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Population Structure and Reproduction of the Fissiparous Seastar, *Linckia columbiae* Gray, on Santa Catalina Island, California

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Abstract – *Linckia columbiae* is a sexual species that also reproduces asexually by ray autotomy. Seventy percent of *L. columbiae* surveyed at the Catalina Marine Science Center Marine Life Refuge, Santa Catalina Island were regenerating autotomized rays. Autotomy occurred throughout the year with the highest incidence in late summer. The incidence of autotomy correlates with growth, but not gender or depth. Regeneration experiments suggest that 3 yr, or longer, may be required for a single ray to reach the adult stage. Gametogenesis was generally confined to non-regenerating rays. Oocyte production was low and spawning occurred in late summer. Lacking evidence of recent larval recruitment at the study site, population densities and morphometric features of *L. columbiae* are best explained by continuous asexual reproduction.

Introduction

The variable seastar, *Linckia columbiae* Gray, generates new multirayed individuals from single autotomized rays (Monks 1903, 1904; MacGinitie & MacGinitie 1949). In contrast, regeneration of new individuals from fissioned segments in most fissiparous asteroids requires a portion of the central disc (Emson & Wilkie 1980). Among other species of fissiparous asteroids, fission is often a significant mode of reproduction, but the emphasis on asexual and sexual reproduction varies between populations as well as between species (James & Pearse 1969; Emson 1978; Rideout 1978; Emson & Wilkie 1980; Ottesen & Lucas 1982; Crump & Barker 1985; Mladenov *et al.* 1986). When fission is frequent, regeneration may limit the extent of sexual development; gametogenesis may be diminished or absent. Because fission alters body shape and provides a source of new individuals, the incidence of fission affects other population parameters, especially morphometry and population density. The present study relates the incidence of ray autotomy in *L. columbiae* to population structure, growth, and sexual reproduction.

Methods

Study Sites: Pumpernickel Cove and its adjoining coastal reef are is located in the Catalina Marine Science Center Marine Life Refuge on the northwest shore near the west end of Santa Catalina Island, California. The site is an extension of steep cliffs which, underwater, give rise to boulder fields and bedrock escarpments of moderate to high relief. Patches of coarse sand and cobble occur throughout the area. The dominant community over most of the cove and reef is kelp forest, *Macrocystis pyrifera*, with an understory of encrusting and erect corallines, scattered small fleshy rhodophytes and various shrubby brown algae. Much of the vertical rock surface is a mosaic of encrusting corallines and sessile invertebrates. A single collection of *Linkia columbiae* was made from similar habitat depths of 8-15 m at Admiral's Reef near Cat Rock, Anacapa Islands, California in September 1986.

Procedures: 1. *Morphometry and Autotomy.* Data on morphometry and autotomy were taken from 10 samples, containing from 16-183 individuals between June 1985 and September 1989. Specimens were collected using scuba at the east end of Pumpernickel Cove from 6-10 m depth. For each specimen, rays were counted and identified (by number) based on the usual presence of two madreporites on the principle ray (identified as R1, Fig. 1a). In a few individuals, madreporites occurred on both sides of more than one ray, making identification of R1 impossible. The lengths of rays and regenerating segments were measured along the ambulacral groove from the mouth or break scar to the ray tip (Fig. 1b).

Specimens were grouped according to their stage of asexual reproduction as 1) single rays, 2) comets - single rays in which the mean length of new rays was <50% the length of the principle ray [Fig. 1c], 3) adults - individuals in which the mean length of non-autotomized rays was >50% of the length of the principle ray or 4) disc parents - adults with one or more autotomized rays. Since the open ends of most autotomized rays sealed and began to regenerate within 30-40 days in the laboratory, ray stubs with open or sealed breaks and no measurable amount of regeneration were counted as recent autotomies. In cases of multiple autotomy, the sequence of ray autotomy was inferred from the relative lengths of regenerating rays. Differences in the lengths of regenerating rays on the same individual were assumed to arise from differences in times of autotomy, not in rates of regeneration. Individuals were returned to the collection area after each survey. Collection sites were shifted along the east side of the cove to avoid overlap in consecutive surveys.

2. *Seasonal Census.* In April and September 1986, and January 1987, censuses were conducted to assess population density, size structure, and the incidence of autotomy. In each census, a series of six non-overlapping 30 m transects were laid between 6 and 10 m parallel to the shore at the west end of Pumpernickel Cove and the adjoining outer reef. Twelve 0.25 m^2 quadrats were sampled at random per transect. Each quadrat was searched thoroughly for *Linkia columbiae*. For each individual, the substrate, number of rays, length of the longest ray (LR), and number of regenerating rays and recent autotomies were recorded. In the last census, *L. columbiae* were collected from all of the quadrats, measured, and sexed. To assess population structure versus depth, 0.25 m^2 quadrats were sampled one meter apart in September 1986 along depth contours at 10, 15 and 25 m.

3. *Water Temperature.* At each sampling or census, water temperature was recorded. Additional information on water temperature is provided in Engle (1993).

4. *Sexual Reproduction.* To determine sex and gonadal condition, individuals were dissected at different times during the year. Sample sizes ranged from 22-71 individuals. Prior to dissection, each individual was blotted dry with a paper towel and weighed. For each ray dissected, the number, position, and maximum length(s) and state of the gonad(s) (developing, ripe, spawned) were recorded. To estimate the ratio of gonad to body weight, ripe gonads from two males and two females were excised, blotted on a paper towel and weighed. Sex was determined from microscopic examination of gonadal squashes. For females, the diameters of 50 oocytes were measured.

Two methods were used to estimate oocyte production in ripe ovaries: 1) the number of oocytes per mm of ovary length was determined by counting the oocytes in 10 different ovary branches of known lengths from two females and 2) for two other females, the longest ovary branch was measured and squashed on a slide to create a monolayer of oocytes. The oocytes were counted and the number per mm was calculated. To estimate total oocyte production, the mean number of oocytes per mm of ovary was multiplied by total ovary length (sum of branch lengths).

5. *Rates of Growth and Regeneration.* To estimate rates of ray regeneration, in September 1986, a single ray was severed with a scalpel 5-10 mm from the mouth on each of 36 individuals. The proximal ends of the amputated rays were cut again to produce single rays of different lengths from 6-32 mm long. Single rays were maintained in the laboratory and provided with coralline encrusted cobble as a substrate and possible source of nutrition until January 1987 when the lengths of regenerated rays were measured.

In July 1990, 141 *Linkia columbiae* including 35 amputated single rays were stained with nile blue sulfate (Simon 1974) and released for possible recapture in August 1991. Four stained individuals, including two single rays, were maintained in the laboratory to determine how rapidly the stain would fade and whether staining had detrimental effects. Unstained amputated rays and disc parents served as controls.

6. *Number of Rays Regenerated.* In June 1990, two single rays were amputated from each of 10 four-rayed, 10 five-rayed, and 10 six-rayed adults to determine if the number of arms regenerated by a single ray is the same as the number on its disc parent. Regenerating rays were maintained in separate containers according to the number of rays on the disc parent and provided with coralline encrusted cobble. Individuals were examined monthly to determine the progress of regeneration.

7. *Data Analysis.* Data were analyzed using statistical methods appropriate to the size and distribution of the samples (Dixon & Massey 1969; Sokal & Rohlf 1981).

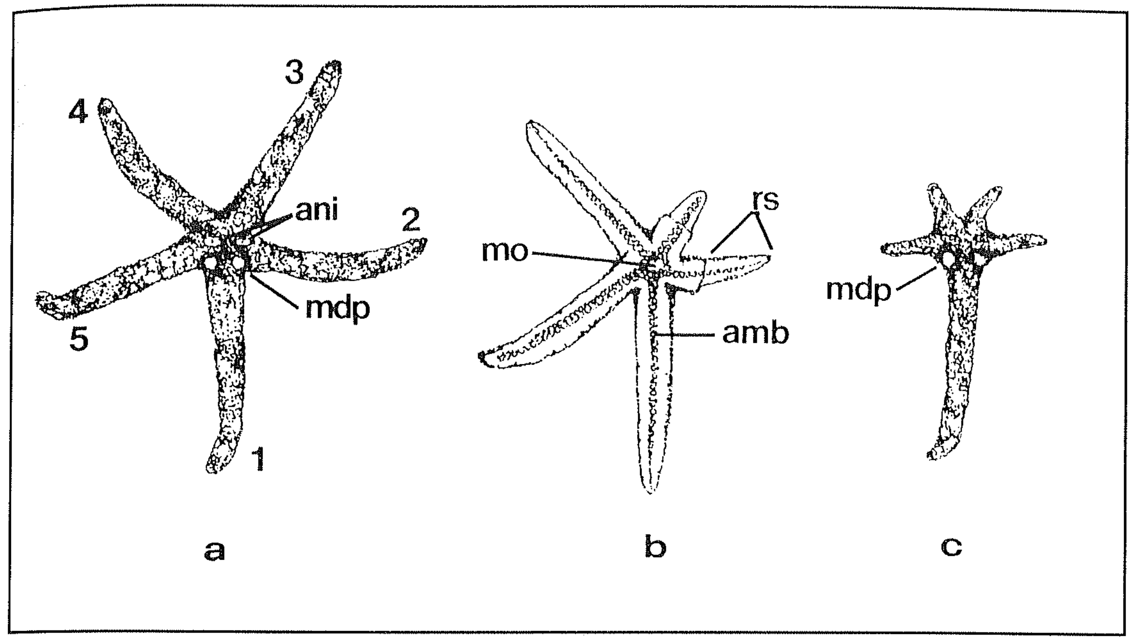

Figure 1. *Linckia columbiae.* a. Aboral surface. Rays are labeled counter-clockwise beginning with R1. b. Oral surface. c. Comet. Abbreviations: amb = ambulacral groove; mdp = madreporite; mo = mouth; and rs = regenerating segment.

Results

Habitat and Population Structure: At Pumpernickel *Linckia columbiae* occurred on substrates from hard bedrock to patches of open sand. Adults represented the majority of individuals sampled (Table 1) and were most abundant in areas of moderate relief on the vertical surfaces of boulders or turnable rocks encrusted with coralline algae. Most single rays occurred in shallow cobble piles (5-10 cm dia.) or crevices, whereas small comets tended to be hidden in piles of larger rocks (15-30 cm dia).

1. *Number of Rays.* Of 725 individuals examined, 520 (72%) had five rays, 128 (17.5%) six rays and 73 (10%) four rays. Less than 1% had three (n = 1), seven (n = 2) or eight rays (n = 1). Of 77 comets examined from field collections, 55 (71.4%) had five rays, 8 (10.4%) had six rays, 12 (15.6%) had four rays, and two (2.6%) had three rays. A small intercalary arm was observed on only one

Table 1. *Linckia columbiae*. Population structure at Pumpernickel (n = the number of individuals sampled).

Census Date	Adults (%)	Comets (%)	Single Rays (%)	n
6/85	48 (92.3)	0 (0)	4 (7.7)	52
7/85	25 (80.6)	3 (9.7)	3 (9.7)	31
9/85	25 (83.3)	1 (3.3)	4 (13.3)	30
2/86	106 (94.6)	4 (3.6)	2 (1.8)	112
4/86†	70 (84.3)	11 (13.3)	2 (2.4)	83
6/86	56 (90.3)	5 (8.1)	1 (1.6)	62
8/86[a]	19 (86.4)	2 (9.1)	1 (4.5)	22
9/86†	95 (79.8)	14 (11.8)	10 (8.4)	119
1/87†	145 (90.1)	14 (8.8)	2 (1.4)	161
9/89[a]	136 (96.4)	3 (2.1)	2 (1.4)	141
Total ($\bar{x}$% ± SD)	725 (89.2) (87.8 ± 5.8)	57 (7.0) (7.0 ± 4.4)	31 (3.8) (5.1 ± 4.4)	813

[a]Extensive search for single rays was not conducted.
†Seasonal quadrat census.

individual indicating that the number of rays is generally fixed early in development.

2. *Size*. The size of *Linkia columbiae* at Pumpernickel, based on the length of the longest non-autotomized ray (LR), followed a normal distribution ($\bar{x}$ = 37.9 mm SD = 8.6, range 13-66 mm, n = 593). Among adults, ray R1 was usually the longest non-autotomized ray, (62%, n = 419). The remaining non-autotomized rays were about the same length (z test, P > 0.95), but shorter than R1. Due to differences in the incidence of autotomy and extent of regeneration, rays on the same individual were rarely equal in length.

3. *Population Density*. Between 6-10 m, the density of *Linkia columbiae* at Pumpernickel remained stable at almost four individuals per m^2 throughout the year (ANOVA, F = 0.082, P > 0.95, between and within census samples). Although the distribution of individuals was not uniform over the reef, measures of dispersion did not reveal a significant pattern of aggregation (G test = 7.56, P > 0.95; Morisit's ID = 1.4). The density of *L. columbiae* declined significantly with depth toward the base of the reef at 25 m (Table 2). There were no significant changes in morphometric characters, sex-ratio, or the incidence of autotomy at different depths.

Pattern of Ray Autotomy: 1. *Size Relations*. In 98% (n = 82) of the recent autotomies examined, fission occurred 6-12 mm from the mouth of the disc parent. Observations of comets in different stages of regeneration indicated that the two madreporites usually regenerate one on either side of the initial single ray identifying R1 as the parent ray. The mean lengths of single autotomized rays and the R1 of comets were 28.6 mm, SD = 7.2, n = 31, and 27.0 mm, SD = 6.6 mm, n = 57, respectively. The length of the smallest single ray collected was 18 mm and R1 on the smallest comet was 13 mm. Among individuals with one recent autotomy and no evidence of autotomy on any other ray, the ratio of the mean ray length, excluding R1, to the length of R1 was 0.87, SD = 0.19 (range 0.57-1.32, n = 18). These data indicate that ray autotomy begins sometime after regeneration is 50% complete and regenerated rays are at or near 18 mm in length (*i.e.*, 13 mm plus a ray stub of 6 mm).

The number of autotomies per disc parent was not correlated to the length of R1, the principle ray. The number of autotomies per disc parent was correlated positively with overall growth as represented by small increases in the mean length of the other non-autotomized rays as the number of autotomies per individual increases (Fig. 2).

2. *Sequence of Ray Autotomy*. Among five-rayed individuals with a single autotomy

Table 2. *Linckia columbiae*. Dispersion and population density as function of depth at Pumpernickel, January, 1987. Population density is expressed as the number of individuals per 0.25 m^2. (Q = the number of quadrats; n = the number individuals censused).

Depth (m)	Number of 0 - .25m^2 Quadrants with 0 - 5 Individuals (%) 0	1	2	3	4	5	Q	n	Density $\bar{x}$ ± SD
7- 9	21 (37.5	20 (35.7)	9 (16.1)	4 (7.1)	1 (1.8)	1 (1.8)	56	59	1.05 ± 1.14
16-19	15 (53.6)	9 (32.2)	2 (7.1)	2 (7.1)	0 (0)	0 (0)	28	19	0.68 ± 0.91
22-24	61 (76.2)	13 (16.2)	3 (3.7)	1 (1.3)	1 (1.3)	1 (1.3)	80	31	0.39 ± 0.89

(recent or regenerating), the incidence of autotomy was equal for all rays except R1 which was significantly less than the 20% expected if autotomy was equally probable for all rays (Table 3). In multiple autotomies, the sequence of ray loss varied, but two tendencies were evident: 1) a disproportionate number of multiple autotomies involved the loss of R3 (44/116 cases, X^2 = 18.65, df = 4, P < 0.01) and 2) multiple autotomies involved adjacent rays more often than non-adjacent rays (z test, P < 0.001); Table 4). Sample sizes for individuals with a single autotomy for four- and six-rayed individuals were too small for analysis.

The progression of autotomy to different rays on the same individual was not a function of the length or percentage of regeneration of previously autotomized rays. Second or third recent autotomies were observed on individuals with as little as 1-2 mm to more than 80% percent regeneration. Of the adults sampled, 19% had two or three recent autotomies or regenerating rays of equal length suggesting that more than one ray may be autotomized at the same time (or in rapid sequence). Although repeated autotomy of the same ray was not evident at Pumpernickel, multiple break scars near the disc on rays of large individuals from Anacapa Island and other sites (unpublished data) indicate that autotomy may occur at the same ray more than once.

3. *Number of Rays*. The majority of single rays amputated in June 1990 from four-, five- or six-rayed adults regenerated rays 3-5 mm long by October or November 1990. The number of rays regenerated was not always the same as the number of rays on the disc parent (Table 5). However, the frequency of four- and six-rayed comets from disc parents with four or six rays respectively strongly suggests that the two variables are associated (G test = 12.8, df = 4, P = 0.013, omitting the comet with three rays).

Incidence of Autotomy: From 60-80% of the *Linkia columbiae* sampled at Pumpernickel had autotomized one or more rays. The proportion of seastars with one or more autotomies was similar for four-, five- and six-rayed individuals (~68%, Table 6). The sample sizes for five-rayed *L. columbiae* were large enough to establish that the distribution of autotomies per individual (from none to five) was similar over all census periods (X^2 = 39.7, df = 35, P = 0.27, Table 7). The incidence of autotomy was similar among males and females ($\bar{x}$ = 1.5 regenerating rays per individual, t test, df = 87, P >>0.99). About 30% of the Pumpernickel population were relatively large adults (LR >35 mm) with no apparent evidence of autotomy.

The frequency of autotomy was expressed as the percentages of single rays and disc parents with recent autotomies. Temporal changes for both incidence of autotomy were largely coincident but varied considerably in different years (Table 8). Individuals with recent autotomies and single rays were found year round. The highest incidence of recent autotomy and single rays were observed in the summer to early fall and lowest in winter and spring when water temperatures were respectively highest and lowest.

The incidence of recent autotomy in *Linkia columbiae* at Pumpernickel was only weakly correlated to the proportion of rays available for autotomy in the population as a whole

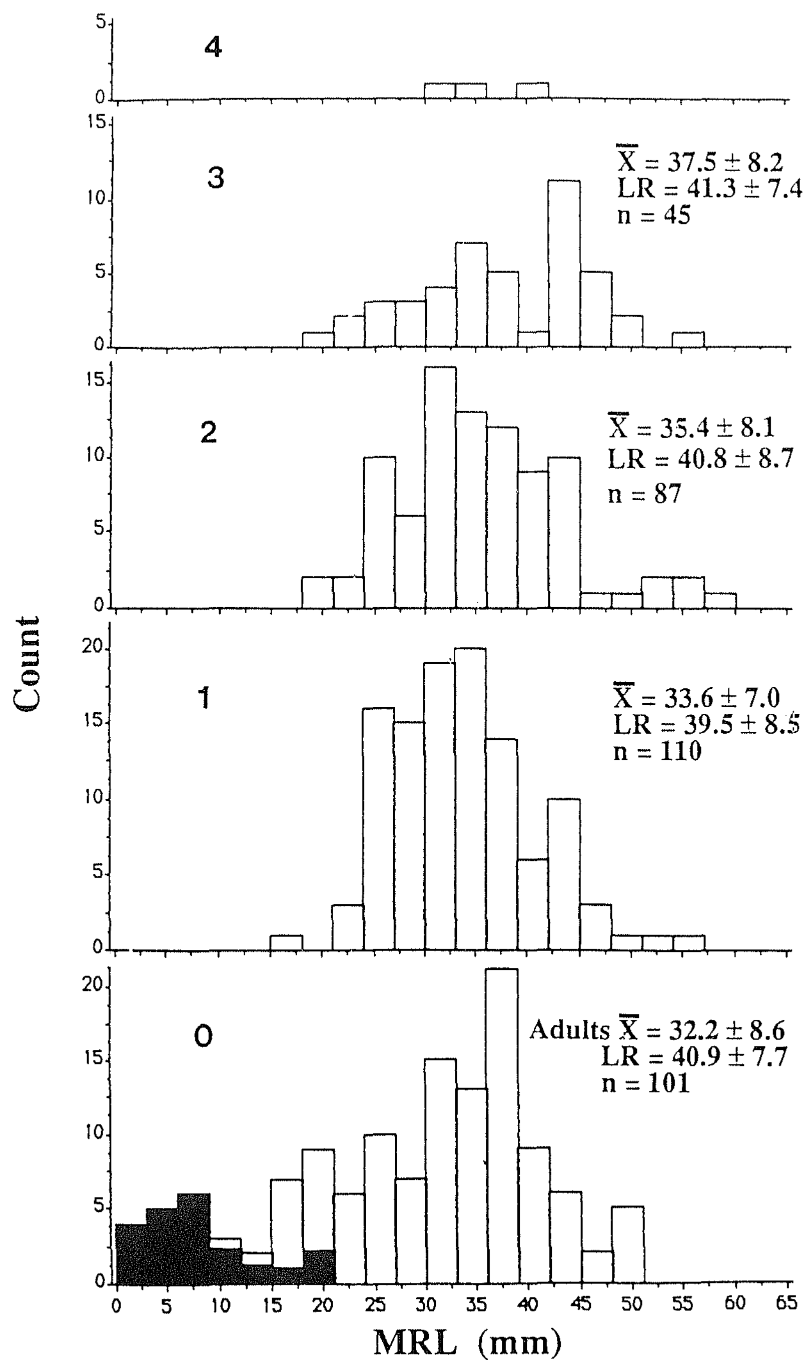

Figure 2. *Linckia columbiae.* Size frequency histograms of the mean length of non-autotomized rays R2-R5 for five-rayed comets and adults with one, two, three or four autotomies. (MRL = the mean length of non-regenerating rays R2-R5; $\bar{x}$ = the mean MRL ± SD; LR = the mean length of the longest ray ± SD, including R1; solid area = comets; open area = adults. For comets, $\bar{x}$ = 7.91 ± 5.4 mm, n = 21A).

(rank correlation test, r = 0.56, P = 0.05, n = 10, Table 8). On average, the ratio of single rays to recent breaks on disc parents in census samples was 1:2. This margin suggests that about half of the single rays were undetected, or perhaps, had died. Movement of individuals into or out of the census area after autotomizing a ray is also a factor. Occasionally, single rays could be matched to fresh autotomies on adults in the same quadrat or nearby, but most often single rays and disc parents with recent autotomies were not found together.

Regeneration and Growth Experiments: 1. *Single Rays.* Within one month following amputation, the cut ends of single rays and ray stubs on disc parents maintained in the laboratory were sealed. The mean rates of regeneration for amputated single rays at the end of four months, from September 1986 to January 1987, was similar to the rate at the end of 13 months (for 25 rays amputated in June 1990 to determine the number of rays regenerated), but more variable (0.63 mm per month, SD = 0.38, n = 35, and 0.51 mm per month, SD = 0.07, n = 25, respectively, based on the longest regenerated ray; F test, P = << 0.001). If these rates of regeneration were sustained, the new rays on most comets would be long enough to initiate autotomy (~18 mm) in about 3 years and reach the mean length for autotomized single rays (28.6 mm) in 4-6 years. A stained single ray recovered from Pumpernickel after one year in August 1991 had five new rays the longest of which was only 3.5 mm, indicating that regeneration times may be much longer.

Regeneration length was not correlated to the length of the parent ray, R1 (Fig. 3, correlation coefficient for the rate of regeneration (mm per month) vs. length of R1, r = 0.07, P = 0.6). The length of R1 did not change significantly during regeneration. The shortest amputated ray to regenerate a comet was 6.8 mm long.

2. *Growth.* Twenty-three adults stained with nile blue sulfate were recovered from Pumpernickel in August 1991, one year after release. All of the animals had faded, but still appeared blue underwater. Under the dissecting microscope, stained portions of the skeletal elements were obvious including the tips of skeletal plates, especially along the ambulacral groove, and tube feet. New tissue, colored cream to reddish-orange was distinct. Growth, estimated as the sum of unstained lengths for all rays for the year, averaged 11.9 mm, SD = 5.3 per individual (median = 10.5 mm, range 4-23 mm, n = 24) which represented a median increase in individual size of about 9% (range 4-26%; where % increase in size = (sum of unstained lengths/ initial size) x 100, and initial size = total ray lengths - sum of unstained lengths). Although total annual growth was inversely correlated to the initial size of individuals (Fig. 4), there was considerable variation in the distribution. For individual rays, the correlation between growth and initial size was stronger (Fig. 5). Growth was generally greatest for the shortest ray of each individual, whereas growth for the longest ray was negligible (shortest ray, median annual

Table 3. *Linckia columbiae.* The frequency of autotomy at different rays for five-rayed adults. (n = the number individuals sampled).

Number of Autotomies	Ray Autotomized (%) 1	2	3	4	5	n
One	9(7)*	36(29)	29(24)	26(21)	23(19)	123
≥One[a]	48(11)*	98(22)	120(27)*	114(25)	78(17)	453

[a] Includes the rays autotomized on individuals with single and multiple autotomies.
*z test, P < 0.01.

Table 4. *Linckia columbiae.* The frequency of autotomy at adjacent rays. Expected values are calculated as if rays autotomized independently, in which case, the total probabilities of autotomy for different combinations of adjacent or non-adjacent rays are equal. (n = the number of cases).

Number of Autotomies per Individual	Number of Cases in which Adjacent Rays Autotomized: Observed	Expected	n
2	61	39.0	78
3	34	20.5	41

length increase = 38%, range 23-88; longest ray, median annual length increase = 0%, range 0-32; median test, P = 0.0001, n = 23). From the regression equation, a 5 mm ray stub on a disc parent would take 7-8 years to regenerate a 28-29 mm ray (Fig. 5).

Individuals stained with nile blue sulfate that remained in the laboratory after one year appeared healthy and dark blue. Their growth patterns were similar to individuals recaptured from the field, except that the two nile blue single rays reared in the laboratory had new rays about twice the length of the only recaptured single ray (Figs. 4 and 3, respectively). The regeneration lengths of amputated rays on unstained disc parents maintained in the laboratory were within the range of values observed for stained rays of similar lengths (Fig. 5, n = 12 rays).

Sources of Mortality: None of the single autotomized rays or R1 rays of comets examined in 1986-1987 had signs of injury. About 1% (8/762) of the recent breaks and regenerating rays examined on adults were ray tips or rays with fission scars distal to the usual region of autotomy. Diseased or degenerating *Linkia columbiae* were absent from samples until the summer of 1990 when a few individuals with white, eroded patches were noticed. In the summer of 1991, afflicted individuals were more common. In September of 1991, 21% (27/129) of the animals censused at Pumpernickel had lesions, or noticeably eroded rays, including one individual on which only the disc and proximal ends of the rays remained.

Table 5. *Linckia columbiae.* The number of rays regenerated by single rays amputated from four-, five- and six-rayed disc parents. (n = the number of comets examined five months after amputation).

Number of Rays on Disc Parent	Number of Rays Regenerated (%) 3	4	5	6	n
Four	1(6)	8(44)	8(44)	1(6)	18
Five	0(0)	3(20)	11(73)	1(7)	17
Six	0(0)	1(5)	13(65)	6(30)	20

Predation by fishes or large invertebrates was not observed (or specifically tested) in this study. Garibaldi (*Hypsypops rubicundus*) were observed occasionally removing *Linkia columbiae* from their territories. Although carried in the Garibaldi's mouth, the seastars showed no signs of injury.

Sexual Reproduction: Examination of gonadal squashes indicated that *Linkia columbiae* is dioecious and the sex ratios are biased toward females, especially among adults (Table 9). Sexually mature individuals were found in almost every size class. The shortest sexually mature ray was 21 mm. The mean wet weights and mean sizes of males and females were similar (3.58 ± 1.76 gm SD, n = 40, 37.6 ± 8.1 mm SD, n = 50, for males and 3.27 ± 1.40 gm SD, n = 48, and 36.6 ± 8.0 gm SD, n = 71, for females; z test, P > 0.99). Large stars (LR > 40 mm) occasionally showed no gonadal development, but some single rays and some R1 rays of comets had well developed ovaries or testes. Ripe gonads reached lengths of 4-20 mm and weighed from 1-3% of the total body wet weight. Both methods used to estimate oocyte production yielded values of 2,500-3,500 mature oocytes in an ovary 10-13 mm in length.

Oocyte diameters, and observations of spawning revealed a seasonal cycle in which gametes mature in early summer followed by spawning in late summer and early fall (Fig. 6). In mid September 1986, approximately 39% (11/28) of the males and females had spawned or partially discharged gonads. The mixed sizes of oocytes in September suggest that a new round of gametogenesis had begun. In January, most large oocytes were in the process of absorption. Spermatogenesis was coincident with the cycle of oogenesis. In August and September males shed sperm in collection jars and a single ray released sperm in the field when a cobble to which it was attached was moved. Both males and females spawned spontaneously and in response to injections of 1-adenosine monophosphate in the laboratory in August and September of 1990 and 1991.

The partially regenerated rays of adults and comets showed little or no gonadal development. In the few regenerating rays of

Table 6. *Linckia columbiae.* The incidence of autotomy among four-, five- and six-rayed adults at Pumpernickel. (n = the number of individuals sampled).

Number of Rays	Number of Autotomies per Individual (%) 0	1	2	3	4	5	6	$\bar{x}$ ± SD	n
Four	18 (36.7)	18 (36.7)	11 (22.4)	1 (2.1)	1 (2.1)	-	-	0.96 ± 0.93*	49
Five	155 (29.8)	167 (32.1)	123 (23.6)	58 (11.2)	13 (2.5)	4 (0.8)	-	1.26 ± 1.12	520
Six	30 (32.0	27 (29.0)	15 (16.1)	16 (17.2)	3 (3.2)	2 (2.1)	0 (0)	1.37 ± 1.30	93

*Mean number of autotomies per individual in four-rayed adults is less than six-rayed, z test, P~0.04

Table 7. *Linckia columbiae.* Number of autotomies per individual for adult five-rayed adults at Pumpernickel. (n = the number of adults sampled; $\bar{x}$% = the mean percentage of individuals per sample).

Cencus Date	Number of Autotomized Rays per Individual (%) 0	1	2	3	4	5	n
6/85	6 (37.5)	4 (25.0)	2 (12.5)	4 (25.0)	0 (0)	0 (0)	16
7/85	4 (23.5)	6 (35.3)	5 (29.4)	2 (11.8)	0 (0)	0 (0)	17
9/85	4 (20.0)	11 (55.0)	2 (10.0)	3 (15.0)	0 (0)	0 (0)	20
2/86	26 (32.5)	27 (33.7)	19 (23.8)	3 (3.8)	0 (0)	2 (2.3)	77
4/86	17 (28.8)	19 (32.2)	14 (23.7)	8 (13.6)	1 (1.7)	0 (0)	59
6/86	9 (23.7)	15 (39.5)	10 (26.3)	4 (10.5)	0 (0)	0 (0)	38
9/86	14 (32.6)	14 (32.6)	5 (13.2)	9 (23.7)	1 (2.6)	0 (0)	43
1/87	42 (29.2)	39 (27.1)	40 (27.8)	15 (10.4)	6 (4.2)	2 (1.4)	144
9/89	33 (31.1)	32 (30.2)	26 (24.5)	10 (9.4)	5 (4.7)	0 (0)	106
Total	155 (29.8)	167 (32.1)	123 (23.6)	58 (11.2)	13 (2.5)	4 (0.8)	520
$\bar{x}$% ± SD	(28.8 ± 5.5)	(34.5 ± 8.8)	(21.2 ± 7.3)	(13.7 ± 6.8)	(1.5 ± 1.9)	(0.4 ± 0.9)	

Table 8. *Linckia columbiae.* Sea temperatures and indices of autotomy at Pumpernickel. (T = sea temperature °C at 6-10 m depth; n = the number of adults sampled).

Census Date	T	Number of Adults with Recent Autotomie(s) (%)	Total Number of Recent Autotomies, all Rays (% available rays)	Ratio of Available Rays to Total Number of Rays[a] (%)	Single Rays (% of n)	n
6/85	15	5 (10.4)	6 (6.9)	87/114 (76.3)	4 (8.3)	48
7/85	16	5 (20.0)	6 (5.6)	108/141 (76.6)	3 (12.0)	25
9/85	18-20	10 (40.0)	11 (9.8)	112/133 (84.2)	4 (16.0)	25
2/86	13	5 (4.7)	6 (1.3)	450/670 (67.2)	2 (1.9)	106
4/86†	14-15	1 (1.4)	1 (<.1)	216/430 (50.2)	2 (2.9)	70
6/86	15-16	3 (5.3)	3 (1.3)	228/314 (72.6)	1 (1.8)	56
8/86[b]	17	4 (21.1)	6 (15.5)	52/75 (69.3)	-	19
9/86†	17-18	6 (6.3)	7 (8.0)	88/134 (65.7)	10 (10.5)	95
1/87†	13	7 (4.8)	7 (1.1)	635/899 (70.6)	2 (1.4)	145
9/89[b]	16-18	26 (19.1)	29 (5.4)	537/681 (78.9)	-	136
$\bar{x}$% ± SD		(13.3 ± 11.8)	(5.5 ± 4.8)	(71.2 ± 9.3)	(6.9 ± 5.5)	

[a]The numerator is the total number of available rays which equals the total number of non-regenerating rays plus the total number of recent autotomies on adults; the denominator is the total number of adult rays including regenerating rays and recent autotomies.
[b]Specific search for single rays was not conducted.
†Quadrat census.

adults that had mature gonads, the gonads were located close to the disc in the portion of the ray that had not autotomized. In the non-regenerating rays of adults, the amounts of gonadal tissue (0-4 pairs of gonads), the extent of gonadal development and the timing of gamete release (based on the extent of gonadal evacuation) varied between individuals, between different rays of the same individual, and between paired gonads on the same ray. The proportion of *Linkia columbiae* with at least one sexually mature ray (gonads with eggs or sperm) differed in the two reproductive seasons sampled. In September 1986, 90% (28/31) of the individuals examined from Pumpernickel were sexually mature, whereas only 42% (17/41) were sexually mature in September 1989.

***Linckia columbiae* at Anacapa Island:** Morphometric comparisons showed that the individuals collected from Admiral's Reef, Anacapa Island in September of 1986, had similar numbers of rays, but were more robust than individuals from comparable depths at Pumpernickel (Table 10). Concomitant with larger size, the percentage of individuals with two or more regenerating rays was also higher at Anacapa (77%) than at Pumpernickel (35%). Among the 28 *Linkia columbiae* examined from Anacapa, two of the adults had a recent autotomy (9%), three were comets (11%) and three were single rays (11%).

The sex ratio at Anacapa was almost 1:1. Eighteen out of the 20 sexually mature individuals collected at Anacapa had completely or partially discharged gonads. In contrast, only about half of the mature stars collected the same month at Pumpernickel had noticeably reduced gonadal volumes and none were completely discharged. Maximum oocyte diameters were similar for the two populations.

Discussion and Conclusions

The incidence of autotomy and patterns of morphometric variation among *Linckia columbiae* are consistent with the view that most individuals at Pumpernickel develop from

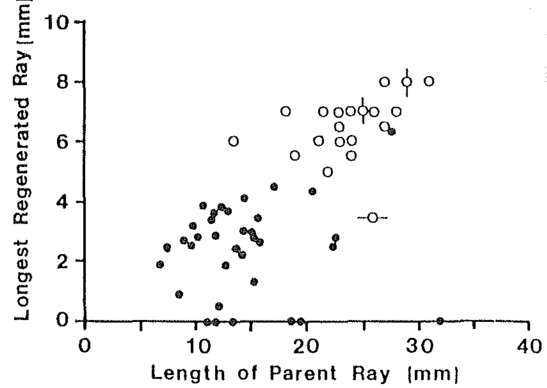

Figure 3. *Linckia columbiae*. Regeneration lengths of comets based on the length of the parent ray. Closed circles = four months after amputation, September 1986 to January 1987. Open circles = 13 months after amputation, June 1990-July 1991. Circles with vertical bars = comets derived from single rays stained with nile blue sulfate. Circle with horizotal bars = the comet derived from a stained single ray recaptured from Pumpernickel after one year.

single autotomized rays. 1) Recent autotomies, single rays and comets are found throughout the year and regenerating rays are common on adults. 2) The growth pattern initiated by regenerating single rays is evident in most adults, *i.e.*, ray R1, the parent ray, is the longest ray and other non-regenerating rays, presumably regenerated by R1, are similar in length. 3) The percentages of four-, five- and six-rayed individuals regenerated by comets is similar to the adult population. Finally, the absence of very small symmetrical *L. columbiae* (LR < 18 mm) in population samples suggests that larval recruitment is rare.

Patterns of Autotomy: Early descriptions of ray autotomy in *Linkia columbiae* proposed that autotomized rays longer than 20 mm continuously produced new individuals by casting off the disc when the regenerated rays reached 9-10 mm (MacGinitie & MacGinitie 1949). In contrast, my results indicate that parent rays, independent of length, usually remain with the discs and asexual reproduction occurs principally by autotomizing regenerated rays. Autotomy begins sometime after comets

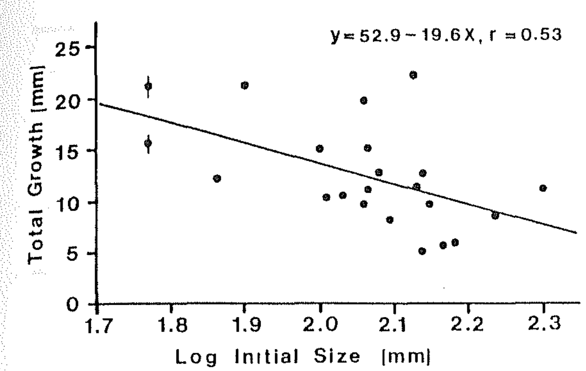

Figure 4. *Linckia columbiae*. Correlation between initial size and total annual growth. Closed circles = adults stained with nile blue sulfate recaptured from Pumpernickel. Closed circles with vertical bars = stained adults maintained in the laboratory.

enter the adult stage when new rays are at least half as long as the principle ray.

Amputation experiments demonstrate that rays of *Linckia columbiae* as short as 6-10 mm are capable of regeneration (MacGinitie & MacGinitie 1949; the present study). At Pumpernickel, the minimum length of autotomized rays appeared to be ~13 mm. However, most single rays observed at Pumpernickel were much longer, 28-30 mm, because comets generally delayed autotomy until regeneration was nearly complete. The coincidence of even longer single rays, 32-65 mm, with larger sized comets and adults at Admiral's Reef (Table 10) suggests that the lengths at which rays autotomize is largely determined by population size structure.

Amputation experiments suggest that the number of rays regenerated on comets is influenced by, but not strictly dependent upon, the number of rays on the disc parent. Variation in the numbers of rays regenerated by spontaneously autotomized single rays is unknown.

Regeneration and Growth: Regeneration experiments and the recovery of dyed individuals indicate that *Linckia columbiae* increases in size by only a few millimeters each

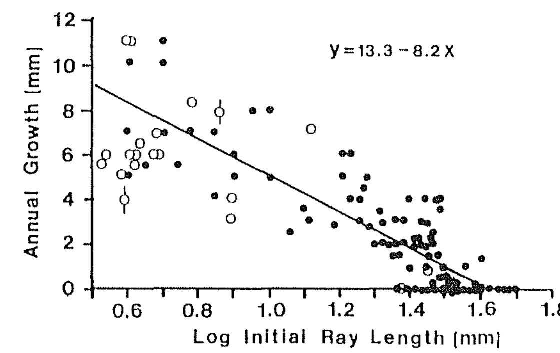

Figure 5. *Linckia columbiae*. Correlation between initial ray length and annual regeneration. Closed circles = adults stained with nile blue sulfate from Pumpernickel recaptured after one year (r = 0.86, P = 0.0001, n = 111 rays). Open circles = unstained disc parents maintained in the laboratory. Open circles with vertical bars = stained adults maintained in the laboratory.

year. Growth is generally channeled into the shortest rays - the regenerating rays of disc parents and comets. The longest rays on most individuals had no measurable growth over the year of this study. However, the presence of individuals at Pumpernickel with rays longer than 43 mm (the length at which zero growth is projected from Fig. 5), indicates that long rays continue to grow albeit very slowly. Thus, the largest individuals are probably very old. If growth is consistently slow and comets require 3-6 years to reach the adult stage, the relatively high population densities of adults and low percentages of comets suggest that *L. columbiae* is a long-lived species (See Menge 1975).

Correlates of Autotomy: Factors that lead to fission in nature and account for temporal variance in asexual reproduction remain largely a mystery (Emson & Wilkie 1980). In *Linckia columbiae*, sudden changes in environmental conditions, external irritants, or ligaments tied around a ray can induce ray autotomy in some individuals (Monks 1904; Edmondson 1935). The persistent location of autotomy between the third and eighth ambulacral ossicles (Shepard 1964), changes in tissue elasticity and

Table 9. *Linckia columbiae.* Sex ratios at Pumpernickel. Data for comets and single rays represents individuals examined during August or September 1985-1989. (n = number of individuals sampled).

Census Date	n	Immature	Females	Males	Sex Ratio F:M	% Mature[a]
6/86	71	12	37	22	1.7:1	(0)
9/86	31	3	20	8	2.5:1	90.3
1/87	58	20	21	17	1.2:1	(0)
9/89	41	24	11	6	1.8:1	41.5
Comets	13	8	4	1	4:1	38.4
Single rays	16	8	4	4	1:1	51.7

[a]Individuals with a ripe gonad in at least one ray.

fission behavior (Monks 1904; Edmondson 1935), the lack of injury on most individuals together with evidence that autotomy can be suppressed by a parasitic infection (at least in *L. multiflora*, see Davis 1967), suggest that endogenous factors are important.

The incidence of autotomy in *Linckia columbiae* at Santa Catalina Island does not correlate with depth. However, *L. columbiae* is strictly subtidal at Pumpernickel and does not experience the environmental stress (temperature, wave action, desiccation, reduced feeding opportunities) associated with increased fission in intertidal populations of other fissiparous asteroids (Emson 1978; Crump & Barker 1985). Annual fluctuations in the indices of autotomy for *L. columbiae* suggest a seasonal trend that peaks in late summer coincident with the highest water temperatures (Engle, 1993)...but variation in the incidence of autotomy between years at Pumpernickel and between different sites in the same year (unpubl. data) indicate that additional factors are important. Populations of the seastars *Allostichaster polyplax* (Emson 1978) and *Coscinasterias calamaria* (Crump & Barker 1985) seem to be more fissiparous when food abundance is low or of apparently poor quality.

Intra-Interspecific Comparisons: Comparative evidence for *Linckia columbiae* from Pumpernickel and Admiral's Reef and a now extinct intertidal population at San Pedro, California (Monks 1903,1904) reveal similar patterns of fission: the percentages of individuals with four, five and six rays are similar; most individuals show evidence of autotomy; and the percentages of single rays (9-11%) and comets (11-17%) are comparable. The primary difference is that the Anacapa and San Pedro collections include larger individuals (LR > 80 mm). At Anacapa, larger size was associated with longer single rays, a higher incidence of multiple autotomies on disc parents and different sex ratios and spawning times. Subsequent analysis of *L. columbiae* populations at additional locations around Santa Catalina Island, Santa Cruz and Santa Barbara islands, and Palos Verdes Point on the mainland of California substantiate significant variability in the structure, fecundity, and incidence of autotomy among local populations (unpubl. data).

Within the genus *Linckia*, the occurrence and pattern of ray autotomy varies. *Linckia multiflora*, a slightly smaller species, is highly asexual. Its mean density in coral reefs around Guam was 36 individuals per m^2 (Rideout 1978, calculated from Table 1), about ten times the density of *L. columbiae* at Pumpernickel. As with *L. columbiae*, typically *L. multiflora* is five-rayed and local population densities are maintained by ray autotomy which occurs year round at variable frequencies (Edmondson 1935; Rideout 1978). The percentages of single rays in population samples of *L. multiflora* and *L. columbiae* are not significantly different ($\bar{x} \pm$ SD = 8.3 ± 6.7%, Rideout 1978, from Table 1; for *L. columbiae*, $\bar{x} \pm$ SD = 6.2 ± 5%; proportion z test, P > 0.95). Nevertheless, a higher incidence of autotomy is predicted for *L.*

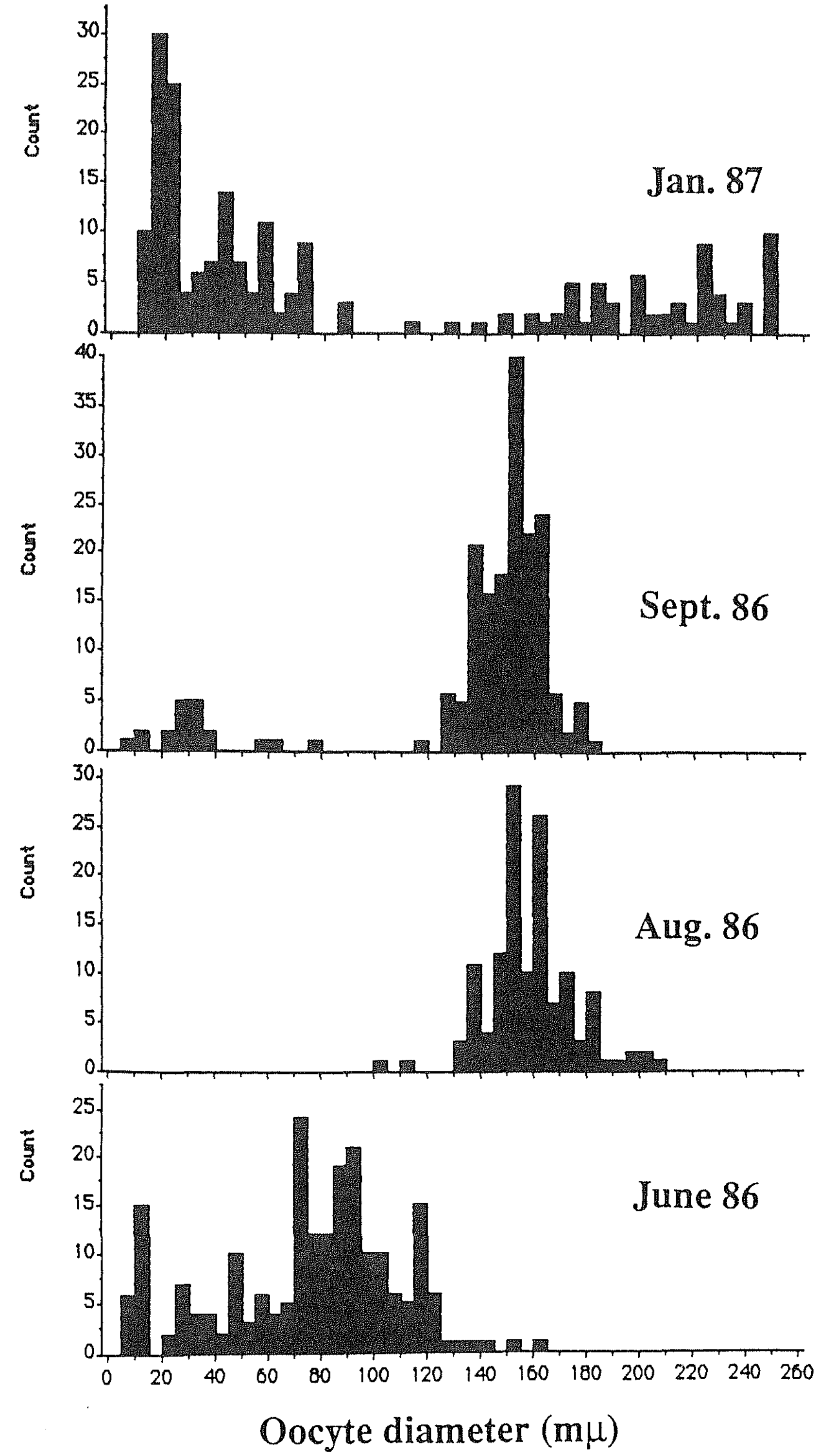

Figure 6. *Linckia columbiae.* Seasonal cycle of oogenesis.

Table 10. *Linckia columbiae*. Morphometry of population samples from Pumpernickel, Santa Catalina Island and Admiral's Reef, Anacapa Island, September 1986. (*n* = the number of individuals examined).

	Number of Rays per Individual (%)							
	Santa Catalina Island				Anacapa Island			
Number of	4	5	6	*n*	4	5	6	*n*
Individuals	14 (15)	66 (69)	15 (16)	95	5 (23)	15 (68)	2 (9)	22
Characteristic	$\bar{x} \pm$ SD		Range	*n*	$\bar{x} \pm$ SD		Range	*n*
Longest Ray* (mm)	35.0 ± 9.0		15.5-55.0	87	61.7 ± 14.8		31.7-90.9	28
Disc Diameter* (mm)	9.9 ± 1.8		4.7-12.6	26	14.1 ± 1.9		10.1-17.3	12
Ray Weight* (wet, mg/mm)	2.3 ± 0.5		1.4-3.2	10	4.0 ± 1.5		1.4 = 8.1	15
Single Rays (mm)	30.0[a]		21.0-35.6	10	35.0[a]		31.7-65.2	3

[a]Median
*z test for difference in sample means, $P < 0.001$.

multiflora because the average length of its autotomized rays is smaller than for *L. columbiae* (16.5 mm vs. 28.6 mm) and the comets of *L. multiflora* attain the size necessary to initiate autotomy in only one year. The sequence and timing of autotomy relative to growth are strikingly different for the two species. The first ray autotomized in *L. multiflora* is R1, the parent ray. R1 separates from the newly regenerated disc after regenerating rays reach a minimum length of 8-10 mm. After the loss of R1, further autotomy is delayed until the remaining rays reach lengths of about 15 mm. At 15 mm, the remaining rays autotomize in rapid succession beginning with the rays adjacent to R1 (Rideout 1978; Fig. 10). The pattern of autotomy bimodally skews the population structure of *L. multiflora*, toward comets and individuals that are regenerating all of their rays. In contrast, succession of autotomy in *L. columbiae* is usually not rapid; the majority of the population are adults with fewer than two autotomies; comets and disc parents that have autotomized all rays are minority classes. Comets of *L. columbiae* delay all autotomy until regenerated rays are longer than 18-20 mm and regeneration is nearly complete. When autotomy does begin, most often, one of the regenerated rays is autotomized. Although multiple autotomies frequently involve adjacent rays in *L. columbiae*, the order in which rays autotomize varies. Disc parents of both species may autotomize regenerated rays.

Little is known about fission in *Linckia guildingi* the only other member of the genus in which autotomy has been described. Of 93 *L. guildingi* examined by Clark (1913), only three were symmetrical, 14% were autotomized single rays, and 18% small comets suggesting that fission is common. Comparisons with *L. laevigata* would be informative because it has size structured populations and very low rates of larval recruitment similar to *L. columbiae*, but reproduction is strictly sexual (Yamaguchi 1977).

Sexual Reproduction and Autotomy: Although the highest incidence of autotomy in *Linckia columbiae* at Pumpernickel was recorded in the late summer coincident with spawning, autotomy is largely independent of sexual activity since autotomy occurs throughout the year, involves males and females equally and produces single rays with or without mature gonads. Growth, apparently, takes precedence over sexual reproduction as evidenced by the smaller size of sexually immature individuals and the lack of gonadal tissue in the regenerating rays of comets and adults.

Fecundity in *Linckia columbiae* is low compared to other non-fissiparous species that broadcast spawn. This, in part, can be attributed to its relatively small size, variable gonadal development, and the lack of gonadal tissue in regenerating rays. In addition, oocyte production is relatively low. If 2,500-3,500 oocytes represent egg production in a typical ovary of *L. columbiae* at Pumpernickel, a female with five non-regenerating rays and a minimum of two pairs of mature ovaries in each ray would produce about 50,000-70,000 eggs per season. For the average female at Pumpernickel (3.3 gm), this is about 21,000 eggs per gm per year. In comparison, a single *L. laevigata* sheds on the order of a million eggs at each spawning and may spawn repeatedly within a season (Yamaguchi 1977). An adult female *Pisaster ochraceus* produces 100,000 eggs per gm each year which, given the weight of sexually mature individuals (> 400 gm), results in tens of millions of eggs (Menge 1975).

Very small complete individuals with ray lengths shorter than 13 mm, R1 of the smallest comet, were never observed despite extensive searches. I infer from this that juvenile *Linckia columbiae* are very rare or that recruitment is infrequent. However, in many asteroid species, including *L. laevigata* that only reproduces sexually, juveniles are seldom seen in the field because they are extremely small and cryptic and often have different habitat preferences than adults (Yamaguchi 1977; Chia *et al.* 1984). Sexual reproduction and pelagic larvae have been noted in at least one population of *L. multiflora* (Mortensen 1938), but, as with *L. columbiae*, fecundity appears to be low (Rideout 1978) and juveniles have not been reported. The details of spawning and larval development for *L. columbiae* are unknown. The relatively small eggs suggest the larvae are planktotrophic (Thorson 1950; Strathmann 1974; Chia 1974).

If dependence on sexually produced larvae for replacement and growth of the population is reduced, energy may be diverted from gametogenesis into the production of asexual propagules. By increasing the expenditure of energy per reproductive unit, *Linckia columbiae* takes advantage of the increased survival of larger reproductive units (juveniles vs. planktonic larvae) and increases the probability of successful recruitment to the parent population (Caswell 1985). By increasing clonal allocation at the expense of annual investments in sexual reproduction *L. columbiae* may also take advantage of environmental conditions that favor year round population growth.

The persistent bias towards females at Pumpernickel has no immediate explanation. The incidence of autotomy was similar for males and females; consequently, autotomy would only perpetuate an excess of females in the population however established (*e.g.*, differential migration, mortality, larval recruitment).

Genetic Consequences of Fission: Subpopulations of the predominantly fissiparous asteroid *Coscinasterias calamaria* are characterized by significant numbers of replicate genotypes and strong genetic disequilibrium between populations (Johnson & Threlfall 1986). Genotype analysis of *Linckia columbiae* around Santa Catalina Island and other locations in southern California shows a similar trend emphasizing the significance of asexual reproduction in maintaining this species (McAlary 1988, unpubl. data). As with other groups of clonal invertebrates, asexual reproduction among fissiparous asteroids may promote successful genotypes and, presumably, adaptiveness within and between local populations (Jackson 1985).

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Contribution No. 148 of the Catalina Marine Science Center.

Temporal and Spatial Variation in the Recruitment of the Sea Hare, *Aplysia californica*, at Santa Catalina Island, California

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Abstract — Recruitment of *Aplysia californica* was studied at Santa Catalina Island, California. *Aplysia californica* recruited almost exclusively to the red algae *Plocamium cartilagineum* and *Laurencia pacifica*. Monthly sampling of *Plocamium* revealed two peaks of recruitment in 1986: one in January and another in June. Recruitment varied between locations, with some sites having consistently more recruits than others. This variation in recruitment is expected to have important consequences for the dynamics of *A. californica* populations.

Introduction

Variation in recruitment can be an important factor structuring marine populations (Connell 1985; Gaines & Roughgarden 1985; Roughgarden *et al.* 1985). Variation in recruitment of sessile marine invertebrates has been relatively well studied (see Hawkins & Hartnoll 1982; Kendall *et al.* 1982; Keough 1983; Caffey 1985; Connell 1985; Gaines *et al.* 1985; Gaines & Roughgarden 1985; Wethey 1985). However, comparatively little work has been done on variation in the recruitment of mobile marine organisms (see Loosanoff 1964; Branch 1975; Underwood 1975; Sarver 1979; Bowman 1985) with the exception of reef fish (Eckert 1984; Jones 1984; Sale *et al.* 1984; Cowen 1985; Victor 1986). In addition to the obvious complication of their motility, the recruits of many mobile marine invertebrates are small and cryptic. As a result, there is often a gap of months to a year between actual settlement (defined as the point when an individual first takes up permanent residence on or near the substratum) and the first observation by the scientist (Branch 1975; Underwood 1975; Bowman & Lewis 1977; Watanabe 1984). This makes it difficult to separate the effects upon the adult population of settlement, post-settlement mortality and movement (Keough & Downes 1982; Connell 1985).

Studies of recruitment typically have found it to be highly variable, both between sites and between years: 1) sessile marine invertebrates (Hawkins & Hartnoll 1982; Kendall *et al.* 1982; Keough 1983; Caffey 1985; Gaines & Roughgarden 1985; Gaines *et al.* 1985; Hughes 1985; Wethey 1985); 2) starfishes (Loosanoff 1964); 3) gastropods (Branch 1975; Lewis & Bowman 1975; Underwood 1975; Bowman & Lewis 1977; Sarver 1979; Watanabe 1984; Bowman 1985); 4) reef fishes (Eckert 1984; Jones 1984; Sale *et al.* 1984; Cowen 1985; Victor 1986). This variation in recruitment often was crucial in structuring the adult populations under study. Here I report results of an investigation of variation in the recruitment of the sea hare *Aplysia californica*, an opisthobranch gastropod, at Santa Catalina Island, California. Recruits were found almost exclusively upon the red alga *Plocamium cartilagineum*. I show that recruitment to this alga varied both seasonally and between sites. This variation in recruitment would be expected to profoundly affect the ecology of this species, potentially producing variation in abundance, competition and age-structure from one year to the next, and from one location to another (Hughes 1984; Connell 1985; Roughgarden *et al.* 1985).

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