

Reproductive biology of the holothurians from the major communities of the New Caledonian Lagoon

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Abstract. The reproductive biology of nine species of aspidochirote holothurians from the major communities of the New Caledonian lagoon has been analysed. The data were obtained from monthly sampling from 1978 to 1982 of their populations on reef slopes and passes for *Holothuria nobilis*, *H. fuscogilva*, *H. fuscopunctata* and *Thelenota ananas*, in the inner lagoon for *Stichopus variegatus*, *H. scabra* and *H. scabra versicolor* and on reef flats for *Actinopyga mauritiana*, *A. echinites* and *H. atra*. The morphology and anatomy of the gonads and their annual cycle are described. The reproductive cycles, composed of the five phases of gonad growth, maturing, spawning, post-spawning and resting, were determined from the changes in the sexual stages, the gonad indices and the percentage of indeterminate sex. Three main reproductive patterns are recognized, annual cycles with spawning occurring during the warm season or during the cool season and a semiannual cycle. Other population parameters, such as the size of the mature oocytes, the mean size of the individuals at first sexual maturity, and absolute and relative fecundities were calculated and related to the mean size of the species, the taxonomy and the ecology. The reproductive strategies of the species show a gradient that is probably related to the stability of the biotopes, with smaller species living in the more unstable outer reef flats and larger species in deeper lagoon floors.

Introduction

Holothurians are conspicuous echinoderms commonly found in the various coral-reef and lagoon benthic communities, but little is known about their biology and their ecological role (Bakus 1973, Birkeland 1989). The New Caledonian lagoon and reefs are very diversified and complex. A number of studies have been conducted, on

both benthic ecology to understand their structure and functioning, and on the biology of the various halieutic resources. The holothurian fauna is particularly rich, ca. 60 species, amongst which aspidochirotés are dominant with ca. 50 species (Guille et al. 1986, Conand 1989a). The main affinities and associations of these aspidochirotés have been detailed in an ecological study conducted on the scale of the whole lagoon (Conand and Chardy 1985). The purpose of the present paper is to describe the reproductive biology of nine common species characteristic of the major communities. This set of data concerning species at the same taxonomic level allows a synthesis of their reproductive biology and makes it possible to relate their adaptative strategies to their distribution and abundance.

Materials and methods

The different species were collected from the southwest lagoon (Fig. 1) at sites where the populations are dense. These species are characteristic of the main holothurian communities defined by Conand and Chardy (1985).

Holothuria nobilis, *H. fuscogilva*, *H. fuscopunctata* and *Thelenota ananas* are characteristic of the reef slopes and passes (infralittoral reef community). In general, their populations are composed of large individuals with rather low densities (Conand 1989a).

Holothuria scabra versicolor (described in Conand 1986) and *Stichopus variegatus* are characteristic of the inner lagoon (terrigenous infralittoral community), while *H. scabra* is more coastal. Compared with the first group, the populations are composed of medium-sized individuals with intermediate densities.

Actinopyga miliaris and *Holothuria atra* are a very common and characteristic species of the inner reef flats (terrigenous mediolittoral community). Compared with the second group, the populations are composed of smaller individuals with high densities.

Actinopyga mauritiana and *A. echinites* are characteristic of the outer reef flats (mediolittoral reef community). The populations of these two species are composed of smaller individuals with variable densities that can be very high.

The sampling methods and laboratory measurements used were those of Conand (1981, 1986, 1989a) and are described briefly below. Microscopic examination of fresh and formalin preserved gonads was used to establish the sex and maturity stage and to measure the oocyte diameters. A maturity scale in five stages, estab-

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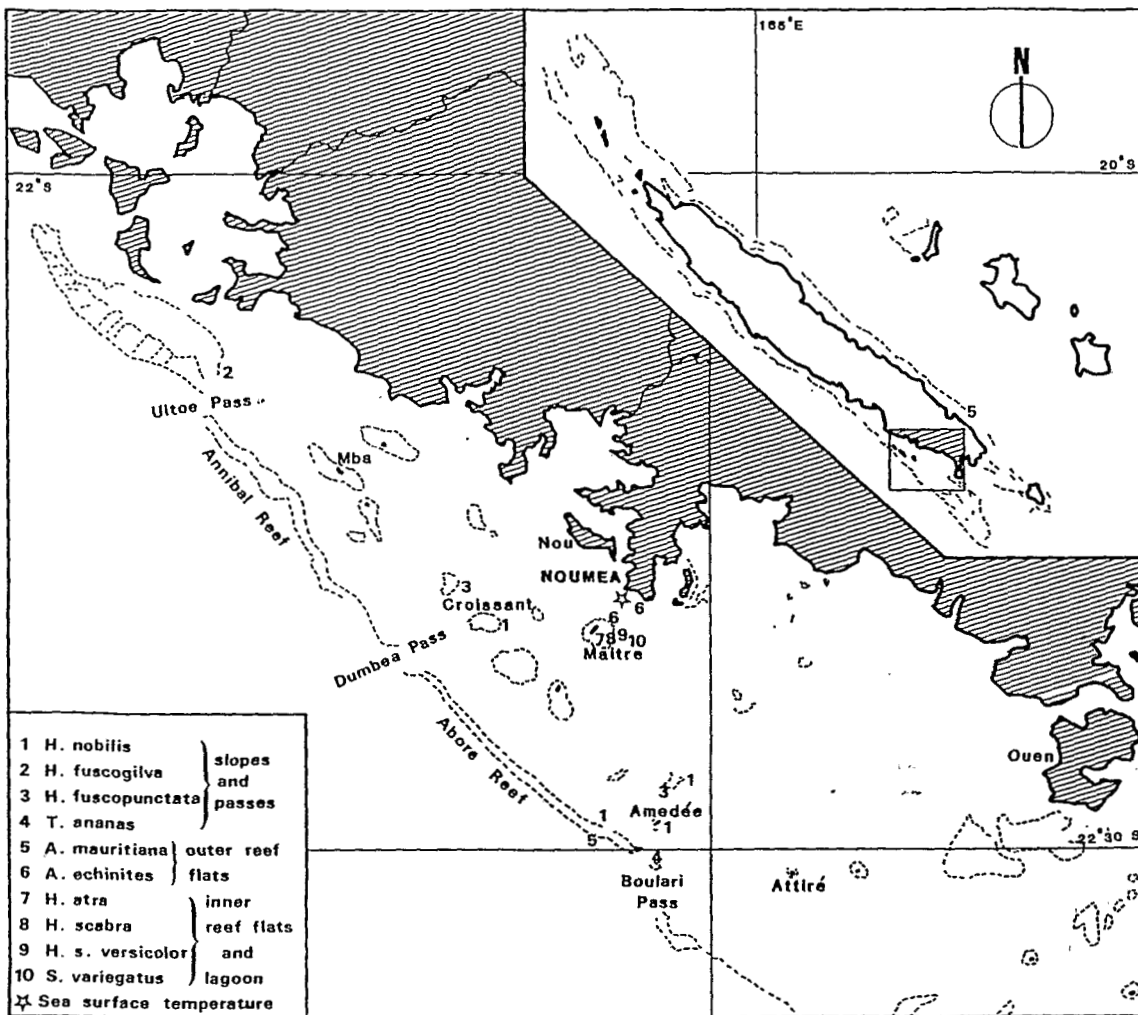


Fig. 1. Sampling sites of holothurians in the lagoon of New Caledonian

lished for *Holothuria nobilis*, *H. fuscogilva*, *Thelenota ananas* (Conand 1981), *Actinopyga echinites* (Conand 1982) and *Stichopus variegatus* (Conand 1993), was used. The stage of maturity was determined by criteria including: form, color, consistency and weight of the gonads, the length and diameter of the fecund tubules, and the size and microscopic characteristics of the oocytes. Stages I and II (undetermined) are gonads whose sex could not be established. Stage I corresponds to immature gonads and stage II to resting gonads, stage III corresponds to developing gonads, stage IV to maturing and spawning gonads, and stage V to post-spawning gonads.

The reproductive cycles were established through the combined use of three criteria: the monthly percentages of the maturity stages for each sex, the monthly gonad index (GI), the ratio of the wet gonad weight (GW) to the drained body weight (WD) and the monthly percentage of individuals that could not be sexed. Five phases were distinguished. A growing phase with an increase of gonad index and preponderance of stage III gonads, a maturing phase with the highest gonad index and increase in percent of stage IV gonads, a spawning phase with a sharp decrease in the gonad index and increase in percent of stage V gonads, a post-spawning phase with a continuous decrease in the gonad index and a resting phase with the lowest gonad index and a maximum of stages I and II.

First sexual maturity for a population was defined as the size (LT_{50}), or weight (WD_{50}), at which the gonads of 50% of the individuals were undergoing gametogenesis during the reproductive season. It was determined by plotting the percentage of individuals

with developing or developed gonads against classes of drained weight (Conand 1981). In order to indicate the relative position of the first maturity in the entire life-cycle, the ratio of LT_{50} and WD_{50} to the maximum values of LT and WD (LT_M and WD_M) were calculated.

Fecundity was estimated from mature ovaries in stage IV. It was assumed that oocytes in the most advanced mode, as indicated by the size frequency distribution, are spawned during the reproductive season and that their number corresponds to the absolute fecundity. An ovary sample of known weight (g) was fixed in Gilson's fluid (Bagenal 1973), the oocytes volumetrically subsampled and the number of oocytes (n) in the most advanced mode counted. The absolute fecundity (FA) was calculated as $FA = n (GW/g)$. The relative fecundities (FRO: fecundity related to eviscerated weight; FRG: fecundity related to ovary weight) were calculated as $FRO = FA/GW = n/g$, per gram ovary, and $FRG = FA/WG$, per body wall (eviscerated) gram weight.

Bimonthly mean seawater temperatures were calculated from daily measurements at the Noumea coastal station (Fig. 1).

Results

Sex ratio, gonad anatomy, maturity stages

All the species studied are dioecious. The sex-ratios (percentage of males) are given in Table 1. The Chi-square

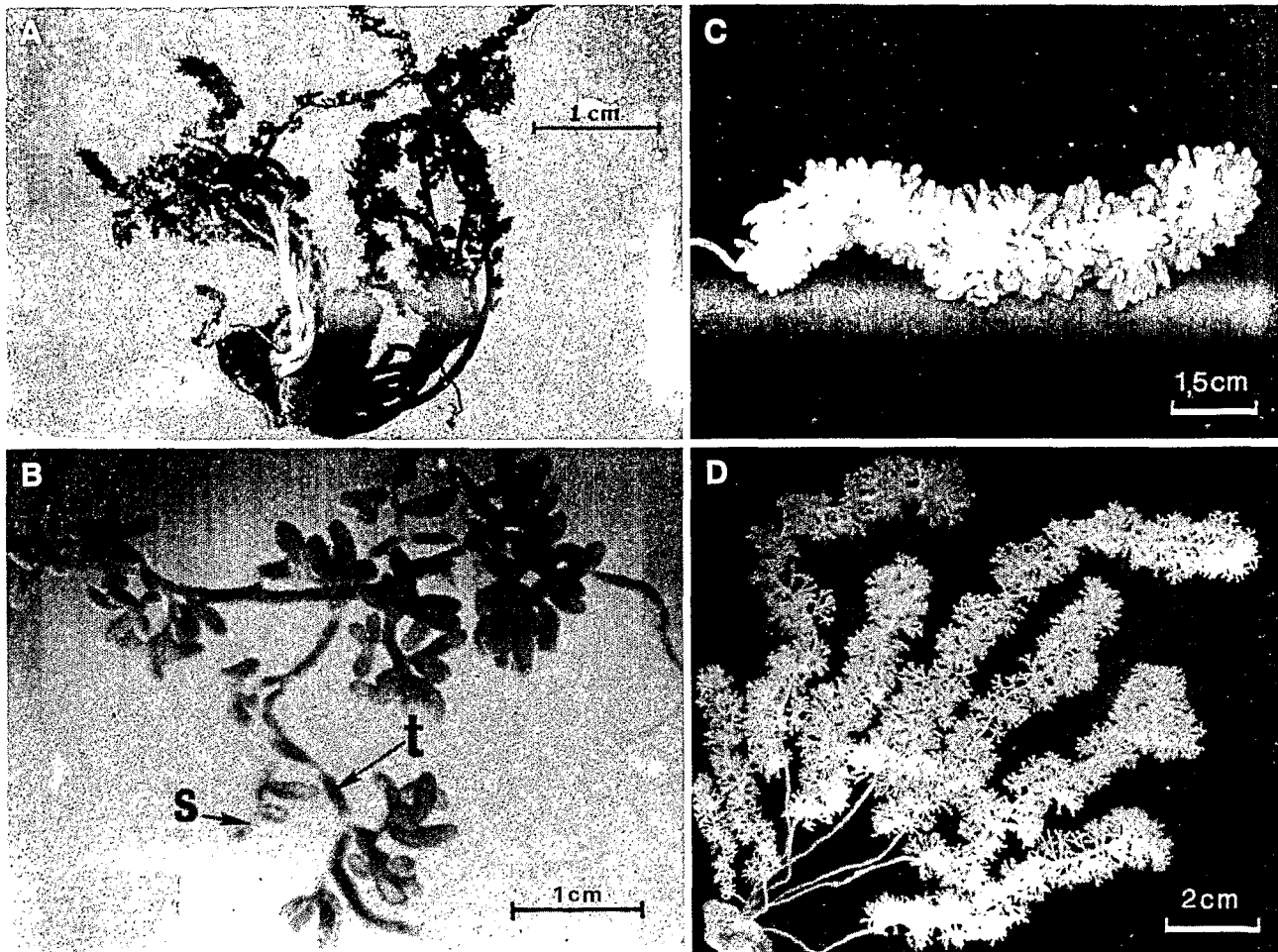


Fig. 2. Anatomy of Stichopodid gonads. Branched tubules with saccules in *Thelenota ananas*: (A) stage I, II; (B) ovary, stage IV. t: tubule; s: saccule. Unbranched tubules with saccules in *Stichopus variegatus*: (C) ovary, stage IV; (D) testis, stage V

Table 1. Sex-ratio of New Caledonia holothurians. M: males; F: females

Habitat Species	M	F	M/M + F (%)
Slopes and passes			
<i>Holothuria nobilis</i>	239	242	50
<i>Holothuria fuscogilva</i>	57	50	53
<i>Holothuria fuscopunctata</i>	119	104	53
<i>Thelenota ananas</i>	127	116	52
Outer reef flats			
<i>Actinopyga mauritiana</i>	134	124	52
<i>Actinopyga echinites</i>	243	227	52
Inner lagoon and reef flats			
<i>Holothuria atra</i>	67	56	54
<i>Holothuria scabra</i>	160	132	55
<i>Holothuria scabra versicolor</i>	149	113	57
<i>Stichopus variegatus</i>	100	114	47

test indicated that the sex-ratios are not significantly different from 1, except for *Holothuria scabra versicolor* ($\chi^2 = 4.94$, $p = 0.05$, $n = 262$).

The gonads consist of one tuft of tubules in the family Holothuridae and two tufts in the family Stichopodidae.

The gonads show very similar morphologies in the seven species of Holothuridae studied. They are more variable amongst Stichopodidae (Conand 1993). In one group, the tufts are composed of elongated tubules similar to those in the Holothuridae. In a second group, short branches of saccules develop from the tubules which are branched in *Thelenota ananas* and *Stichopus chloronotus* but not in *S. variegatus*, as shown in Fig. 2. Spicules are very abundant in the gonad wall of these species.

The main features of the mature gonads (stage IV) are presented in Table 2. Sexual dimorphism is evident at this stage. The fecund ovarian tubules are shorter and wider, the ovaries are heavier than the testes, and the gonad index mean values are higher for females than males. Interspecific differences are also conspicuous at this stage, as shown in Fig. 3 where the mean ovary weight and female gonad index at stage IV are related to the mean body wall weight of each species at the sampling site (data from Conand 1989a). Amongst Holothuridae, the large species such as *Holothuria fuscopunctata* or *H. nobilis* generally have the largest gonads and small species have smallest ones (Table 2). The maximal values show the same relation with size, such as for example the "record gonads" weighing 270 g in an ovary of *H. fuscopunctata* and *H. nobilis*. The same figure was obtained for

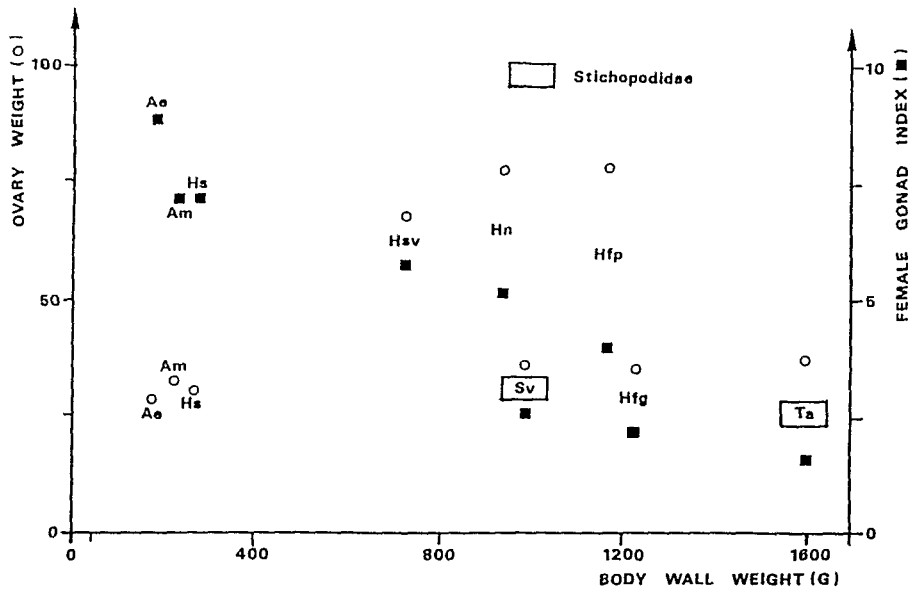


Fig. 3. Mean ovary weight and female gonad index at stage IV, in relation to the mean body wall weight of the species. Hn: *Holothuria nobilis*; Hfg: *H. fuscogilva*; Hfp: *H. fuscopunctata*; Hs: *H. scabra*; Hsv: *H. scabra versicolor*; Ae: *Actinopyga echinites*; Am: *A. mauritiana*; Sv: *Stichopus variegatus*; Ta: *T. ananas*. □: member of Stichopodidae family

Table 2. Characteristics of mature gonads of New Caledonia holothurians. M: males; F: females; n: number of specimens; GW: mean wet gonad weight (standard deviation); oocyte \emptyset : modal diameter of the most advanced mode after formalin fixation; mean gonad index: $(GW \times 100)/WD$ (standard deviation); WD: drained weight (g)

Family Species	Sex	n	GW (g) mean (SD)	Tubules		Gonad index mean (SD)	Oocyte \emptyset (μm)
				Length (mm)	\emptyset (mm)		
Holothuridae							
<i>Holothuria nobilis</i>	M	83	50.6 (36.8)	123	1.1	3.5 (2.1)	
	F	109	77.7 (63.1)	103	2.0	5.3 (3.0)	150
<i>Holothuria fuscogilva</i>	M	27	13.8 (14.0)	88	0.9	0.8 (0.8)	
	F	21	36.0 (30.6)	79	1.6	2.2 (1.7)	170
<i>Holothuria fuscopunctata</i>	M	52	45.2 (29.6)	159	1.1	2.2 (1.1)	
	F	54	78.5 (57.8)	118	1.9	4.0 (2.2)	210
<i>Actinopyga mauritiana</i>	M	61	32.2 (22.8)	153	1.0	7.1 (4.2)	
	F	64	32.9 (22.5)	124	1.5	7.2 (4.2)	170
<i>Actinopyga echinites</i>	M	96	20.9 (12.5)	115	0.8	6.9 (3.6)	
	F	80	28.2 (16.6)	106	1.2	9.0 (4.7)	165
<i>Holothuria scabra</i>	M	74	23.8 (12.6)	82	1.0	5.4 (2.4)	
	F	65	31.2 (21.3)	80	1.3	7.2 (3.8)	190
<i>Holothuria scabra versicolor</i>	M	72	45.9 (27.0)	137	1.3	4.0 (1.7)	
	F	53	69.7 (43.6)	125	1.9	5.8 (2.8)	210
<i>Holothuria atra</i>	M	26	5.5 (5.0)	67	1.6	3.3 (2.6)	
	F	21	7.4 (6.4)	65	2.1	3.3 (1.4)	150
Stichopodidae							
<i>Thelenota ananas</i>	M	42	26.1 (15.9)	165		1.1 (0.5)	
	F	49	37.9 (27.7)	158		1.6 (1.0)	200
<i>Stichopus variegatus</i>	M	20	34.1 (29.0)	278		2.8 (1.9)	
	F	32	36.4 (22.4)	254		2.7 (1.5)	180

males, with smaller gonad weights and gonad indices. In Stichopodidae, the gonads are not as large as in Holothuridae of the same size. The modal diameter of the oocytes of the last mode of the size frequency distribution (Table 2) is between 150 and 210 μm . Tubule resorption in spawned individuals occurred over several months. Apart from small oocytes, the ovary of these individuals

consisted of large residual oocytes, degenerating oocytes and occasional empty follicles.

Reproductive cycles and spawning behaviour

The annual reproductive cycle for each species was analysed from observations over two or more years, at

one or more sites. As the timing and duration were similar over years and sites, the monthly data have been pooled and a single annual cycle is presented. The three sets of monthly observations, respectively, the percentages of stages III, IV, V in males and females, the percentage of individuals that could not be sexed and the mean gonad index are given for each species (Table 3). The

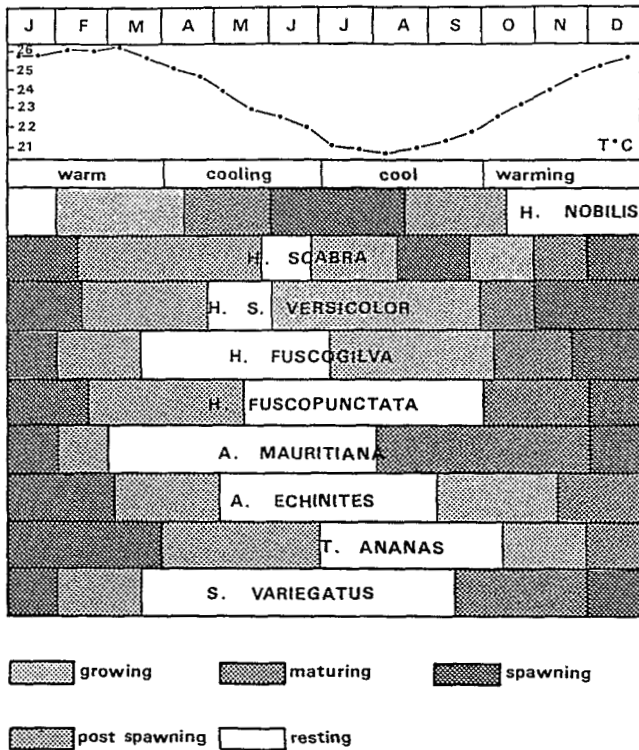


Fig. 4. Reproductive cycles of New Caledonia holothurians in relation to hydrological seasons. H.: *Holothuria*; A.: *Actinopyga*; T.: *Thelenota*; S.: *Stichopus*

reproductive cycles and the hydrological seasons are summarised in Fig. 4. Three main patterns are evident. An annual cycle, with spawning during the warm season, occurred in most species. An annual cycle, with spawning during the cool season, occurred in one species, *Holothuria nobilis*. A semi-annual cycle, with the main spawning during the warm season, occurred in *H. scabra* and perhaps in *H. atra*.

Some characteristics of broadcast spawning in the field are summarised in Table 4. The anterior half of the spawning individual was raised in a vertical position with the tentacular crown curved toward the substratum. The genital papilla posterior to the tentacles was extended. The individual weaved slowly, before and during shedding. The sperm formed a white string more easily distinguished than the translucent eggs. This behaviour is illustrated in Fig. 5 for *Bohadschia argus*, *Holothuria scabra* and *Stichopus variegatus* where a small sperm stream is coming out the genital papilla.

Size at first sexual maturity and fecundity

The percentage of individuals ripening during the reproductive season increases with size, from 0 to nearly 100%. The length at first maturity (LT_{50}), as well as the weights at first maturity, total weight (WT_{50}) and drained weight (WD_{50}) are given for the different species in Table 5. The values are higher for the large species inhabiting the reef slopes and passes. They exceed 50% of the maximum length and 30% of the maximum drained weight in *Holothuria fuscogilva*, *Actinopyga mauritiana* and *H. atra*.

The fecundity values are given in Table 6. Absolute fecundity values are variable within and between species. Within a species, e.g. in *Holothuria fuscopunctata*, the maximal fecundity is 45-fold greater than the minimal

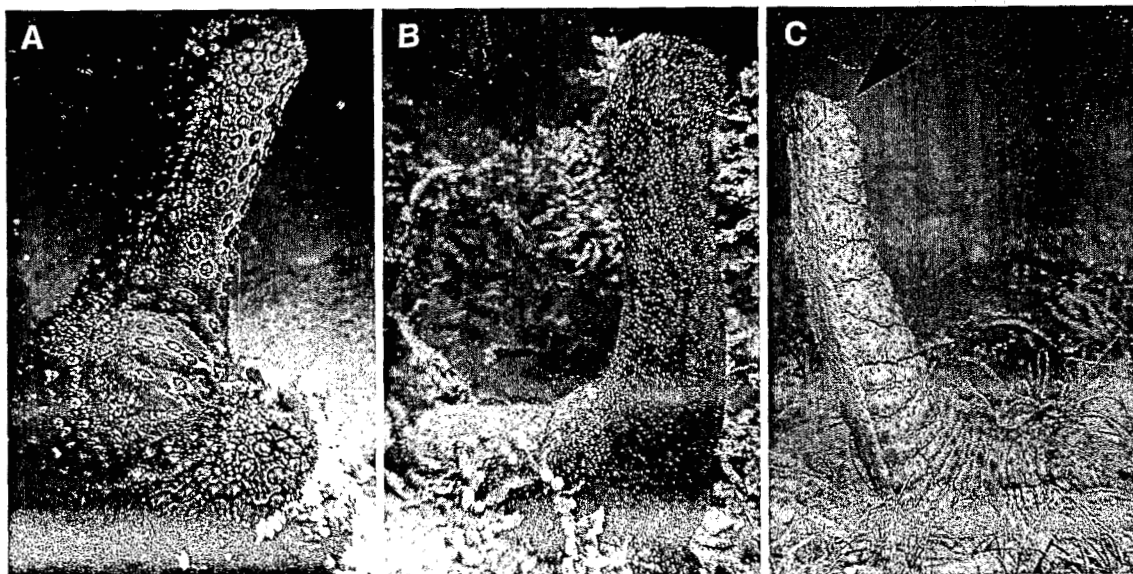


Fig. 5. Spawning behavior in the field (photographs by ORSTOM divers). (A) *Bohadschia argus*; (B) *Holothuria scabra versicolor*, (C) *Stichopus variegatus*

Table 3. Reproductive cycle of New Caledonia holothurians. *n*: number; I: undetermined individuals (%); M: male; F: female; III, IV, V: maturity stages (%); GI: mean gonad index; s: standard deviation

Species	Month												
	J	F	M	A	M	Ju	Jl	A	S	O	N	D	
<i>Holothuria nobilis</i>	<i>n</i> :	35	36	52	41	39	31	63	42	12	55	46	44
	I:	3	8	2	2	2	3	4	4	7	5	2	20
	Sex:	M F	M F	M F	M F	M F	M F	M F	M F	M F	M F	M F	M F
	III:	0 0	13 11	25 25	20 8	4 0	0 0	0 0	0 0	0 0	0 4	0 0	0 3
	IV:	0 6	13 22	50 20	46 72	86 100	100 87	70 76	19 26	50 29	20 27	10 12	6 10
	V:	100 94	73 67	25 45	33 20	9 0	0 13	30 24	81 74	50 71	80 69	90 88	94 87
	GI:	0.71	2.15	1.38	2.63	3.89	5.68	5.17	1.40	1.90	1.90	1.54	1.63
	s:	1.05	2.09	1.85	2.15	2.50	3.84	4.18	1.24	1.10	1.10	1.59	1.55
	<i>Holothuria scabra</i>	<i>n</i> :	17	34	41	40	39	17	16	32	21	21	26
I:		6	2	9	15	23	24	0	3	9	4	7	5
Sex:		M F	M F	M F	M F	M F	M F	M F	M F	M F	M F	M F	M F
III:		0 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0	11 10	7 17	11 16	0 0
IV:		60 83	63 50	8 41	11 42	18 14	0 0	67 50	62 55	33 10	93 83	89 84	80 89
V:		40 17	37 50	92 59	89 58	82 86	100 100	33 50	38 45	56 80	0 0	0 0	20 11
GI:		5.33	3.01	2.75	2.73	2.27	0.95	3.55	4.42	2.30	6.66	7.58	7.69
s:		2.81	2.01	1.33	1.67	1.82	0.51	2.38	3.27	2.03	3.34	5.03	4.60
<i>Holothuria scabra versicolor</i>		<i>n</i> :	-	33	32	34	35	16	-	16	17	31	28
	I:	-	3	0	9	9	0	-	6	6	0	3	0
	Sex:	-	M F	M F	M F	M F	M F	-	M F	M F	M F	M F	M F
	III:	-	0 0	0 0	0 8	0 0	0 0	-	60 40	50 38	0 0	0 0	0 7
	IV:	-	50 47	28 43	11 25	0 6	30 0	-	10 20	50 50	100 100	100 100	88 62
	V:	-	50 53	72 57	89 67	100 94	70 100	-	30 40	0 12	0 0	0 0	12 31
	GI:	-	3.86	1.79	1.33	0.80	1.99	-	1.99	2.72	5.59	5.18	3.72
	s:	-	3.14	1.01	1.24	0.75	0.78	-	1.28	1.64	2.62	2.51	1.90
	<i>Holothuria fuscogilva</i>	<i>n</i> :	18	-	6	17	-	-	27	-	19	-	26
I:		11	-	0	35	-	-	15	-	11	-	8	0
Sex:		M F	-	M F	M F	-	-	M F	-	M F	-	M F	M F
III:		0 0	-	0 0	0 25	-	-	50 46	-	13 0	-	14 20	0 0
IV:		0 27	-	0 0	0 0	-	-	10 0	-	87 78	-	79 80	89 0
V:		100 73	-	100 100	100 75	-	-	40 54	-	0 22	-	7 0	11 100
GI:		0.99	-	0.13	0.04	-	-	0.21	-	0.59	-	1.18	1.21
s:		1.72	-	0.10	0.03	-	-	0.24	-	0.51	-	1.22	1.69
<i>Holothuria fuscopunctata</i>		<i>n</i> :	-	33	28	33	24	-	18	-	17	18	32
	I:	-	3	11	0	4	-	50	-	29	11	3	4
	Sex:	-	M F	M F	M F	M F	-	M F	-	M F	M F	M F	M F
	III:	-	12 7	0 0	0 0	0 11	-	20 25	-	20 0	57 56	25 12	11 0
	VI:	-	53 73	54 75	32 36	7 0	-	0 0	-	0 0	0 0	75 88	89 100
	V:	-	35 20	46 25	68 64	93 89	-	80 75	-	80 100	43 44	0 0	0 0
	GI:	-	1.98	2.47	1.10	0.54	-	0.37	-	0.53	0.97	3.22	2.82
	s:	-	1.79	2.11	0.60	0.45	-	0.29	-	0.40	0.73	2.39	1.43
	<i>Holothuria atra</i>	<i>n</i> :	31	24	27	24	24	-	22	15	21	28	37
I:		32	58	48	84	83	-	82	73	81	61	30	38
Sex:		M F	M F	M F	M F	M F	-	M F	M F	M F	M F	M F	M F
III:		0 0	0 0	0 0	0 0	0 0	-	0 0	0 0	0 0	71 33	42 14	9 40
VI:		33 22	71 67	56 20	0 0	0 0	-	0 0	0 0	0 0	29 0	50 79	18 30
V:		66 78	29 33	44 80	100 100	100 100	-	100 100	100 100	100 120	0 60	8 7	73 30
GI:		1.12	2.23	0.78	0.39	0.64	-	0.99	0.99	0.40	2.25	2.66	2.50
s:		0.76	1.58	0.77	0.26	0.29	-	0.94	0.54	0.31	2.07	1.82	2.43
<i>Actinopyga mauritiana</i>		<i>n</i> :	42	33	26	99	-	53	-	-	26	33	6
	I:	53	45	57	0	-	13	-	-	0	48	0	19
	Sex:	M F	M F	M F	M F	-	M F	-	-	M F	M F	M F	M F
	III:	0 0	0 0	0 0	0 0	-	56 76	-	-	36 42	33 9	0 0	0 3
	IV:	9 0	0 0	0 0	0 0	-	0 0	-	-	64 50	67 91	66 100	100 94
	V:	91 100	100 100	100 100	100 100	-	44 24	-	-	0 8	0 0	33 0	0 3
	GI:	1.37	0.71	0.36	0.19	-	0.21	-	-	0.33	4.16	1.53	8.56
	s:	3.36	0.74	0.34	0.28	-	0.25	-	-	2.23	2.08	1.22	4.60
	<i>Actinopyga echinites</i>	<i>n</i> :	61	70	36	66	39	25	19	38	17	16	59
I:		3	13	11	42	33	60	21	18	6	0	0	12
Sex:		M F	M F	M F	M F	M F	M F	M F	M F	M F	M F	M F	M F
III:		0 0	0 0	0 0	0 0	0 0	0 0	0 0	75 82	84 53	50 100	92 100	3 14
IV:		89 100	10 3	0 6	0 0	0 0	0 0	0 0	0 0	0 0	0 0	97 83	100 100
V:		11 0	90 97	100 94	100 100	100 100	100 100	100 100	25 18	16 47	50 0	0 0	0 0
GI:		6.56	2.93	1.61	1.11	0.54	0.32	0.36	0.67	1.06	1.77	8.19	9.48
s:		4.04	3.18	1.64	1.64	0.63	0.40	0.27	1.02	0.78	1.07	4.55	3.15

Table 3 (continued)

Species	Month																						
	J	F		M		A		M		Ju	Jl	A		S	O	N		D					
<i>Thelenota ananas</i>	n:	31	29		37		28		32		17	16		17	-	23	18		41				
	I:	23	3		8		11		16		12	44		59	17	0		17					
	Sex:	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F				
	III:	17	25	5	0	0	0	0	0	8	7	0	14	0	0	67	83	89	80	25	57	42	47
	IV:	83	75	50	86	19	70	15	67	8	14	12	14	0	0	0	0	0	0	75	43	58	53
	V:	0	0	45	14	81	30	85	33	84	79	88	72	100	100	33	17	11	20	0	0	0	0
	G:	1.39	0.79		0.58		1.03		0.26		0.41	0.12		0.07	0.11		0.02	0.11	0.90	0.95			
s:	1.13	0.51		0.59		0.98		0.34		0.41	0.11		0.02	0.07		0.02	0.72	0.94					
<i>Stichopus variegatus</i>	n:	17	28		27		34		36		15	-		16	10	16	16		17				
	I:	0	25		11		24		39		13	-		25	30	0	6		0				
	Sex:	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F				
	III:	0	12	0	14	0	0	0	11	10	0	0	0	0	0	57	89	50	44	0	0		
	IV:	0	0	14	14	15	18	0	0	0	0	0	0	0	0	0	0	50	56	100	100		
	V:	100	88	86	72	85	82	100	89	90	100	100	100	100	100	50	43	11	0	0	0	0	
	GI:	2.31	1.41		1.15		0.51		0.35		0.30	0.25		0.22	0.49		1.38	3.33					
s:	2.05	1.34		1.08		0.40		0.20		0.21	0.08		0.09	0.32		0.78	2.00						

Table 4. Direct field observations of holothurians spawning in New Caledonia. HT: high tide; MT: medium tide; LT: low tide; NM: new moon; FQ: first quarter; FM: full moon; LQ: last quarter

Species	Observation	Source	Locality	Date/time/environment
<i>Actinopyga miliaris</i>	3 ind. amongst 15 seen	Conand 1989a	Devarenne Reef	8 Mar 1983/16:00 hrs/HT; LQ
<i>Holothuria flavomaculata</i>	2 ind. amongst 2			
<i>Actinopyga miliaris</i>	Several ind.	Conand 1989a	Bailly Islet	3 Dec 1979/15:00 hrs/MT; FQ
<i>Bohadschia similis</i>	Several ind.			
<i>Actinopyga miliaris</i>	Several ind.	Babin (personal communication)	Ué Bay	26 Nov 1979/night/LT; LQ
<i>Bohadschia argus</i>	3 ind.	Menou (personal communication)	Coco Islet	5 Dec 1979/night/MT; NM
<i>Stichopus variegatus</i>		Laboute (personal communication)	Croissant Islet	20 Feb 1980/day/4 d after NM
<i>Holothuria scabra versicolor</i>		Laboute (personal communication)	Croissant Islet	25 Feb 1980/2 d after FQ

Table 5. Parameters at first sexual maturity of New Caledonia holothurians. LT₅₀: length first maturity; WT₅₀: total weight at first maturity; WD₅₀: drained weight at first maturity; LT_M and WD_M: maximum length and maximum drained weight

Habitat Species	LT ₅₀ (mm)	LT/LT _M (%)	WT ₅₀ (g)	WD ₅₀ (g)	WD ₅₀ /WD _M (%)
Slopes and passes					
<i>Holothuria nobilis</i>	260	46	800	580	24
<i>Holothuria fuscogilva</i>	320	56	1 175	900	35
<i>Holothuria fuscopunctata</i>	350	46	1 220	870	27
<i>Thelenota ananas</i>	300	45	1 230	1 150	20
Outer reef flats					
<i>Actinopyga mauritiana</i>	220	55	370	250	31
<i>Actinopyga echinites</i>	120	32	90	75	12
Inner lagoon and reef flats					
<i>Holothuria scabra</i>	160	41	185	140	13
<i>Holothuria scabra versicolor</i>	220	46	490	320	17
<i>Stichopus variegatus</i>	270	47	560	450	22
<i>Holothuria atra</i>	165	51	160	110	32

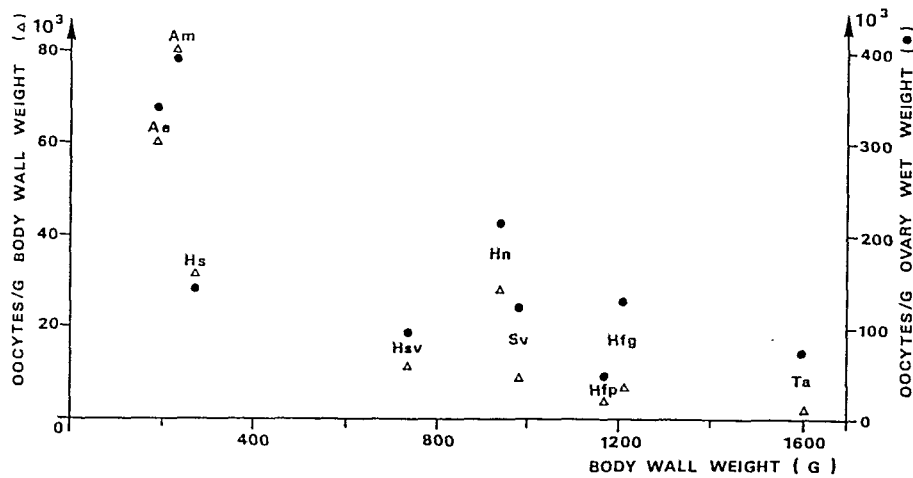


Fig. 6. Relative fecundities, per ovary and body wall weight unit, in relation to the mean body wall weight of the species. Ae: *Actinopyga echinites*; Am: *A. mauritiana*; Hfg: *Holothuria fuscogilva*; Hfp: *H. fuscopunctata*; Hn: *H. nobilis*; Hs: *H. scabra*; Hsv: *H. scabra versicolor*; Sv: *Stichopus variegatus*; Ta: *Thelenota ananas*

Table 6. Absolute and relative fecundities per ovary and per eviscerated weights (g) of New Caledonia holothurians. m: mean value; s: standard deviation

Habitat Species	n	Absolute fecundity (10^{-3} oocytes)		Relative fecundity/ g ovary weight (10^{-3} oocytes)		Relative fecundity/ g eviscerated weight (10^{-3} oocytes)	
Slopes and passes							
<i>Holothuria nobilis</i>	24	Minimum	13 281	m	208	m	28
		Maximum	78 517	s	38	s	14
<i>Holothuria fuscogilva</i>	5	Minimum	6 387	m	128	m	7
		Maximum	14 210	s	22	s	2
<i>Holothuria fuscopunctata</i>	17	Minimum	295	m	44	m	4
		Maximum	13 172	s	15	s	2
<i>Thelenota ananas</i>	5	Minimum	2 239	m	74	m	2
		Maximum	7 861	s	10	s	1
Outer reef flats							
<i>Actinopyga mauritiana</i>	5	Minimum	23 683	m	389	m	80
		Maximum	33 790	s	57	s	13
<i>Actinopyga echinites</i>	25	Minimum	3 831	m	333	m	59
		Maximum	25 044	s	64	s	24
Inner lagoon and reef flats							
<i>Holothuria scabra</i>	5	Minimum	9 207	m	133	m	31
		Maximum	17 313	s	18	s	9
<i>Holothuria scabra versicolor</i>	12	Minimum	2 296	m	93	m	11
		Maximum	18 708	s	23	s	5
<i>Stichopus variegatus</i>	5	Minimum	7 243	m	120	m	9
		Maximum	12 585	s	17	s	2

value. This is the result of sampling individuals of different sizes and of the variability of the mature gonad weight. The interspecific variation ranged from a minimum of 295×10^3 oocytes in *H. fuscopunctata* to a maximum of $33\,790 \times 10^3$ oocytes in *Actinopyga mauritiana*. Relative fecundity values FRO and FRG are correlated with the mean body wall weight of the species (Fig. 6). Fecundity related to ovary weight (FRO) varied interspecifically with oocyte size, the importance of the most advanced mode of oocytes, and the amount of somatic tissues in the gonad. The small saccules of the gonads in the Stichopodidae have more epithelial tissue and the fecundity is low. The species of *Actinopyga* have small

ripe oocytes and high fecundity, while *H. fuscopunctata* has large oocytes and low fecundity. Fecundity related to eviscerated weight (FRG) is also variable between the species.

Discussion

The present study described the reproductive cycles, measured fecundity and reproductive output of nine species from the lagoon of New Caledonia. Since Bakus (1973) review which pointed out the rarity of reproductive stud-

ies of tropical holothurians, a number of publications have concerned Indo-Pacific tropical aspidochirots from the Holothuridae family: *Holothuria leucospilota* by Franklin (1980), *H. atra*, *H. edulis*, *H. impatiens*, *H. scabra* by Harriot (1980, 1985). This species has also been studied by Shelley (1981), Ong Che and Gomez (1985) and Conand (1986). Conand also described the reproductive biology of *H. nobilis*, *H. fuscogilva* (1981, 1986), and of *Actinopyga echinites* (1982, 1986). In the Stichopodidae family *Stichopus chloronotus* has been studied by Franklin (1980), *Thelenota ananas* and *S. variegatus* by Conand (1981, 1993). These studies described the phases of the reproductive cycles.

Gonad anatomy, maturity stages

All the species studied here are dioecious and iteroparous. Differences observed in the morphology of the fecund tubules in the gonads amongst the Stichopodidae has led to the distinction of several groups. The first one comprises some temperate species and is based on descriptions by Mitsukuri (1903) and Levin (1982) for *Stichopus japonicus*, Smiley and Cloney (1985), Cameron and Fankboner (1986) for *S. californicus* and Sewell (1992) for *S. mollis*. In this group, the tubules are elongated and similar to the Holothuridae. The second group, characterised by the presence of fecund saccules is subdivided into species with branched tubules as *Thelenota ananas*, *S. chloronotus* as observed by Franklin (1980), Conand (personal observation) and *T. anax* (personal observation) but not observed by Lamberson (1978). Only one species, *S. variegatus*, has unbranched tubules with saccules (Conand 1993). One implication of the presence of saccules is a probable increase of the peritoneum and connective tissue compartments compared to the gametes. Experimental studies are needed following Smiley's model (1988) on the resorption of spent tubules and the role of the nutrients derived from phagocytosis to determine if this organisation has functional consequences.

Within the nine species, the size frequency distributions of the males and females are similar (Conand 1989a), but ripe females have larger gonads in stage IV which is indicative of the reproductive output and the mean values of the gonad index, indicative of the reproductive index (Lawrence 1987). The gonadal tubules are also shorter and wider in females. As the gonad structure is comparable in both sexes, the difference indicates a smaller reproductive output in males. This dimorphism shown by Holothuridae and Stichopodidae from the New Caledonian lagoon has also been observed in other aspidochirots: *Stichopus japonicus* (Choe 1963), *Holothuria floridana* and *H. mexicana* (Engstrom 1980), *H. atra*, *H. impatiens*, *H. edulis*, *H. scabra* (Harriot 1980), *H. scabra*, *Actinopyga echinites* (Shelley 1981), *Parastichopus californicus* (Cameron and Fankboner 1986), *S. mollis* (Sewell and Bergquist 1990), and *H. forskali* (Tuwo and Conand 1992). This could mean that either females eat more, or use the absorbed material more efficiently, or use it preferentially for the gonads.

Body size is an important parameter for interpreting the variations in reproductive output and index, both interspecifically and intraspecifically. Interspecific differences must be examined separately for males and females on account of the dimorphism. For most of the species (with the exception of *Holothuria fuscogilva* where the sample size was small and the standard error high), the reproductive output increases with the body size. An inverse relationship is shown by the reproductive index, smaller species having higher values, with the exception of *H. atra*. In this species asexual reproduction by fission may complicate the interpretation (Ebert 1978, 1983, Conand and De Ridder 1990). The energetic costs of fission and subsequent regeneration may decrease the sexual reproduction capacity. Although the data published on other species are not directly comparable, as different weights and indices have been used, the same trend appears in the reproductive index of *H. atra*, *H. impatiens* and *H. edulis*, studied by Harriot (1985) and in *A. echinites* and *H. scabra* studied by Shelley (1981).

Intraspecific differences are not easy to determine for several reasons: the high variance observed in gonad weights and gonad indices in most holothurians, the modality of the onset of the first sexual maturity which is poorly known, the size distribution in the holothurian populations often composed of a large proportion of mature adults. Intraspecific differences in reproductive output and indices therefore necessitate more comparative studies using large samples and standardized weight parameters, such as body wall (or eviscerated weight) and gonad weight, both in wet, dry and ash-free dry weight units.

The size of the eggs is an important parameter of the reproductive strategies. Its implications in functional and adaptative aspects has been discussed in detail for echinoids and asteroids by Emler et al. (1987). In the aspidochirote species studied the modal size of the mature oocytes varies only between 150 and 210 μm . This is an indication of a probable planktotrophic development if compared with the planktotrophic echinoids and asteroids. No correlation is found with the size of the species or with the family. The same statement holds with the other data on oocyte diameters for *Holothuria edulis*: 103 μm ; *H. impatiens*: 184 μm ; *H. atra*: 88 μm (Harriot 1985); *H. scabra*: 155 μm ; *A. echinites*: 149 μm . The lower values found by these authors result from the method used: Bouin fixation shrinks eggs. *H. parvula* (formalin fixation) oocytes measure only 93 μm (Emson and Mladenov 1987). This species and *H. atra* are fissiparous and have relatively small eggs.

Reproductive cycles, spawning behaviour

All the species studied in New Caledonia show an annual reproductive cycle. Three main patterns in reproductive seasonality were observed.

(1) Most species spawn during the warm water season (December to February in New Caledonia). This agrees with observations of other tropical species: *Holothuria leucospilota* (Franklin 1980); *H. impatiens* (Harriot 1980);

Actinopyga echinites (Shelley 1981). For the last species the reproductive phases are more precisely defined in New Caledonia (Conand 1982) than in Papua New Guinea. This agrees with Pearse's observations (1968) of more restricted spawning seasons at higher latitudes. Several examples for echinoids are given in Giese and Kanatani (1987). The temperate species *Stichopus japonicus* (Tanaka 1958), *Parastichopus californicus* (Cameron and Fankboner 1986), and *S. mollis* (Sewell and Bergquist 1990, Sewell 1992) also spawn during summer.

(2) *Holothuria scabra* has a biannual cycle in India (Krishnaswamy and Krishnan 1967), Australia (Harriot 1980), Papua New Guinea (Shelley 1981) and in the Philippines (Ong Che and Gomez 1985). In New Caledonia, as in the other localities, the warm season spawning is dominant and the secondary peak is smaller and more variable. This pattern has also been found for *Stichopus chloronotus* (Franklin 1980) and *H. atra* in Australia (Harriot 1980, Conand and De Ridder 1990).

(3) One species, *Holothuria nobilis* shows a cycle marked by a long spawning period during the cool season and the beginning of the warm season.

In New Caledonia none of the species studied spawns continuously, or without seasonality, as does *Holothuria edulis* (Harriot 1985) and many deep-sea species (Tyler et al. 1985). Most species have, nevertheless, a few mature individuals in most samples except during the resting phase. They cause the high variability of the gonad weights and indices.

In holothurians, as in other marine invertebrates, the circannual reproductive cycles probably result from interactions between endogenous rhythms and exogenous environmental timers (Giese and Kanatani 1987). The variety described in these holothurians from New Caledonia argues in favour of the existence of specific innate rhythms. Environmental cues could then allow intraspecific temporal synchronization. For most species, the growing and maturing phases occur during the warming period when the days become longer. This results in spawning during the warm season. The planktotrophic larvae can therefore take advantage of the rich phytoplankton. Thus at the Noumea coastal station (see Fig. 1) the chlorophyll *a* content (Dandonneau personal communication) was relatively stable, between 0.1 and 0.3 mg m⁻³, between July 1986 and February 1987, and more variable with higher concentrations, up to 0.7 mg m⁻³, between March and June. The inverse timing described for *Holothuria nobilis* is more questionable. Does it result from different critical values of the environmental parameters, or is it an adaptation to the competition with other species, particularly with *H. fuscogilva* with which it has often been confused? Similar arguments can be evoked to explain the semiannual cycle of *H. scabra* and its difference with the variety (or sibling species?) *H. scabra versicolor*. Some authors (Krishnaswamy and Krishnan 1967, Ong Che and Gomez 1985) considered salinity as the environmental cue for *H. scabra*. No comparable semiannual changes in salinity occur in New Caledonia and Australia (Harriot 1982).

Observations of spawning in the field are few for the Indo-Pacific aspidochirotids (Giese and Kanatani 1987).

Pearse et al. (1988) observed simultaneous spawning of six species of echinoderms, and McEuen (1988) presented a review of the published observations for all holothurian orders. The observations made in New Caledonia confirm the spawning behavior of aspidochirotids first described from *Bohadschia marmorata* in aquarium by Mortensen (1937). The raised genital papilla probably helps dissemination of eggs and sperm. The observations presented here are the first report of field spawning for *Actinopyga miliaris*, *Bohadschia similis*, *B. argus*, *Holothuria flavomaculata*, *H. scabra versicolor*. On several instances, *H. nobilis* collected for monthly sampling spawned in the tanks on the way to the laboratory. Three factors could be involved in the tanks: the increase in water temperature, crowding and agitation. Other observations from the Great Barrier Reef can also be added. Silver (personal communication) observed *B. graeffei* spawning at Lizard Island during an afternoon low tide in January, and Franklin (1980) observed a loose correlation with full and new moon for *H. leucospilota* spawning simultaneously in separate aquaria in December 1977 and January 1978. Simultaneous spawning has therefore been observed for conspecifics of the Holothuridae. This synchronization might be a response to a pheromone. No "pseudocopulation" as mentioned by McEuen (1988) has been observed for New Caledonia holothurians. Environmental conditions during the spawning events could help determine the triggering stimulus: the observations were made primarily during the afternoon and the night, so light changes could be evoked. No clear relation appears with the tidal or the lunar cycles.

First sexual maturity and fecundity

In these populations of iteroparous species, first sexual maturity is attained progressively by the individuals between a size where they are all immature and a size where all are maturing. Size at first maturity is related to the mean size of the species; it is attained earlier in the small species *Actinopyga echinites*, *A. mauritiana* and *Holothuria scabra*. In other studies only approximative mean size for maturity has been given. Yet this parameter is important for understanding the change in allocation of energy from somatic growth to reproduction. The study of their fecundity has shown a few characteristics of these species. Gross differences appear between families. Stichopidae are less fecund, a fact which can be related to their gonad anatomy. Absolute fecundities are rather variable amongst Holothuridae. Interspecies comparisons of relative fecundity show that the small species are more fecund. Within a species, fecundity increases with body size.

Life history strategies

The aspidochirototes are usually considered to share the same strategy. As a whole, they display the same deposit-feeding and locomotion habits, iteroparity and high longevity, as pointed out by Lawrence (1990). They also

Table 7. Demographic features of some New Caledonia holothurian populations arranged by increasing mean size of species. *: low value; **: medium value; ***: high value

Habitat Species	Length (or weight)	First maturity	Relative fecundity	Oocyte diameter	Population density	
					Numbers	Weights
Outer reefs flats and passes						
<i>Stichopus chloronotus</i>	*	*		*	**	**
<i>Actinopyga echinites</i>	*	*	***	*	***	***
<i>Actinopyga mauritiana</i>	*	**	***	*	***	***
Inner lagoon and reef flats						
<i>Holothuria scabra</i>	**	*	**	**	***	***
<i>Holothuria scabra versicolor</i>	**	*	**	***	**	**
<i>Stichopus variegatus</i>	**	**	*	**	**	**
Slopes and passes						
<i>Holothuria fuscopunctata</i>	***	***	*	***	*	**
<i>Holothuria nobilis</i>	***	**	**	*	*	*
<i>Holothuria fuscogilva</i>	***	***	*	**	*	*
<i>Thelenota ananas</i>	***	**	*	***	*	**

show relatively large size, stable densities and various defenses against predation (toxicity, cuvierian tubules, evisceration), which correspond to *K*-strategies in the *r*-*K*-selection theory. They yet have high fecundities and small eggs, but probably low and sporadic recruitment. The demographic characteristics of the different species studied in New Caledonia are presented synthetically in Table 7, arranged by increasing mean size of the species. Interspecific comparisons clearly show a gradient related to the mean size of the species. Smaller species, such as *Actinopyga echinites* and *A. mauritiana* are situated toward the *r*, whereas larger species, such as *Holothuria nobilis* and *Thelenota ananas* are toward the *K* of a *r*-*K*-continuum. The former live in outer reef flats which are high energy habitats with higher productivity and shorter duration than lagoon floors or deeper coral slopes. Growth and mortality values for *T. ananas* and *Stichopus chloronotus* (Conand 1989b) show that the former has a slower growth and higher longevity compared to the latter.

This comparative approach, at the population level, has shown that there is a gradient in the strategies amongst coral-reef aspidochirotes. A better basic understanding of their acquisition of energy and growth, as well as of the productivity of the various habitats is yet required for a more complete interpretation.

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Literature cited

Bagenal, T. B. (1973). Fish fecundity and its relation with stock and recruitment. Rapp. P.-v Réun. Cons. int. Explor. Mer 164: 186–198

- Bakus, G. J. (1973). The biology and ecology of tropical holothurians. In: Jones, I. O. A., Endean, R. (eds.) Biology and geology of coral reefs, Vol. II. Academic Press, New York, p. 325–367
- Birkeland, C. (1989). The influence of echinoderms on oral-reef communities. In: Jangoux, M., Lawrence, J. M. (eds.) Echinoderm studies, 3. Balkema, Rotterdam, p. 1–79
- Cameron, J. L., Fankboner, P. V. (1986). Reproduction biology of the commercial sea cucumber *Parastichopus californicus* (Stimpson) (Echinodermata, Holothuroidea). I – Reproductive periodicity and spawning behavior. Can. J. Zool. 64: 168–175
- Choe, S. (1963). Biology of the Japanese Common Sea Cucumber *Stichopus japonicus*, Selenka. Pusan National University, Pusan (in Japanese)
- Conand, C. (1981). Sexual cycle of three commercially important holothurian species (Echinodermata) from the lagoon of New Caledonia. Bull. mar. Sci. 31: 523–544
- Conand, C. (1982). Reproductive cycle and biometric relations in a population of *Actinopyga echinites* (Echinodermata: Holothuroidea) from the lagoon of New Caledonia, Western Tropical Pacific. In: Lawrence, J. M. (ed.) Echinoderms: proceeding of the international conference Tampa Bay. Balkema, Rotterdam, p. 437–442
- Conand, C. (1986). Les ressources halieutiques des pays insulaires du Pacifique. Deuxième partie: les Holothuries. F.A.O. Doc. Tech. Pêches, 272.2, F.A.O., Roma
- Conand, C. (1989a). Les holothuries aspidochirotes du lagon de Nouvelle-Calédonie: biologie, écologie et exploitation. Etudes et thèses, ORSTOM, Paris
- Conand, C. (1989b). Comparison between estimations of growth and mortality of two Stichopodid holothurians: *Thelenota ananas* and *Stichopus chloronotus* (Echinodermata: Holothuroidea). In: Proc. 6th int. coral Reef Symp. (1989) 2: 661–665 [Choat, J. H. et al. (eds.) Sixth International Coral Reef Symposium Executive Committee, Townsville]
- Conand, C. (1993). Ecology and reproductive biology of *Stichopus variegatus* and Indo-Pacific coral reef sea cucumber (Echinodermata: Holothuroidea). Bull. mar. Sci. 52 (in press)
- Conand, C., Chardy, P. (1985). Les holothuries aspidochirotes du lagon de Nouvelle-Calédonie sontelles de bons indicateurs des structures récifales? In: Proc. 5th int. coral Reef Congr. 2: 291–296 [Gabrié, C. et al. (eds.) Antenne Museum-EPHE, Moorea, French Polynesia]
- Conand, C., De Ridder, C. (1990). Reproduction asexuée par scission chez *Holothuria atra* (Holothuroidea) dans des populations de platiers récifaux. In: De Ridder, C., Dubois, P., Lahaye, M. C., Jangoux, M. (eds.) Echinoderm research. Balkema, Rotterdam, p. 71–76

- Ebert, T. A. (1978). Growth and size of the tropical sea cucumber *Holothuria (Halodeima) atra* Jaeger at Enewetak Atoll, Marshall Islands. *Pacif. Sci.* 32: 183–191
- Ebert, T. A. (1983). Recruitment in echinoderms. *Echinoderm. Stud.* 1: 169–203
- Emler, R., McEdward, L., Strathmann, R. (1987). Echinoderm larval biology viewed from the egg. In: Jangoux, M., Lawrence, J. M. (eds.) *Echinoderm studies*, 2. Balkema, Rotterdam, p. 55–136
- Emson, R. H., Mladenov, P. V. (1987). Studies of the fissiparous holothurian *Holothuria parvula* (Selenka) (Echinodermata: Holothuroidea). *J. exp. mar. Biol. Ecol.* 111: 195–211
- Engstrom, N. A. (1980). Development, natural history and interstitial habits of the apodous Holothurian *Chiridota rotifera* (Pourtales, 1851) (Echinodermata: Holothuroidea). *Brenesia* 17: 85–96
- Franklin, S. E. (1980). The reproductive biology and some aspects of the population ecology of the holothurians *Holothuria leucospilota* (Brandt) and *Stichopus chloronotus* (Brandt). Ph. D. Thesis, Univ. of Sydney, Sydney
- Giese, A. C., Kanatani, H. (1987). Maturation and spawning. In: Giese, A. C., Pearse, J. S. (eds.) *Reproduction of marine invertebrates*, 9. Academic Press, New York, p. 251–329
- Guille, A., Laboute, P., Menou, J. L. (1986). Guide des étoiles de mer, oursins et autres échinodermes du lagon de Nouvelle-Calédonie. ORSTOM, Coll. Faune tropicale, Paris
- Harriot, V. J. (1980). The ecology of Holothurian fauna of Heron Reef and Moreton Bay. M.S. Thesis, Univ. of Queensland, Townsville
- Harriot, V. J. (1982). Sexual and asexual reproduction of *Holothuria atra* Jaeger at Heron Island Reef, Great Barrier Reef. *Aust. Mus. Sydney Mem.* 16: 53–66
- Harriot, V. J. (1985). Reproductive biology of three congeneric sea cucumber species *Holothuria atra*, *H. impatiens*, and *H. edulis*, at Heron Reef, Great Barrier Reef. *Aust. J. mar. Freshwat. Res.* 36: 51–57
- Krishnaswamy, S., Krishnan, S. (1967). A report on the reproductive cycle of the holothurian *Holothuria scabra* Jaeger. *Curr. Sci.* 36: 155–156
- Lamberson, J. O. (1978). Notes on the morphology, ecology and distribution of *Thelenota anax* H.L. Clark (Holothuroidea, Stichopodidae). *Micronesica* 14: 115–122
- Lawrence, J. M. (1987). A functional biology of echinoderms. Croom Held, London
- Lawrence, J. M. (1990). The effect of stress and disturbance on Echinoderms. *Zool. Sci.* 7: 17–28
- Levin, V. S. (1982). Japanese sea-cucumber. U.S.S.R. Academy of Sciences, Vladivostok (in Russian)
- McEuen, F. S. (1988). Spawning behaviors of northeast Pacific sea cucumbers (Holothuroidea: Echinodermata). *Mar. Biol.* 98: 565–585
- Mitsukuri, K. (1903). Notes on the habits and life history of *Stichopus japonicus*. *Annotnes. zool. jap.* 5: 1–22
- Mortensen, T. (1937). Contributions to the study of the development and larval forms of Echinoderms. III, K. danske. Vidensk. Selsk. *Skr.* 9 7: 1–65
- Ong Che, R. G., Gomez, E. D. (1985). Reproductive periodicity of *Holothuria scabra* Jaeger at Calatagan, Batangas, Philippines. *Asian mar. Biol.* 2: 21–29
- Pearse, J. S. (1968). Patterns of reproductive periodicities in four species of indo-pacific echinoderms. *Proc. Indian Acad. Sci.* 67: 247–279
- Pearse, J. S., McClary, D. J., Sewell, M. A., Austin, W. C., Perez-Ruzafa, A., Byrne, M. (1988). Simultaneous spawning of six species of Echinoderms in Barkley Sound British Columbia. *Invert. Reprod. Dev.* 14: 279–288
- Sewell, M. (1992). Reproduction of the temperate aspidochirote *Stichopus mollis* (Echinodermata: Holothuroidea) in New Zealand. *Ophelia* 55: 103–121
- Sewell, M., Bergquist, P. (1990). Variability in the reproductive cycle of *Stichopus mollis* (Echinodermata: Holothuroidea). *Invert. Reprod. Devel.* 17(1): 1–7
- Shelley, C. (1981). Aspects of the distribution, reproduction, growth and fishery potential of holothurians (Bêche-de-mer) in the Papuan coastal lagoon. M.S. Thesis, Univ. of Papua New Guinea, Port Moresby
- Smiley, S. (1988). The dynamics of oogenesis and the annual ovarian cycle of *Stichopus californicus* (Echinodermata: Holothuroidea). *Biol. Bull. mar. biol. Lab., Woods Hole* 175: 79–93
- Smiley, S., Cloney, R. A. (1985). Ovulation and the fine structure of *Stichopus californicus* (Echinodermata: Holothuroidea) fecund ovarian tubules. *Biol. Bull. mar. biol. Lab., Woods Hole* 169: 342–363
- Tanaka, Y. (1958). Seasonal changes occurring in the gonad of *Stichopus japonicus*. *Bull. Fac. Fish. Hokkaido Univ.* 9: 29–36
- Tuwo, A., Conand, C. (1992). Reproductive biology of the holothurian *Holothuria forskali* (Echinodermata). *J. mar. biol. Ass. U.K.* 72: 745–758
- Tyler, P. A., Muirhead, A., Gage, J. D., Billet, D. S. M. (1985). Reproductive biology of the deep-sea holothurians *Laetmogone violacea* and *Benthogone rosea*, (Elasipoda: Holothuroidea). *Mar. Ecol. Prog. Ser.* 23: 269–277

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