Asexual reproduction in *Holothuria atra* on a reef of Reunion Island in the Indian Ocean

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Holothuria atra is a sea cucumber species which is frequently encountered throughout the Indo-Pacific region. A population displaying fission characteristics was studied in one of the reefs of Reunion Island. Analysis of various studies on the external morphology and the internal anatomy of this back reef population contributed to the determination of parameters linked to the processes of fission and regeneration.

External morphology

An examination of the external morphology of each specimen observed in the field produced the following classification system:

– N: 'Normal' specimens which have a mouth and an anus and show no transverse constriction of their integument;

– F: Specimens in the process of fission which have a mouth and an anus and show transverse constriction of their integument;

– A: Anterior specimens which have a mouth but no anus;

– P: Posterior specimens which have an anus but no mouth;

– Ap: Anterior specimens which are regenerating their posterior portion;

– Pa: Posterior specimens which are regenerating their anterior portion.

Note that specimens in the process of regeneration can be identified, as the regenerated portion has an integument which is lighter in colour and smaller in diameter than the rest of the body.

Asexual reproduction in the overall population

Using the above classification, two characteristic parameters for asexual reproduction were determined: the rate of fission (F%) and the rate of regeneration (R%), based on sampling carried out during the six-month austral summer.

Overall, the process of asexual reproduction appeared to involve 20.2 per cent of the total surveyed population.

Rate of fission

As few specimens in the process of fission are generally available, the rate was calculated from the following formula: 100 x (A+P)/2T, with T being the total number of specimens. In La Réunion, this rate is 4.7 per cent on average, which corresponds to 9.5 per cent if the As and the Ps are considered as new specimens. Temporal variations in the rate were observed, as shown in Figure 1.

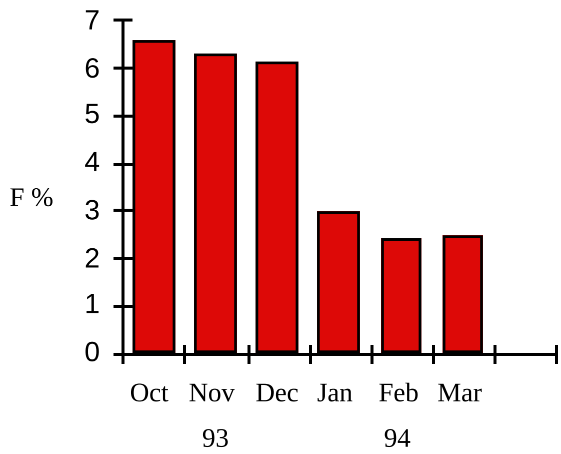


Figure 1: Temporal variations in the fission rate, F %

This rate seems to be relatively stable from October to December, then it decreases by 50 per cent between the months of December and January, after which it levels out again.

Having determined that division takes part in the anterior portion of the animal, at a point located at 45 per cent of the length of the specimen, and based on the weight distribution of recently divided specimens, it was determined that fission takes place in normal animals weighing between 9 g and 135 g.

Regeneration rate

This rate was obtained by using the following formula: 100 x (Ap+Pa)/T. The average value obtained, 10.6 per cent, indicates that the regeneration period is longer than the fission period.

The regeneration rate also varies over time. In fact, a decrease was noted from October to February, followed by a slight increase in March. Moreover, mortality in animals produced by asexual reproduction is greater in anterior specimens than in posterior specimens, which are more numerous.

A new parameter was considered during this study—the regenerated length. Contrary to what had been expected, given the location of the division, we noted that anterior specimens (Ap) regenerate to a shorter length than posterior ones (Pa). However, we have some reservations about this observation, since, above a certain regenerated length, the distinction between a normal specimen and an anterior specimen in the process of regeneration is less clear than it is for posterior specimens.

Asexual reproduction at the individual level

Some of the specimens surveyed (belonging to categories F, A, Ap, P and Pa) were harvested and dissected. Examination of the organs supplied additional information about fission and regeneration.

Description of fission

Sea cucumbers beginning fission hide and are contracted. They show constriction at one place on their integument which then develops into a ring. The integument stretches and then splits. At this stage, the digestive system is the only link between the two parts. In the end it also divides (sometimes pieces remain outside the body and are lost) and the anterior and posterior parts separate, but generally remain close to each other.

Dissection revealed where the split was located in relatio to the internal organs. Two possibilities are proposed as shown on Figure 2.

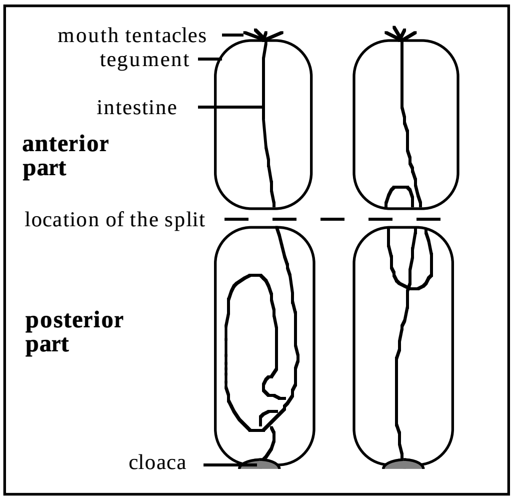


Figure 2 : Two fission possibilities

The difference in the layout of the digestive tube in the two cases is explained by the fact that the stretching forces which affect the animal disturb the arrangement of the organs.

Both external and internal signs of future fission were observed. The external signs are a point on the integument which is particularly contracted or a ringlike constriction of the body; internal signs are constrictions of the longitudinal muscular bands at the point of future fission. A few of the dissected subjects showed these characteristic signs, even though they had already undergone fission only a short time earlier.

Description of regeneration

After fission, the anterior part A has very few organs. The only ones remaining are the mouth area and its appendages, the gonads (if any), and part of the intestine. The intestine lengthens during the regeneration and recovers its initial appearance. The respiratory trees regenerate completely, as does the *rete mirabile*. Feeding recommences rather quickly, well before all the organs are completely regenerated.

In the posterior part P, generally most organs remain, except those of the anterior region. The left respiratory tree associated with the *rete mirabile* and attached to the digestive tract dissolves. Meanwhile, the length of the digestive tract measurably decreases, then regeneration restores it to its initial appearance. The right respiratory tree is also regenerated. The oral area is regenerated rather quickly, becoming functional even when it is very small and only has a dozen buccal tentacles.

Synopsis of organ regeneration

After fission, specimens in category A have to regenerate the intestine, the *rete mirabile*, the respiratory trees and the cloaca. Specimens in category P dissolve most of the remaining organs (intestine, *rete mirabile*, respiratory tree). They then regenerate them, probably through materials left over after dissolution. In both groups, the intestine, the left respiratory tree and the *rete mirabile* are regenerated.

Category verification

The various categories that we have defined according to their external morphology show some variability, related to the state of advancement of regeneration which affects the physiology of nutrition in particular. Thus category A includes all anterior specimens that have recently undergone fission or that are in the process of internal regeneration. The Ap category includes all anterior specimens that have begun regeneration of the integument; category P includes all posterior specimens that have recently undergone fission and have not regenerated any of their organs; and, finally, category Pa includes all posterior specimens that have regenerated the oral portion and begun regeneration of internal organs.

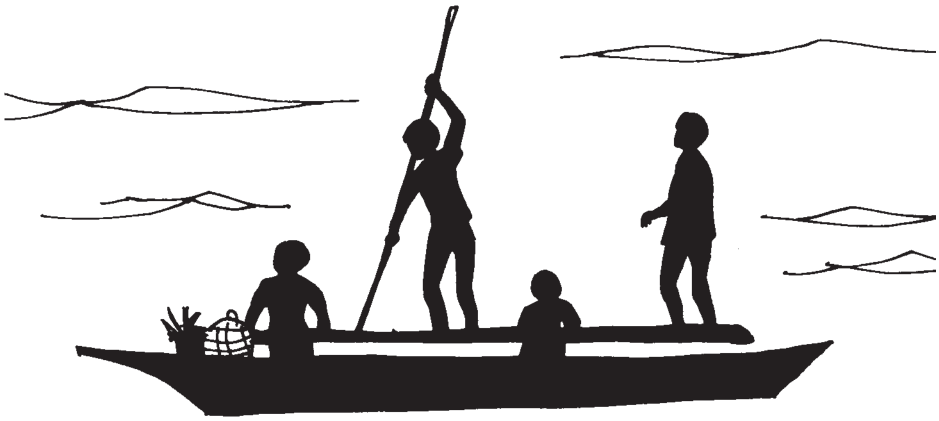
Sexual and asexual reproduction

The presence of gonads both in some subjects showing recent fission and in some that are in the process of regeneration suggests that sexual and asexual reproduction can occur in the same specimen.

Anatomical study has thrown light on the ways in which fission and regeneration take place in *Holothuria atra*. Study of regeneration and fission rates will be carried out over an entire year-long cycle for full understanding of these events. Finally, numerous other parameters, such as fission stimuli, energy requirements, etc. will have to be considered in order to understand the place of this strategy in population dynamics.

Acknowledgements

We thank Mrs C. Conand and the team at the Marine Ecology Laboratory who assisted us in carrying out this research.



Request for information on fission and regeneration of tropical holothurians

by Chantal Conand

Asexual reproduction by fissiparity and regeneration is displayed by some marine animals. It can occur in populations also reproducing sexually, but the evolutionary and ecological significances of this strategy are still a subject of debate (Ghiselin, 1987; Mladenov & Emson, 1988; Gouyon et al., 1993).

Although holothurians are noted for their ability to reproduce asexually by fission, there have been relatively few reviews on the subject and specific data are still very limited (Emson & Wilkie, 1980; Lawrence, 1987; Smiley et al., 1991; Mladenov & Burke, 1994). Approximately ten species, amongst Dendrochirotes and Aspidochirotes, have been reported, from field and laboratory observations, to reproduce asexually. Most of these observations are still anecdotal, and refer to very low fission rates in the field; they are therefore not significant at the population level.

Two tropical Aspidochirotes have attracted more attention: *Holothuria parvula*, in the Atlantic Ocean (Crozier, 1917; Deichmann, 1922; Emson & Mladenov, 1987) and *Holothuria atra* in the Indo-Pacific (Bonham & Held, 1963; Pearse, 1968; Doty, 1977; Harriot, 1982; Conand & De Ridder, 1990; Conand, 1993; Chao et al., 1993). As this species is