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Effect of the degree of autotomy on feeding, growth, and reproductive capacity in the multi-armed sea star Heliaster helianthus

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ABSTRACT

The term *autotomy* refers to the process by which some species lose limbs or parts of limbs in response to adverse biotic or abiotic conditions, as for example, predation or abnormally high temperatures. The multi-armed sea star *Heliaster helianthus* is a key predator of the intertidal and the shallow rocky subtidal communities of north-central Chile. Natural populations of this sea star have been found with up to 60% of the individuals showing some degree of autotomy. The present study evaluated the effects of autotomy on feeding rate and growth of juvenile and adult *H. helianthus* after experimentally induced autotomy of 17% and 33% of their arms, as well as on the energy content of the pyloric caeca and gonads of adults during the reproductive period. Experimental juvenile sea stars were maintained and fed in the laboratory over a period of five months and adult sea stars for one month, Intact individuals were maintained as parallel controls. The results showed that juveniles undergoing 33% autotomy decreased their feeding rates, and as a consequence showed lowered net individual growth. In contrast, adults with 17% and 33% autotomy showed marked reductions in feeding. The results showed that autotomized adults had between five and seven times lower contents of carbohydrates, lipids, and proteins (and thus energetic content) in their pyloric caeca and gonads. The loss of the arms not only decreased the capacity for feeding in sea stars, but also allocated energy away from growth and reproduction into the process of regeneration of arms. This suggests that autotomy reduces the fitness of *H. helianthus*. Growth was reduced in the juveniles, while adults became limited in their ability to store energy which then limited their reproductive potential. Finally, based on the important effect of autotomy on reducing the feeding capacity of *H. helianthus*, the role of this sea star as a predator in the environment may be strongly affected.

1. Introduction

The process of autotomy in organisms includes the loss of appendages, or parts of these appendages in response to adverse environmental conditions such as unusually high temperatures, red tides, pollution, and predation (Viviani, 1978; Emson and Wilkie, 1980; Arnold, 1984; Hotchkiss et al., 1991; Lares and Lawrence, 1994; Lawrence and Larraín, 1994; Ramsay et al., 2001; Díaz-Guisado et al., 2006). This process occurs in vertebrates (lizards, salamanders and rodents; Lares and Lawrence, 1994; Ramsay et al., 2001; Naya and Bozinovic, 2006) and invertebrates (annelids, molluscs, ophiuroids and asteroids; Viviani, 1978; Lawrence and Vásquez, 1996; Ramsay et al., 2001; Díaz-Guisado et al., 2006). When caused by the activities of a predator, autotomy is termed sublethal predation, in which the prey loses part of its biomass but is able to survive the attack (Lawrence, 1992; Lawrence and Vásquez, 1996). Loss of biomass is a direct effect of autotomy, with indirect effects related to the loss of appendage functions (*e.g.* reduced motility, feeding efficiency, reproductive and mating potential, social status, and defensive structures) (Vitt et al., 1977; Lares and Lawrence, 1994; Díaz-Guisado et al., 2006; Naya and Bozinovic, 2006).

In asteroids, autotomy is mainly an adaptive response to predation in which the death of the individual is avoided (Vitt et al., 1977; Lawrence, 1992; Lawrence and Vásquez, 1996). Autotomy represents costs which may be reflected in behavioral changes such as bottom distribution patterns (Viviani, 1978) and feeding activities (Harrold and Pearse, 1980; Lawrence, 1992; Lawrence and Larraín, 1994; Ramsay et al., 2001; Díaz-Guisado et al., 2006).

Heliaster helianthus is a predatory sea star endemic to the southern coast of South America. It inhabits the intertidal and shallow rocky subtidal zone to ~10 m in depth (Viviani, 1978; Castilla, 1981; Tokeshi, 1989; Tokeshi and Romero, 1995; Tokeshi et al., 1989; Pérez, 1991). It is a keystone predator in rocky communities of north-central Chile, having as many as 40 arms, which makes it fast moving and effective in its feeding activities (Viviani, 1978; Castilla, 1981; Paine et al., 1985; Pérez, 1991; Tokeshi and Romero, 1995). In natural populations up to 60% of the individuals have been observed with varying degrees of autotomy (Lawrence and Vásquez, 1996). *H. helianthus* autotomizes arms mainly in response to predation by the rockfish *Graus nigra* (Fuentes, 1982) and the

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sea star *Meyenaster gelatinosus* (Vásquez, 1989; Vásquez, 1993). When attacked by *M. gelatinosus*, adult *H. helianthus* may lose up to five arms (Viviani, 1978) which is in contrast to other sea stars with five or six arms, which may autotomize only one or two of arms (Lawrence and Vásquez, 1996; Díaz-Guisado et al., 2006; Maginis, 2006). The large number of arms in *H. helianthus*, makes this species an excellent model for studying the effect of the degree of autotomy (which has not been evaluated in the literature) as related to aspects of fitness in adults and juveniles. *H. helianthus* which have undergone autotomy would be expected to have a lower capacity for feeding than intact individuals, due to the losses of structures involved in location, capture, and consumption of prey, as well as in their locomotion. A decrease in feeding capacity would decrease the energy available for growth in juveniles and for reproduction in adults. These effects should be proportional to the degree of autotomy. Based on the preceding points, the present study evaluated the effects of the degree of autotomy on feeding rate and growth in juvenile individuals and feeding rate and energy storage in pyloric caeca and gonads in adult individuals.

2. Materials and methods

2.1. Collection of individuals

A total of 48 juveniles (~2 cm of radius) and 56 adults (~11 cm of radius) of *Heliaster helianthus* were collected from the intertidal and rocky subtidal zones, respectively, at Coquimbo, Chile (30°05'S, 71°2'W). The specimens were taken to the laboratories of the Universidad Católica del Norte, Coquimbo, where they were maintained in 500 L tanks containing flowing sea water with continuous aeration, and were fed *ad libitum* with the common mussel *Semimytilus algosus*.

2.2. Induction of autotomy

32 juvenile specimens (2–4 cm in diameter) each having 18 arms on average, were individually induced to autotomize either 3 or 6 arms (17% or 33% of total arms). 32 adults (20–26 cm in diameter, 30 arms in average) were induced to autotomize either 5 or 10 arms (17% or 33% of total arms). Autotomy was induced by the application of 12 V electric shocks (Hotchkiss et al., 1991), applied by two electrodes, one of which was placed in the distal portion of the arm and the other on the proximal portion of the arm for a time period of five minutes in the juveniles and 10 minutes in the adults. Treated individuals were permitted to recover in the sea water tanks as described above, and this was indicated by resumption of feeding after ~3–5 days.

2.3. Feeding rate and growth in juveniles

The juveniles of *Heliaster helianthus* (n=48) were separated into three groups of 16 individuals, including an intact (control) group, a group with three arms autotomized, and a group with six arms autotomized. Radius and underwater mass of all the specimens was determined following the methods of Yamaguchi (1974). Four individuals of each group were maintained in 30-l plastic aerated seawater tanks over a period of five months from January to May 2005 (4 tanks per treatment and control). Sea stars were fed daily with a ration of ten ~1 cm in length *Semimytilus algosus* per tank. This feeding ration was considered limited as determined by a preliminary experiment that showed that each juvenile normally consumed a maximum of four ~1-cm mussels daily. Within the first four days of each month of the experiment, sea star feeding rates were recorded as the number of mussels consumed daily in each tank divided by the number of *H. helianthus* per tank. The juveniles were measured monthly over the five-month period, and their growth rates were estimated as monthly increases in radius and underwater mass per

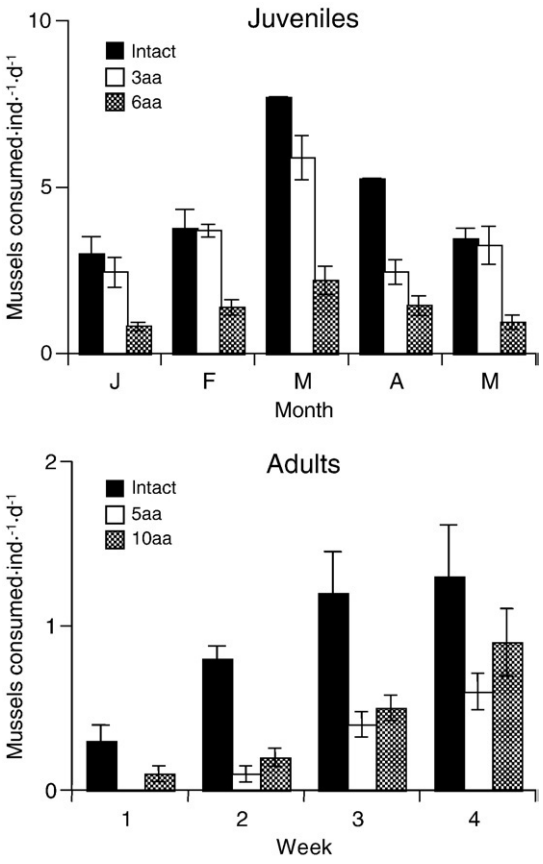

Fig. 1. Mean number of mussels consumed per day by intact and autotomized (17 or 33% of the arms) juveniles and adults of *Heliaster helianthus* provided with 1-cm mussels *Semimytilus algosus* in the laboratory. 3aa, 6aa, 5aa, 10aa=3, 6, 5 or 10 autotomized arms. Vertical bars represent standard errors.

Table 1
Repeated measures analyses used to compare feeding rates between intact and autotomized (17 or 33% of the arms) juvenile and adult *Heliaster helianthus* (Treatment), over time (Time)

Source	df	F	P	Comparisons
Juveniles				
Treatment	2	36.011	<0.001	Intact=3>6
Time	4	11.603	<0.001	Mr>Jn=Fb=Ap=My
Treat.*Time	8	1.891	0.093	
Error	36			
Adults				
Treatment	2	9.123	0.007	Intact>5=10
Time	3	9.819	<0.001	1 week=2 week=3 week<4 week
Treat.*Time	6	.291	0.937	
Error	38			

The experiment with juveniles lasted five months and that of adults four weeks.

Table 2
ANCOVA used to compare size (underwater mass, and radius) between intact and autotomized (17 or 33% of the arms) juvenile *Heliaster helianthus* (Treatment), over five month (Time)

Source	df	F	P	Comparisons
Underwater mass				
Treatment	2	17.194	<0.001	Intact=3>6
Time	4	5.059	0.002	Jn=Fb<My
Error	53			
Radius				
Treatment	2	5.409	0.007	Intact=3>6
Time	4	12.542	<0.001	Jn=Fb<Mr=Ap=My
Error	53			