Asexual reproduction by fission in *Holothuria atra* : variability of some parameters in populations from the tropical Indo-Pacific

Asexual reproduction
Regeneration
Holothurian
Strategy
Indo-Pacific

Reproduction asexuée
Régénération
Holothurie
Stratégie
Indo-Pacifique

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ABSTRACT

Holothuria atra is the most common aspidochirotid holothurian on tropical Indo-Pacific reefs. Asexual reproduction by transverse fission, followed by regeneration, has been studied at Reunion Island (Indian Ocean) and compared with different populations of the Indo-Pacific zone, thus permitting a better identification of the most significant parameters and a better understanding of this reproductive strategy. At Reunion Island, the species is studied at two stations on the same fringing reef: 1) on the back-reef where the fission rate is high (20 % of the population), the individuals small (generally weighting less than 150 g) and the population density high (4/m^2); and 2) on the reef front, where fission is extremely rare, the mean size of the individuals larger (up to 300 g) and the density low (0.01/m^2). Different categories of individuals, fissioning (F), after fission, anterior and posterior parts (A and P), and regenerating (Ap and Pa) have been identified from external observations. Dissection has demonstrated the unequal allocation of organs during fission and the variability of the regenerative states, mostly in the anterior part. Concerning fission, the position of the split in an individual is in the anterior half (at 44 % of the total length). The monthly incidence of fission is higher from October to January and in June-July. Fission does not result in an increase in the density of the population. The monthly rates of regenerating individuals originating from anterior (3.7 %) and posterior (6.1 %) parts suggest that survival is higher in the latter instance. The occurrence of asexual reproduction in various populations of this species is discussed in relation to the ecology and the parameters of the populations considered. On the back-reef studied at Reunion Island, the population is subtidal and emersion cannot explain fission. Anthropogenic disturbances are possible triggers of this phenomenon.

RÉSUMÉ

Reproduction asexuée par scission chez *Holothuria atra* : variabilité de certains paramètres dans des populations de l'Indo-Pacifique tropical.

Holothuria atra est l'espèce la plus commune des holothuries aspidochirotes dans les récifs de l'Indo-Pacifique tropical. Sa reproduction asexuée par scission, suivie de régénération, a été étudiée à La Réunion (Océan Indien) et comparée à différentes populations de la zone Indo-Pacifique, pour identifier les paramètres les plus significatifs et interpréter cette stratégie adaptative. A La Réunion, l'étude a été menée en deux sites du même récif frangeant : 1) dans un arrière récif où le taux de scission est élevé (20 % de la population), les individus de petite taille (en général inférieurs à 150 g) et la densité de population forte (4/m^2) ; 2) sur le front récifal où la scission est extrêmement rare, la taille moyenne des individus plus grande (jusqu'à 300 g) et la densité faible (0,01/m^2). Plusieurs catégories d'individus, en cours de scission (F), après la scission, régions antérieure et postérieure ((A et P) et en régénération (Ap et Pa) ont été décrites à partir de leur morphologie externe. Les dissections ont ensuite permis de déterminer la répartition inégale des organes entre les régions antérieures et postérieures durant la scission et la variabilité des stades de régénération, qui est particulièrement nette dans la partie antérieure. Concernant la scission, le niveau de séparation se situe dans la région antérieure d'un individu (à 44 % de la longueur totale); le taux de scission mensuel parait plus élevé d'octobre à janvier et en juin-juillet. La scission n'a pas entrainé d'augmentation de la densité de population pendant la période d'étude. Les taux mensuels moyens d'individus en régénération, provenant respectivement des parties antérieures (3,7 %) et postérieures (6,1 %) semblent indiquer que le taux de survie des régions postérieures est supérieur. L'occurrence de la reproduction asexuée dans différentes populations de cette espèce est discutée en relation avec l'écologie et les paramètres des populations considérées. A la station d'étude à La Réunion, la population étant subtidale l'exondation ne peut pas expliquer la scission. Des perturbations d'origine anthropiques pourraient être causes de ce phénomène.

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INTRODUCTION

Asexual reproduction by fissiparity and regeneration is only displayed by some taxa. It can occur in populations that also reproduce sexually; but the evolutionary and ecological significance of this strategy is still a matter of debate (Ghiselin, 1987; Mladenov and Emson, 1988; Gouyon *et al.*, 1993).

Although holothurians are noted for their ability to reproduce asexually by fission, there have been relatively few reviews of the subject and data are still limited (Emson and Wilkie, 1980; Lawrence, 1987; Smiley *et al.*, 1991; Mladenov and Burke, 1994). Approximately ten species, including dendrochirotes and aspidochirotes, have been reported, from field and laboratory observations, to reproduce asexually. Most of these observations are anecdotal, and report very low fission rates in the field; these rates are therefore not significant at the population level. Two tropical aspidochirotes have attracted greater attention: *Holothuria parvula* in the Atlantic Ocean (Crozier, 1917; Deichmann, 1922; Emson and Mladenov, 1987), and *Holothuria atra* in the Indo-Pacific (Bonham and Held, 1963; Pearse, 1968; Doty, 1977; Harriot, 1982, 1985; Conand, 1989; Conand et De Ridder, 1990; Chao *et al.*, 1993; Chao *et al.*, 1994). As the latter species is widely distributed in the tropical Indo-Pacific (Guille *et al.*, 1986), it offers a good example of this particular life-history strategy and could be used as a model for comparison with the general strategy of sexual reproduction in holothurians.

MATERIALS AND METHODS

Holothuria atra is the most common holothurian in reefal systems. Various ecological and biological parameters of its populations have been reviewed by Conand (1989; 1993). There appear to be two major types of population – one characterized by low densities of large individuals and the other possessing high densities of predominantly smaller individuals. The occurrence of one or the other of these population types generally seems to be related to ecological factors, such as depth, hydrodynamic conditions or food availability. Chao *et al.* (1993; 1994) have recently compared the fission rates in populations of these two types from Taiwan, showing that a low-density population of large individuals does not undergo fission, whereas in a high-density population fission occurs throughout the year, peaking during the summer.

Reunion Island, situated in the Indian Ocean, is part of the Mascarene Archipelago. As a relatively recent volcano, its coastal shelf is narrow and the coral formations are limited to small fringing reefs. Saint-Gilles/La Saline reef (Fig. 1) extends nine kilometres along the leeward coast, with a width of approximately 500 m. Its general ecology, the impact of eutrophication and the structure of the major communities have received increasing attention (Cuet *et al.*, 1989; Naim and Cuet, 1989; Amanieu *et al.*, 1993; Naim, 1993; Cuet, 1994). The study of *Holothuria atra* is part of a research programme on the diversity and role of the echinoderms on this reef.

Planch'Alizés station (Fig. 1) was chosen for: 1) monthly sampling of a back-reef population of *Holothuria atra* composed of different size classes (where fission had been observed during preliminary observations); and 2) occasional sampling of an outer reef-flat population of large individuals. On the back-reef, in eight permanent quadrats, each measuring 10 m^2, all *H. atra* were collected, examined for fission or regeneration, weighed and returned to the site. On the basis of their external morphology, the individuals were classified in six categories, following previous studies (Doty, 1977; Conand and De Ridder, 1990):

– Normal (N): with no, or no longer any, discernible external sign of regeneration (*i.e.* when the length of the regenerated portion was > 30 mm);

– Fission (F): in the process of transverse division;

– Anterior (A): lacking posterior part;

– Anterior regenerating posterior part (Ap);

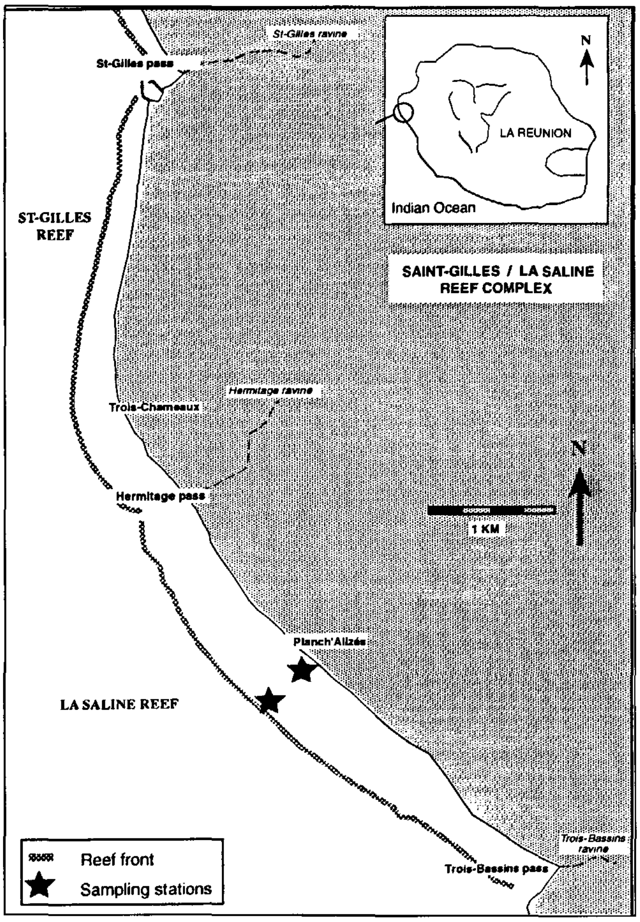

Figure 1

Sampling stations at Planch'Alizés, Reunion Island.

– Posterior (P): lacking anterior part;

– Posterior regenerating anterior part (Pa).

A dozen individuals in each category were collected, preserved and dissected to ascertain: 1) the validity of the categories; and 2) the allocation of the organs during fission. In order to understand the re-establishment of the digestive and reproductive functions, special attention was paid to the intestine and gonads during the monitoring of the regeneration processes. On the outer reef-flat, which is very exposed, samples were collected to establish a size frequency distribution, gonad-indices and abundance from Catch Per Unit Effort (CPUE) data, as carried out by Conand (1989).

RESULTS

Changes in population density

The total abundance of *H. atra* in the eight quadrats (T) of the back-reef station is shown, for each sample date, in Table 1. Analysis of variance has shown that the differences in total abundance between sample dates are not significant (ANOVA F = 1.36; d.d.l. = 11.77), with the mean equal to 331 per 80 m^2, or 4.14 per m^2. It thus appears that there has been no significant change in population density during the course of the year, in this population (Fig. 2).

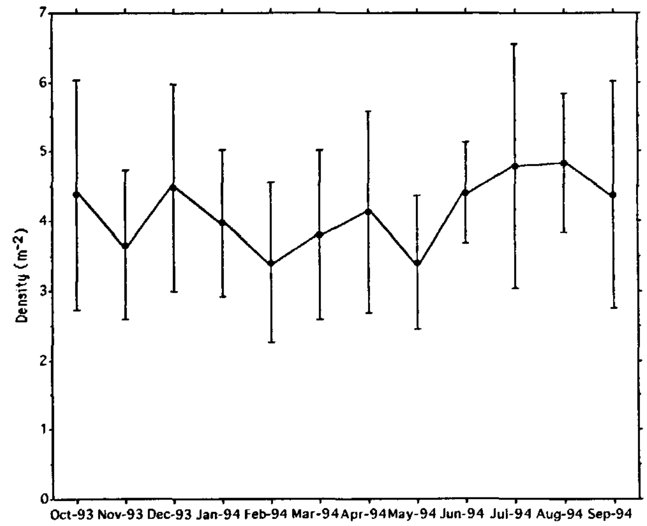

Figure 2

Density fluctuations (mean ± confidence interval, a = 0.05) in the population of Holothuria atra, *from the back-reef station.*

At the outer reef-flat station, the mean CPUE is 38 individuals/hour. Since a one-hour search corresponds to approximately 4000 m^2 (estimation using a flow-meter, by Conand, 1989), the mean density is therefore of the order of 0.01 per m^2.

Size frequency distributions at the stations

Size frequency distributions, expressed in term of weight, are very different at the two stations (Fig. 3). On the back-reef, the weight distribution appears plurimodal, consisting of smaller individuals weighing less than 240 g and with putative modes at 30, 90 and 120 g. On the reef-front, individuals weighed between 40 and 310 g.

Categories of individuals at the stations

At the outer reef-flat station, all the individuals were normal, showing no sign of recent fission. In contrast, at the back-reef station, different categories of individuals were found (Tab. 1). Fluctuations of the proportions of each category are also shown in Table 1. The characteristics of each category, as revealed by dissection, are presented below, as well as their variability.

Fissioning (F) anterior part

For ten individuals measured during the process of fission, the fission point was always located in the anterior part, at 0.44 of the total length (sd = 0.03). This anterior part appears largely empty, as noted for *H. parvula* by Emson and Mladenov (1987), containing the pharyngeal bulb (plus tentacular ampullae, madreporite, polian vesicle), a short portion of the descending intestinal loop and a portion of the dorsal mesentery with gonads in most cases. The intestine is generally cut at the same level, *i.e.* where the hemal vessel bifurcates, between 5 and 20 mm below the gonad-basis. There is no left respiratory tree, but generally a portion of the right tree floats in the cavity. The lon-

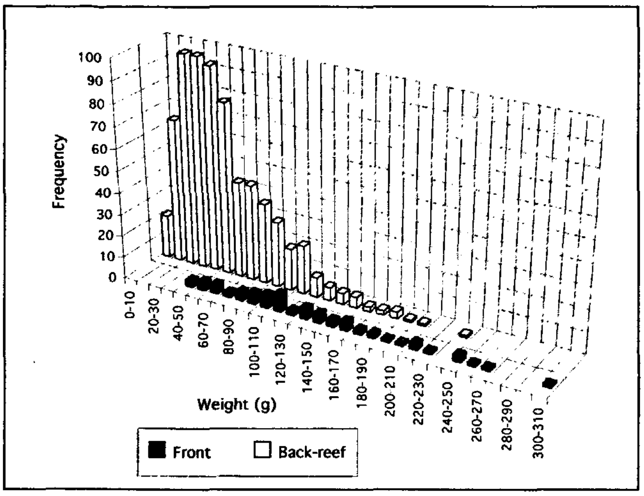

Figure 3

Weight frequency distributions of individuals of Holothuria atra *from the back-reef and reef-front stations.*

gitudinal muscles are generally cut, the median muscle of the trivium has been observed half-severed and stretched in its median part.

Fissioning (F) posterior part

The posterior part is comparatively full of organs. Two empty loops of intestine with the rete mirabile, the left respiratory tree and remains of the right tree form a large, more or less floating, mass. The intestine rapidly seals. Near the end of the fission process, small holes sometimes appear in the tegument, the last organ to undergo fission; through these holes, a part of an intestinal loop, or of a respiratory tree, can be extruded and may be lost during the separation of the two parts.

Recently fissioned anterior part (A)

This category is the most variable one, because some individuals have already started to regenerate their intestine from the descending loop. The regenerated intestine, pink in colour, appears first as a straight tube, then loops appear; sometimes sand grains are seen inside, before the anus is perforated. The regenerated respiratory trees appear at the distal part of the intestine, in the form of small buds. The gonad tubules seem reduced by lysis. Although the tegument only shows a scar, the muscles can already regenerate a narrow band of a few millimetres. The remains of the right respiratory tree may, or may not, show lysis.

Recently fissioned posterior part (P)

A circular scar some 8 mm in diameter is apparent at the fission site. The intestine can be organized in two different ways: generally, the third descending intestinal loop is fixed to the cloaca and in contact with the other loops, the rete and left respiratory tree. In a few individuals however, the third loop is separated from the others, which, tangled with the rete and respiratory tree, are free in the cavity. This could be a consequence of the holes sometimes noticed in fissioning individuals, through which the organs are extruded. The right tree is fixed along its canal to the tegument. A narrow band of muscles can regenerate on a few mm.

Regenerating anterior part (Ap)

This category often displays the same internal appearance as recently fissioned anterior parts (A), though externally the regenerate tegument is generally easily distinguished by its colour and the paucity of tiny podia. The regenerated longitudinal muscles are narrow. The gonad basis mostly persists without tubes. The intestine shows the same development and variability as in the A category; the anus may, or may not, be open, but the cloaca is never regenerated at this stage. The new respiratory trees elongate and the remains of the original ones degenerate. The longitudinal muscles elongate, now in close correlation with the length of the regenerated tegument. In order to include only regenerating individuals in the observations, older fissioned individuals, which could not be characterized without dissection, have not been taken into account. A length of 30 mm of regenerated tegument has been chosen as the maximum; this results in an underestimate of the regenerating categories.

Regenerating posterior part (Pa)

The intestine is generally organized in the first of the two categories as described above, with only the first intestinal loop regenerating, pink and narrow, but filled with sand. The regenerated muscles and tegument have an appearance similar to that of the anterior part. The pharyngeal bulb is smaller than in normal individuals and the number of small

Table 1

Frequency of individuals from different categories of Holothuria atra *at the back-reef station. T: total of all individuals; number and* percentage (%) *in each category, N: "normal" individuals, F: fission from field counts, A: anterior part, P: posterior part, Ap: anterior regenerating posterior part, Pa: posterior regenerating anterior part; s: standard deviation of the yearly mean.*

Date	T	N	F	A	Ap	P	Pa
20/10/93	351	223	3	32	32	14	41
		63,5%	*0,9%*	*9,1%*	*9,1%*	*4,0%*	*11,7%*
17/11/93	293	219	1	15	9	22	23
		74,7%	*0,3%*	*5,1%*	*3,1%*	*7,5%*	*7,8%*
15/12/93	359	284	1	14	12	30	17
		79,1%	*0,3%*	*3,9%*	*3,3%*	*8,4%*	*4,7%*
12/01/94	318	275	0	10	8	9	16
		86,5%	*0,0%*	*3,1%*	*2,5%*	*2,8%*	*5,0%*
23/02/94	273	242	0	9	10	4	7
		88.6%	*0,0%*	*3,3%*	*3,7%*	*1,5%*	*2.6%*
16/03/94	305	263	0	10	3	5	24
		86,2%	*0,0%*	*3,3%*	*1,0%*	*1,6%*	*7,9%*
22/04/94	331	275	1	18	9	11	13
		83,1%	*0,3%*	*5,4%*	*2,7%*	*3,3%*	*3,9%*
17/05/94	273	243	1	7	1	9	11
		89,0%	*0,4%*	*2,6%*	*0,4%*	*3,3%*	*4,0%*
27/06/94	353	277	3	24	9	26	14
		78.5%	*0,9%*	*6,8%*	*2,5%*	*7,4%*	*4.0%*
19/07/94	384	286	1	27	13	26	26
		74,5%	*0,3%*	*7,0%*	*3,4%*	*6,8%*	*6,8%*
31/08/94	387	308	0	15	18	16	29
		79,6%	*0,0%*	*3,9%*	*4,7%*	*4,1%*	*7,5%*
21/09/94	350	288	0	11	22	7	22
		74,4%	*0,0%*	*3,1%*	*6,3%*	*0,02*	*6,3%*
Sum	3977	3183	11	192	146	179	243
Mean	331,4	265,3	0,9	16,0	12,2	14,9	20,3
s	39,3	27,7	1,1	7,9	8,5	9,0	9,3
		80,0%	*0,3%*	*4.8%*	*3,7%*	*4,5%*	*6,1%*

buccal tentacles, always less than 20, is correlated with the length of the regenerated tegument. Gonads have not been observed in individuals of this stage. In a few individuals, the manner of the regeneration of the intestine probably follows on from the second category as described above. In this case, most of the intestine, rete mirabilis and right tree are produced by regeneration; the lysis of the old organs could, therefore, provide the energy required.

The different categories would seem to be clearly identifiable from their external organization. However, some A and Ap individuals could be confused and the variability in the organization is noticeable. This study has also shown that the digestive system regenerates very early and appears to function immediately. The reproductive system, on the other hand, seems to regenerate last, after the other systems have already regenerated.

Importance and size distributions of the different categories

It appears that there are nearly as many A as P individuals (Tab. 1), with a mean of about 5 % of the total in each category. On the basis of their distribution by weight (Fig. 4, A, B), individuals of the P category are larger, which corresponds to the position of the plane of fission already mentioned; they do not however exceed 80 g. The results of Kolmogorov-Smirnov tests permit rejection of the hypothesis that the distributions are the same (D = 0.363).

On the other hand, the difference in abundance between Pa and Ap individuals is remarkable, with the number of the former nearly double that of the latter. The former are also much larger than the latter, but do not exceed 110 g.

Finally a comparison of the abundance and size of categories A and Ap on the one hand, and P and Pa categories on the other, shows that the former are not very different (Kolmogorov-Smirnov test for distribution: D = 0.264), whereas the latter differ both in their numbers and sizes (Kolmogorov-Smirnov test for distributions: D = 0.454).

From these observations, and in relation to the anatomy, it is probable that the post-fission rate of mortality is higher in the Ap than in the Pa category.

Importance of seasonal variations in asexual reproduction

In Table 2 the different categories of regeneration are grouped to interpret the changes in the rates of fission and regeneration during the year. F individuals represent instantaneous fission (F_1) and the A + P categories are considered as recent fission (F_2), whereas the Ap + Pa , or regenerating, (R) categories result from an earlier fission. Taken together, all the fission products ($S = F_1+F_2+R$) account for nearly 20 % of the population at the back-reef. The distributions, in weight, of these products compared with the "normal" individuals (Fig. 5) show that they are predominant in the smaller sizes.

As the numbers of fissioning individuals F are generally low, less than 1 % on average (Tab. 1), the percentage of recent fission products, A + P, is used to show the variation of fission rates (Fig. 6). During the period of sampling, two

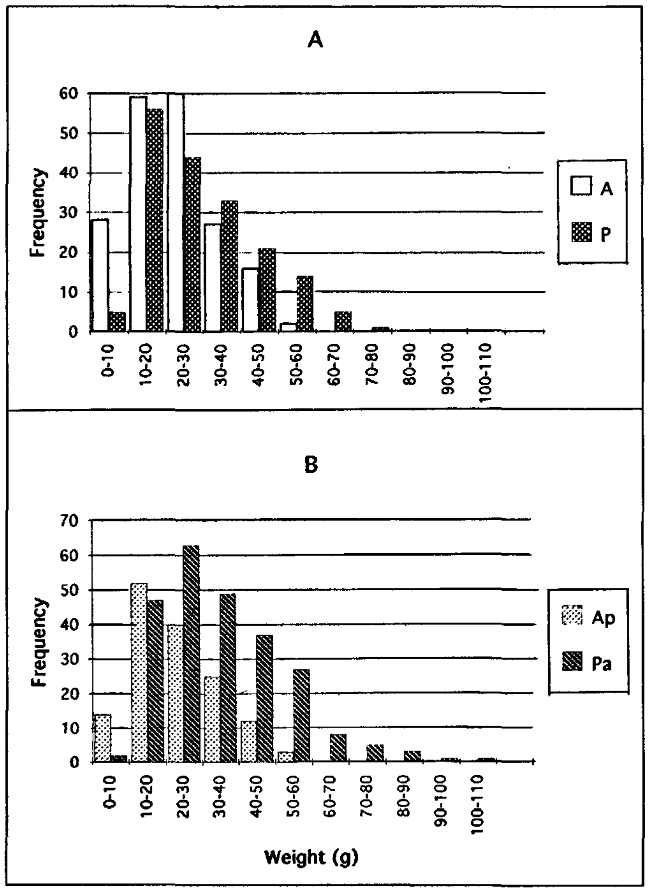

Figure 4

Weight frequency distributions for the different categories of fission products in Holothuria atra. *A: recent fission products, A and P; B: regenerating individuals, Ap and Pa.*

Table 2

Fission and regeneration at the back-reef station. T: total of all individuals; number and percentage (%) *in each category, A + P: recent fission products, Ap + Pa: regenerating individuals; S: scissiparity, from the sum of the fissioning, recent fission products and regenerating individuals; A + Ap: anterior individuals; P + Pa: posterior individuals.*

Date	T	A + P	Ap + Pa	S	A + Ap	P + Pa
20/10/93	351	46	73	122	64	55
		13,1%	*20,8%*	*34,8%*	*18,2%*	*15,7%*
17/11/93	293	37	32	70	24	45
		12,6%	*10,9%*	*23,9%*	*8,2%*	*15,4%*
15/12/93	359	44	29	74	26	47
		12,3%	*8,1%*	*20,6%*	*7,2%*	*13,1%*
12/01/94	318	19	24	43	18	25
		6,0%	*7,5%*	*13,5%*	*5,7%*	*7,9%*
23/02/94	273	13	17	30	19	11
		4,8%	*6,2%*	*11,0%*	*7,0%*	*4,0%*
16/03/94	305	15	27	42	13	29
		4,9%	*8,9%*	*13,8%*	*4,3%*	*9,5%*
22/04/94	331	29	22	52	27	24
		8,8%	*6,6%*	*15,7%*	*8,2%*	*7,3%*
17/05/94	273	16	12	29	8	20
		5,9%	*4,4%*	*10,6%*	*2,9%*	*7,3%*
27/06/94	353	50	23	76	33	40
		14,2%	*6,5%*	*21,5%*	*9,3%*	*11,3%*
19/07/94	384	53	39	93	40	52
		13,8%	*10,2%*	*24,2%*	*10,4%*	*13,5%*
31/08/94	387	31	47	78	33	45
		8,0%	*12,1%*	*20,2%*	*8,5%*	*11,6%*
21/09/94	350	18	44	62	33	29
		5,1%	*12,6%*	*17,7%*	*9,4%*	*8,3%*
Sum	3977	371	389	771	338	422
Mean	331,4	30,9	32,4	64,3	28,2	35,2
s	39,3	14,8	16,5	27,2	14,6	14,0
		9,3%	*9,8%*	*19,4%*	*8,5%*	*10,6%*

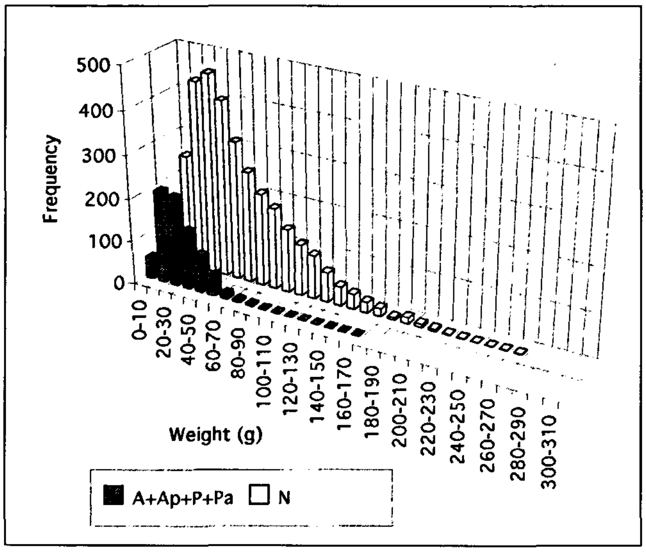

Figure 5

Weight distributions of the products from asexual reproduction (F, A, Ap, P, Pa), compared with the distribution of non fissiparous individuals.

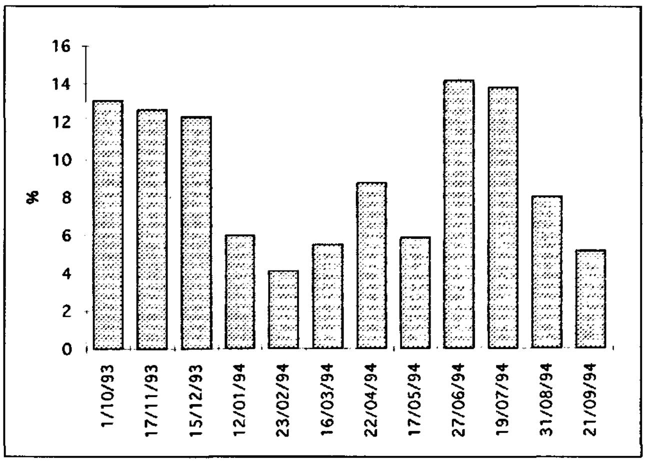

Figure 6

Seasonal variations in percentage fission, from A + P, the recent fission products.

phases with high fission rates, the first from October to January, the second in June-July, were observed; two phases of lower incidence of fission were observed from January to May and in August-September.

DISCUSSION

Characteristics of the populations of *Holothuria atra*: correlation between habitat, size and density

Holothuria atra shows a wide range in population density and individual sizes throughout the Indo-Pacific (Conand, 1989). The present study has confirmed the existence of two different types of populations, correlated with the habitat, the size distribution of individuals, and density (Tab. 3). On nearshore inner reef-flats and on back-reefs, the individuals are generally smaller and the populations reach higher densities than on outer reef-flats and deeper lagoon floors, as suggested for some habitats by Pearse (1968), Harriot (1982), Conand (1989) and Chao *et al.* (1993; 1994). These populations also have different strategies, the fission rates being significantly higher on inner flats or back-reefs (Tab. 3). Other echinoderms also show interpopulational variations in the levels of asexual reproduction (Mladenov and Emson, 1988).

Fission rates, periodicity and triggers to fission

Some comparisons will be attempted between the different Indo-Pacific populations of *H. atra*, although the data have not been collected with the same procedures by the different authors, and the characteristic coefficients of fission or regeneration do not have the same meaning. The «true» fission rates (F_1 %, from F individuals) are generally low in this species and often present seasonal fluctuations, with maximum values during the warm season (Tab. 3). The fission rates calculated from recently fissioned individuals (F_2 % = A + P/T) have higher values that are also seasonally fluctuating, as do the regeneration rates (R = Ap + Pa/T) and total fission rates (S = F_1 + F_2 + R/T). For example, on Heron Reef (Tab. 3), this rate only refers to small (less than 90 g) individuals (Harriot, 1982). Standardization of these parameters is recommended, using the external morphology of the individuals and the whole range of sizes, in order to obtain comparable data from various sites.

Different environmental factors have been put forward as triggering fission, such as the hydrodynamic regime (Pearse, 1968) and – more frequently – emersion (Conand, 1989; Conand et De Ridder, 1990; Chao *et al.*, 1993), with its effects on temperature (Doty, 1977), salinity, solar radiation and desiccation. At the back-reef site in the present study, these factors are probably not responsible, because the water depth remains between 1 and 1.7 m. Yet at this station the degradation of the reef, which is blatant, is due to nutrient enrichment probably from submarine groundwater discharge (Cuet *et al.*, 1989; Amanieu *et al.*, 1993; Cuet, 1994). Eutrophication has the most critical effects during the warm season (Naim, 1993). Direct human impact by walking may also be evoked, as this station is a resort spot. Fission could therefore also be considered in relation to reefal disturbance, a hypothesis which requires further investigation.

Consequences of fission for population structure

The present careful study of the anatomy in the different categories has thrown light on the phenomenon of unequal fission, the loss of organs during fission resulting in weight loss, the lysis of organs during regeneration and the slow regeneration of the anterior part. Differences therefore exist in the physiology of the two parts, and raise the issue of the mechanisms and energetic pathways involved in regeneration.

With regard to the interactions between sexual and asexual reproduction, a few observations have been made concerning the presence of gonads in fissioning individuals, as

Table 3

Densities, sizes of individuals and fission rates in different populations of Holothuria atra *in the Indo-Pacific, from reef-flat or back-reef, and* reef-front or lagoon (italics), *from different sources.* F_1*: fission rate from fissioning individuals;* F_2*: fission from recently fissioned; S: asexual reproduction from fissioning and regenerating individuals.*

Site	Mean density/m^2	Size or weight	F1, F2, S rates (date)	Reference
Eniwetak, reef-flat		186g		Pearse, 1968
Eniwetak, lagoon		*620g*		
Eniwetak, windward reef-flat	52 (max)	23cm, 49g (max)	S=9% (July)	Lawrence, 1979 and pers. com.
Guam, Pago Bay	0.21	103ml	F1=0.4 to 1.3% S=11 to 40%	Doty, 1977
Heron Island, reef-flat	0.8	20 to 300g	F2=10 to 25%; S=50 to 61%	Harriot, 1982
Heron Island, lagoon and front	*0.2*	*40 to 260g*	*S=27%*	
New Caledonia, reef-flat	0.73	6 to 26cm; 0 to 360g	F1=0.5 to 1.9%; S=6 to 25%	Conand and De Ridder, 1990
Papua New Guinea, reef-flat	0.5 to 6	5 to 23cm;	S=24% (July)	
Taiwan, Wanlitung	0.51 to 1.59	5 to 185g	F2=0.5 to 18%	Chao et al., 1993
Taiwan, Nanwan	*0.24*	*350 to 1350g*	*F2=0%*	
La Reunion, back-reef	4.05	0 to 220g	F1=0.3%;F2=5 to 14%;S=10 to 35%	Conand, present study
La Reunion, reef-front	*0.01*	*0 to 310g*	*S=0%*	

well as their lysis during regeneration in anterior parts, the absence of gonads in posterior parts and very low gonad-indices in both populations in Reunion Island. From the different studies on this species (Harriot, 1982; Conand, 1993), it appears that the variability of the gonad-index is higher in *H. atra* than in other holothurians, and that its maximum values are lower. Thus the reproductive effort is reduced. This characteristic could be a consequence of fission.

Concerning the consequences of fission for demography, it appears that the density remained stable during this study, as it did in the other populations displaying fission (Ebert, 1978, 1983; Conand, 1989), in contrast with the increase observed in Taiwan (Chao *et al.*, 1993; 1994). Is the difference in size distributions (with predominantly smaller individuals in populations showing fission) also the consequence of fission ? A long-term survey will help to answer these questions.

Finally, in order to determine the impact of fission on population dynamics it will be necessary to model simultaneously the variability of different parameters: recruitment by sexual and asexual means; growth and mortality of the three categories of recruits (larvae, anterior and posterior parts). Triggers of fission from both natural and anthropogenic disturbances also deserve further reseach.

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