BIOLOGY AND INFESTATION RATE OF *CORALLONOXIA LONGICAUDA*, AN ENDOPARASITIC COPEPOD OF THE WEST INDIAN REEF CORAL *MEANDRINA MEANDRITES*

by

MAUREEN E. BUTTER

Institute of Taxonomic Zoology, University of Amsterdam, The Netherlands

&

Caribbean Marine Biological Institute (Carmabi), Curaçao, Netherlands Antilles

ABSTRACT

During 1½ year the biology of *Corallonoxia longicauda*, a copepod endoparasitic in the stony coral *Meandrina meandrites* was studied in Curaçao, Netherlands Antilles.

The infestation rate of the corals as well as the numbers of parasites present were investigated at several depths and in several stations. The parasites proved to be distributed in a spatial pattern inside the colony. This pattern appeared to be correlated with current and exposure.

It is postulated that the numerical distribution of the copepods in the corals, which differs markedly from a normal distribution, depends on the way of proliferation and settling of the parasites. This offers also an explanation for the remarkable spatial pattern inside the colony.

The results of the comparison of the biomasses of host and parasite indicate that the parasite must be rather harmless to its host, and that no significant influence of its metabolism on the skeleton formation of the coral is to be expected.

INTRODUCTION

Stock (1975) recorded the first endoparasitic copepods in West Indian stony corals. These copepods, ten new species, were classified with two new genera, *Corallovexia* and *Corallonoxia* of the new family Corallovexiidae.

In Curaçao three species are particularly abundant, viz. *Corallovexia brevibrachium* Stock, 1975 in *Diploria labyrinthiformis* (Linnaeus, 1758), *C. longibrachium* Stock, 1975 in *Manicina areolata* (Linnaeus, 1758) and *Corallonoxia longicauda* Stock, 1975 in *Meandrina meandrites* (Linnaeus, 1758). The latter species was sometimes met with in such extraordinary large quantities that it seemed not improbable that these parasites exercise an important influence on the metabolism of their host. It was this assumption that made me choose *Meandrina meandrites* with its copepod parasites as an object of investigation during my stay at the Caribbean Marine Biological Institute (Carmabi), Curaçao, from December 1, 1975 till June 1, 1977.

This investigation was meant to elucidate the relation between host and parasite (harmfulness for the reef, propagation and distribution, rôle in the skeleton formation of the coral, bathymetric and possible other environmental factors). In this context transplantation experiments were carried out, during which live corals were moved from 30 m depth to 10 m and vice versa. Furthermore, samples were taken from locations where the orientation of the reef slope towards the current differs from the principal station, the latter being more or less representative of the general situation at the S.W. coast of Curaçao.

It is a well-known fact that some coral species, among which also *Meandrina*, expell spontaneously (that is without apparent reason) their zooxanthelles. The possibility that parasites form a major cause for this was considered; in that case "bleached" corals should contain parasites more frequently and in larger quantities than specimens capable of maintaining their zooxanthelles. This assumption was also tested.

CHARACTERISTICS OF THE RESEARCH AREA

Curaçao belongs to the Dutch Leeward Islands. Because of the constant trade winds the current is

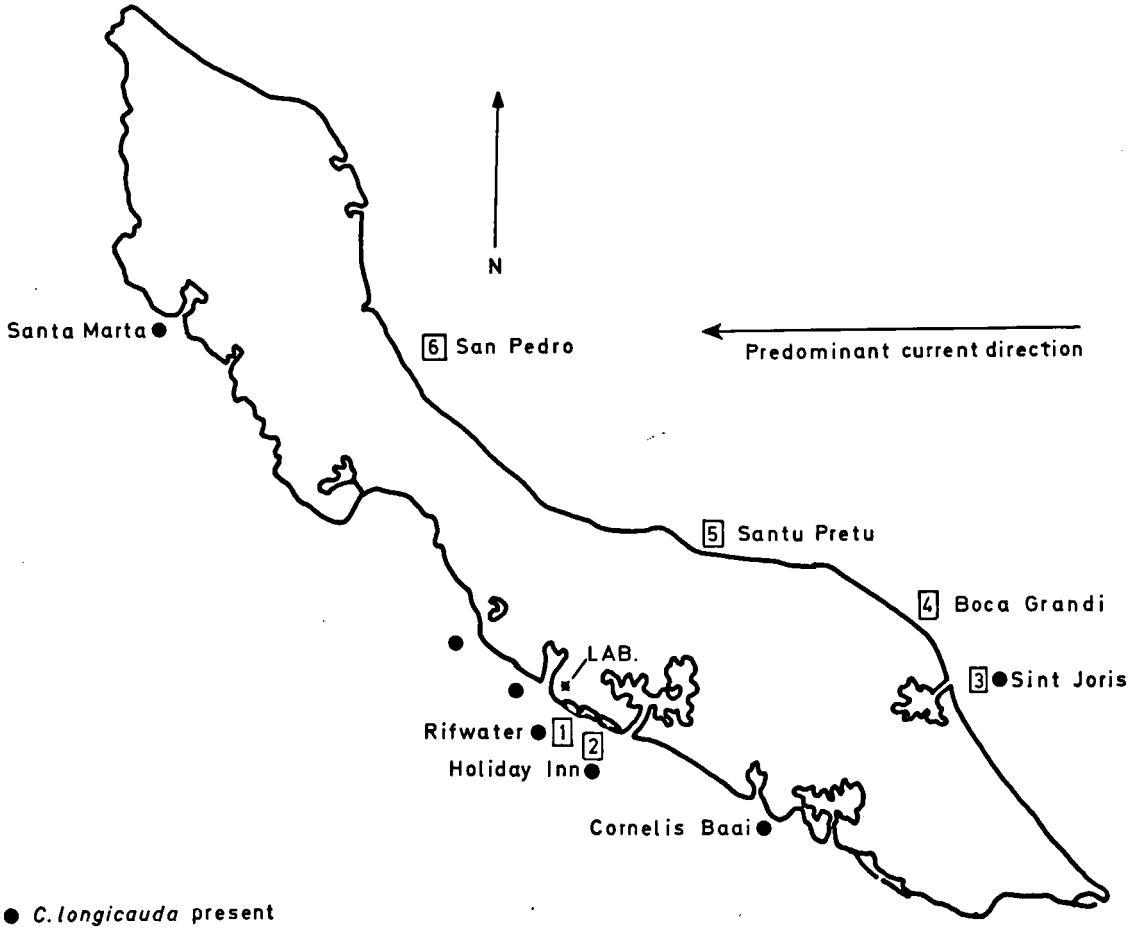

Fig. 1. Location of the sampling stations 1 to 6; occurrence of *Corallonoxia longicauda* in Curaçao (scale 1 : 960000).

from East to West for most of the time (fig. 1). The reefs at the leeward S.W. coast usually show in cross section the profile as drawn for station 1 (fig. 2A). Station 1, situated in front of Rifwater, East of Piscadera, is by far our most important sampling point. For comparison, samples have been taken from station 2, in front of the Holiday Inn Hotel, and the stations 3 to 6 at the N.E. coast of Curaçao (fig. 1).

In samples from station 1 we determined: (1) the rate of infestation at various depths, (2) the biomass of host and parasites, (3) the rate of infestation of young colonies, (4) the rate of infestation of "bleached" *Meandrina* and (5) the spatial distribution of the parasites inside the colonies. Also the transplantation experiment was carried out here.

Station 1 has the following characteristics:

— constant current from Southeast to Northwest;

— compared to other locations at the S.W. coast the water is a bit murky because of the effluent of the nearby situated freshwater distilling plant and the outflow of muddy water from Rifwater, a salty lagoon;
Meandrina meandrites is abundantly present at all depths where I was sampling (3-33 m), but most abundant between 3 and 5 m.

— the general physiognomy of station 1 is shown in table I.

Station 2, in front of Holiday Inn, has a double reef parallel to the shore, a cross section of which is shown in fig. 2B. Samples were taken from the inner slope, which lies faced to the shore and thus

TABLE I

Percentages of coverage at station 1.

	4½ m (%)	12 m (%)	22 m (%)	30 m (%)
Meandrina meandrites	19.9	6.4	3.8	3.9
Agaricia sp. [1]	2.2	3.2	4.8	5.5
Montastrea sp.	3.0	15.1	9.6	17.7
Rock, sand, algae	57.0	67.4	72.1	69.6
Other	17.7 [2]	7.8	9.6	3.3

[1] Mostly *A. agaricites* (Linnaeus, 1758) in shallow waters and almost exclusively *A. lamarcki* Milne Edwards & Haime, 1851, below 20 m.

[2] An important part hereof (6.6%) is constituted of *Madracis mirabilis* (Duchassaing & Michelotti, 1861), at the other depths this species is entirely absent.

reversed to the current and exposition as compared to the situation in station 1.

Further characteristics of station 2 are:

— the current is from Southeast to Northwest, but often quite a bit stronger than in station 1;

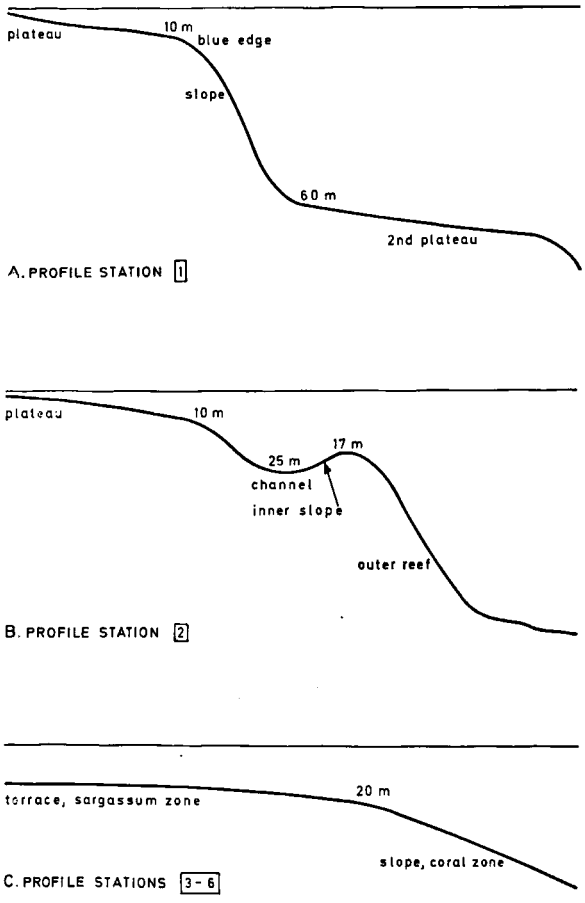

Fig. 2. Profiles of the sampling stations in cross section.

— the assemblage of corals on the inner slope does not differ from that on the outer slope at station 2, or at station 1.

Stations 3 to 6 are situated at the N.E. coast (fig. 1). They are all year round subjected to the strong trade wind (average velocity 7.2 m/sec). So violent is the water movement that diving is most of the time impossible and always dangerous. The reef differs in several respects from that on the S.W. coast (cf. Bak, 1975). Near the shore there is a vehement water movement, the terrace slopes down very gradually and for a distance of about 200 m from the shore it is densely covered with *Sargassum* and other algae, with now and then large flat discs of sponges or fire coral (*Millepora*). Beyond this 200 m, at a depth of about 20 m, the coral reef begins. Here the corals have a different shape than at the S.W. coast, they are larger and flatter. Like on the S.W. coast, *Montastrea* is the dominant species, *Meandrina* on the other hand is rather scarce. The cross section profile of the stations 3 to 6 is drawn in fig. 2C.

METHODS

Collecting. — Collecting was done with the aid of SCUBA gear. Corals of about the same size were jerked loose from the substratum with a divers' knife and the orientation with respect to the reef slope was marked with small cuts in the edge of the colony. Next the coral was put into a numbered plastic bag, and number and depth were noted down with pencil on a piece of formica. The corals, still in their plastic bags, were transferred into a bucket of seawater and in this manner transported to the laboratory for further treatment.

Sawing. — With a diamond-saw the colony was sawed into cubes (approximately 4 × 4 cm colony surface), which could be examined for parasites or tissue weight.

Isolation of the parasites. — Essentially the method of Stock (1975) was followed, a little simplified.

(a) Using decomposed corals:

The piece of coral is incubated in seawater or tapwater. After 2 or 3 days it is squirted off with a water pick (method: Johannes & Wiebe, 1970),

after which the water, tissue and parasite mixture is filtered through a fine mesh cloth (mesh size: 0.2 mm). In this way the major part of the coral tissue, which has become more or less liquid, passes the cloth, but not the chitinous parasites.

Disadvantage: if, by chance, eggs are present, they are lost with this method and remain unnoticed. Nor is it possible to determine the biomass of the parasites thus isolated.

(b) Using fresh corals:

Without previous incubation the living coral is squirted off, the water pick being filled with seawater. Filtering renders living parasites surrounded by pieces of coral tissue. Sometimes ovigerous females are present, sometimes also single eggs or clusters of eggs.

Disadvantage: the coral can not be cleaned thoroughly. Besides, the counting of the parasites is a laborious and lengthy job, because they are hardly distinguishable between the pieces of coral tissue.

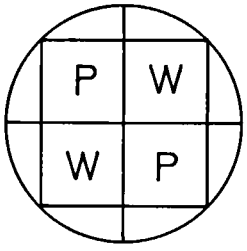

Fig. 3. Sawing scheme of a coral for biomass determination. P, cubes of which parasites are counted; W, cubes of which ash-free dry weight is determined.

Biomass determination. — A fresh coral is sawn into pieces as shown in fig. 3. From the cubes marked P the parasites are counted, from the cubes marked W ash-free tissue weight is determined. For this purpose, immediately after sawing the cube in question is put into a plastic bag with a little bit of seawater. This has to be frozen quickly. After subsequent thawing it is possible to remove all tissue with the water pick. The liquid tissue mixture resulting is centrifuged for 15 minutes at 500 rpm (filtering is impossible because of the slimy consistence of the liquid). The supernatant is filtered through a previously dried and weighed filter with known ash rest. This together with the deposit from the centrifuge tube is put into a porcelain cup, subsequently dried, weighed, ashed and weighed again, after which it is possible to calculate the ash-free dry weight.

Freshly isolated parasites too can be dried, weighed and ashed. I did so for males and females separately and used the results to convert numbers of parasites into units of ash-free dry weight, for comparison with the dry weight of the colony in which they were found.

Transplantations. — Corals from 10 m depth were collected and marked the usual way and transported to 30 m, where they were cemented to plastic grills with Marine Tex (method: Bak, 1973). Care was being taken to keep the corals in the same orientation towards the slope as in their original site at 10 m. The grills were well anchored to the substratum with nylon lines. The same procedure was followed with corals from 30 m when transferring them to 10 m. After six months the transplants were examined for parasites.

Superficies determination. — Both numbers of parasites and tissue weights found were related to the projected surface, that is the surface formed by connecting the farthest protruding edges of the rows of septae of the living part of the colony. This can be measured by covering the colony as accurately as possible with aluminium foil, which is weighed afterwards. For small pieces of coral with a reasonably flat surface I applied the following system: a piece of mosquito net, by means of coloured thread provided with a lattice denoting 1 cm^2, 0.5 cm^2 and 0.1 cm^2 is placed over the surface to be measured, next the compartments are counted. This method is more accurate and much faster than the aluminium foil method, provided that the pieces are not too large.

RESULTS AND DISCUSSION

1. *Occurrence of the parasite on the Curaçao reefs*

Table II gives the numbers of *Corallonoxia longicauda* found during the present study in the stations 1 to 6. Fig. 1 shows all the localities where *C. longicauda* ever has been found. Both Stock's results (1975) and my own findings indicate that *C. longicauda* is very common on the entire S.W. coast. Apparently it is much rarer on the N.E.

TABLE II

Occurrence of *Corallonoxia longicauda* at the different stations. The figures in the last column are the result of computing the number of parasites per 100 cm² coral for each separate colony and averaging these for the number (*N*) of colonies examined.

station	depth (m)	*N* coral colonies examined	% infested	average parasite density
1. Rifwater	3-5	9	100	27.9
	10-12	27	74.1	190.0
	15-22	18	55.6	16.6
	27-33	19	63.2	10.5
2. Holiday Inn	15-22	11	54.5	46.3
3. Sint Joris	15-22	4	75	13.5
4. Boca Grandi	15-22	2	0	0
5. Santu Pretu	15-22	2	0	0
6. San Pedro	15-22	6	0	0

coast, with the exception of Sint Joris that lies closest to the assumed large population on the S.W. coast.

From Boca Grandi and Santu Pretu only two corals were collected, it is true, but this is due to the great scarcity of *Meandrina* in these locations: in station 1 at least seven or eight colonies could have been collected during a dive of comparable length.

At Sint Joris the reef characteristics do not differ from the rest of the N.E. coast, including the scarcity of *Meandrina*, so the parasites occurring there most probably originate from the S.W. coast. This may indicate that the larvae of this parasite have either a very short pelagic stage or none at all.

2. *Observations in vivo on the parasite*

By squirting off a living coral with seawater it was possible to isolate living parasites. In seawater they could sometimes be kept alive for a couple of hours, but usually they live shorter.

2.1 Appearance

Parasites obtained this way differ markedly in appearance from parasites out of corals that have been left macerating for a while. They are more swollen and in males the articulation between urosome and metasome is less clearly visible (fig. 4A). Juvenile females seem devoid of limbs. In juveniles of the size in which the male urosome has not yet grown out it is not always possible to see the difference between the sexes.

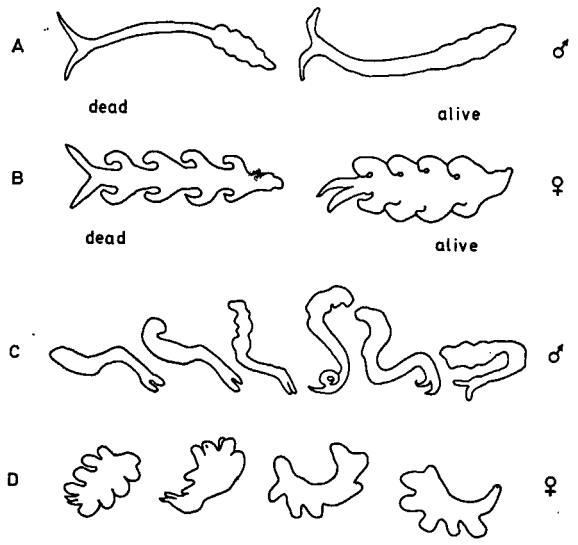

Fig. 4. *Corallonoxia longicauda*. A, Difference in aspect of males, dead and alive (5 ×); B, difference in aspect of females, dead and alive (5 ×); C, a sequence of positions adopted by a male, in a petri dish (2 ×); D, a sequence of positions adopted by a female, in a petri dish (2 ×).

2.2 Movements

Under the bright light of a microscope lamp the parasites make several sorts of movements. Adult males are the most active and mobile, small juveniles (<1.5 mm) do not move. The males are capable of contracting and expanding the metasome and of twisting the urosome. They move the cephalic appendages as well as the caudal rami, the latter can be curved (fig. 4C). The principal movements are: bending of the cephalosome, metasome and urosome with respect to each other and in various directions. Usually the caudal rami are kept fixed on the spot (on the bottom of the petri dish), from which point a contraction wave passes through the body, with the strongest emphasis on the articulation between urosome and metasome.

The females can curve their body in the ventrocaudal plane. Usually they only move their lateral trunk prolongations with respect to each other and to the body (fig. 4D). Females seem to be far less mobile than males, possibly they are more sensitive to the change of environment and die sooner. However, neither males nor females managed to move (in a dish) a distance worth mentioning, despite the sometimes quite violent movements. Still they might be capable of moving through the coral tissue inside the colony.

2.3 Zooxanthelles

Some parasites had zooxanthelles in their skin and in the layer below the skin as well. These correspond in size and shape to the host's zooxanthelles. Some of them looked shrunken and deformed. This is a strong indication that the parasites feed upon the coral's tissue. The zooxanthelles, being quite indigestible, are excreted through the skin.

2.4 Eggs

Some coral colonies contained ovigerous females (only found in fresh material). Part of a colony full of ovigerous females was left in a tray of fresh water and squirted off the next day. Although many females were present, no trace of eggs could be observed anymore.

There is a difference in appearance between ovigerous and non-ovigerous females. The latter are definitely slimmer and the lateral body appendages are less curved. Whenever in a colony ovigerous females were present, all other adult females carried eggs too, or at least had the same appearance as the ovigerous ones.

The eggs measure 0.4-0.7 mm in diameter, they are rich in yolk. They are carried in two packages on the abdomen, about 20-40 eggs per package, in multiserial arrangement (fig. 5).

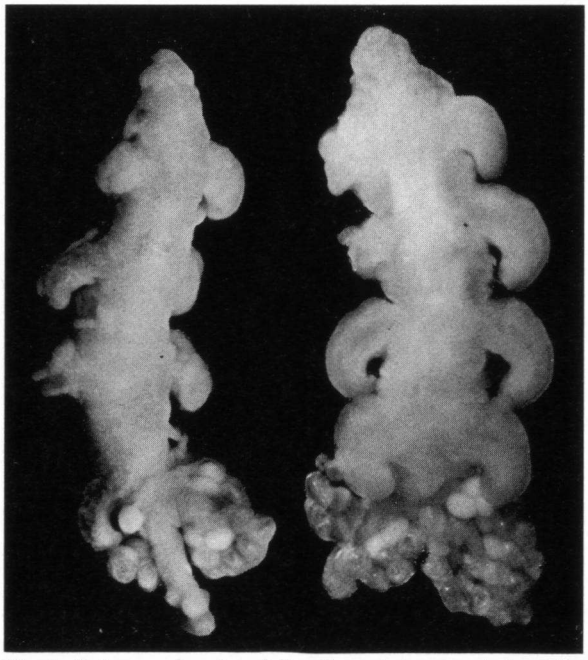

Fig. 5. Ovigerous females of *Corallonoxia longicauda* (12 ×) Packages of eggs are attached to the ventral side.

In coral colonies with ovigerous females sometimes loose eggs were found, similar in size and general appearance to the eggs of *Corallonoxia.* These eggs were surprisingly mobile, rotating constantly, also in clusters of 2-5 eggs. The loose eggs were provided with a ciliated spiral ridge, whereas the eggs in the packages did not have this. It is not sure, of course, that the loose eggs are the parasite's, but they may represent some later stage. Attempts to let the eggs hatch in the laboratory were not successful.

3. *Population dynamics*

3.1 Infestation rate in relation to depth and colony size

Table III gives the numbers of parasites, the superficies of the coral colony and the rate of infestation (as expressed by the number of parasites per 100 cm² coral for any given colony), at four different depths at station 1.

3.1.1 Relation between colony size and infestation rate. — The figures in table III do not indicate a correlation between colony size and the number of parasites per colony: at 3-5 m depth the correlation coefficient is 0.57, at 10-12 m 0.07, at 15-22 m -0.28 and at 27-33 m 0.11. There are two reasons to expect such a correlation. The older the coral, the more parasites it will contain, because it has been exposed to possible infestation for a longer period. The larger the colony, the more chance for a free-swimming larva to "hit" it and settle in this particular colony. Apparently the differences in size within the range examined (about 100-300 cm²) are not large enough to show the effect of either mechanism.

3.1.2 Relation between infestation rate and depth. — Evidently the average parasite density per colony (defined as the sum of the last column of table III divided by the number of observations, Σ/N) has a maximum at 10-12 m depth. At 3-5 m this average is much lower, but still considerably higher than below 15 m. If we take as null hypothesis that the parasites are equally abundant in the corals of all depths, we may, based on the

TABLE III

Number of *Corallonoxia longicauda* (*N* parasites), superficies of coral colony and density of the parasites (= parasites per 100 cm² coral), at station 1.

depth (m)	*N* parasites	surface (cm²)	parasites per 100 cm²	depth (m)	*N* parasites	surface (cm²)	parasites per 100 cm²
3-5	3	113.7	2.6	15-22	0	205.2	0
	14	102.5	13.7		0	191.7	0
	17	156.3	10.9		0	174.4	0
	21	182.9	11.5		0	169.2	0
	35	163.3	21.4		0	143.6	0
	35	118.2	29.6		0	136.0	0
	67	254.6	26.3		0	128.2	0
	117	159.9	73.2		0	104.7	0
	134	217.5	61.6		1	294.8	0.3
	mean 49.2	*163.2*	*27.9*		2	166.5	1.2
					4	212.4	1.9
					6	209.0	2.9
10-12	0	268.1	0		17	109.8	15.5
	0	212.3	0		18	115.3	15.6
	0	203.6	0		38	179.7	21.2
	0	184.4	0		48	242.3	19.8
	0	128.4	0		83	145.7	57.0
	0	125.3	0		164	98.3	166.8
	0	116.9	0		*mean* 21.2	*168.1*	*16.8*
	6	126.8	4.9				
	8	150.8	5.3	27-33	0	199.4	0
	54	110.0	49.1		0	197.4	0
	64	175.0	36.6		0	148.1	0
	122	160.3	76.1		0	124.9	0
	124	211.7	58.6		0	124.0	0
	139	153.7	90.4		0	102.7	0
	145	130.0	111.5		0	77.2	0
	223	104.3	213.8		4	193.3	2.1
	240	103.7	231.4		4	163.6	2.4
	258	113.6	227.1		9	210.1	4.3
	308	95.5	322.5		9	136.8	6.6
	312	209.7	148.8		9	125.8	7.2
	364	140.3	259.4		11	172.5	6.4
	405	188.0	140.6		11	99.9	11.0
	409	246.1	166.2		19	133.0	14.3
	472	55.8	845.9		20	154.5	12.9
	1411	161.4	874.2		27	143.8	18.8
	1423	121.0	1176.0		67	231.5	28.9
	2240	211.7	1058.1		102	122.6	83.2
	mean 323.4	*159.3*	*190.0*		*mean* 15.4	*155.9*	*10.5*

data from table III, construct a synopsis (table IV). The discrepancy between the values found and expected in table IV is so evident, that the χ^2-test is as much as unnecessary.

Obviously the conditions at 10 m are much more favorable for the parasites than elsewhere. This favorable difference may depend on one or more of the following factors: (1) better chances of life for the parasites inside the colony; (2) greater possibilities for free-swimming parasite larvae to

TABLE IV

Expected and observed densities of *Corallonoxia longicauda* at different depths at station 1.

depth (m)	parasites per 100 cm² coral found	parasites per 100 cm² coral expected	*N* colonies
3-5	27.9	80.5	9
10-12	190.0	80.5	27
15-22	16.6	80.5	18
27-33	10.5	80.5	19

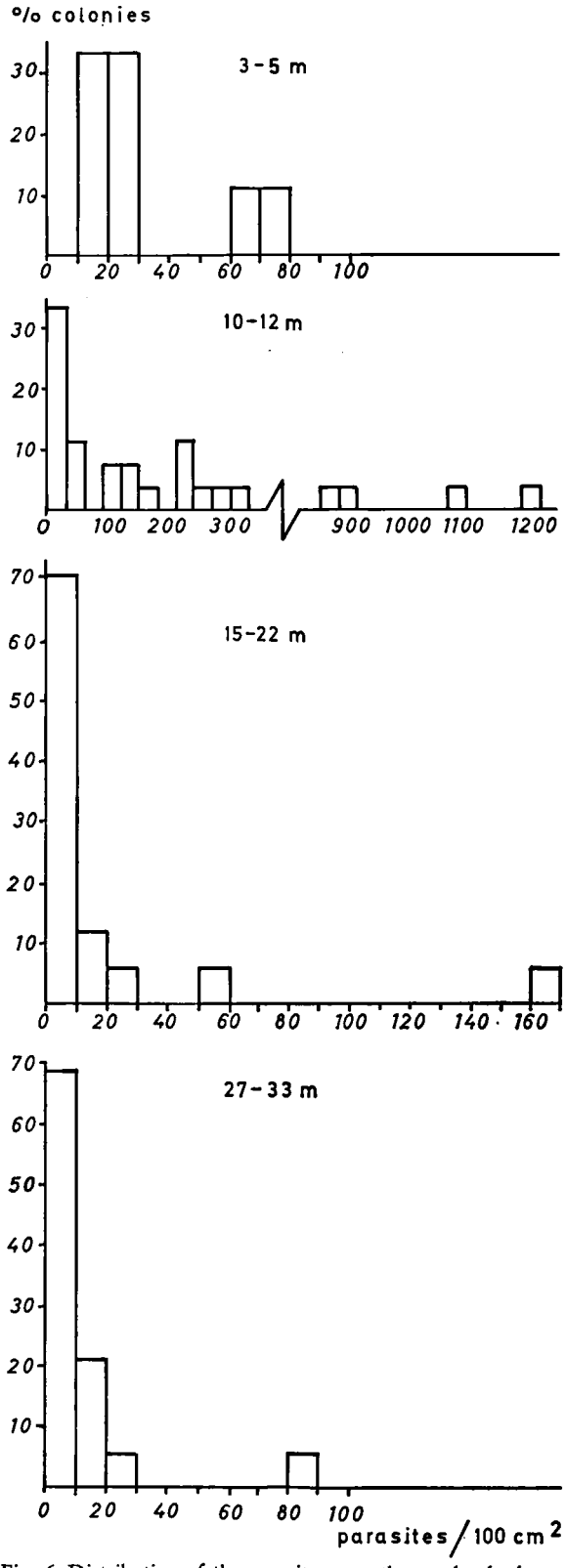

Fig. 6. Distribution of the parasites over the coral colonies at different depths.

infest; (3) greater reproductive success inside the colony (or greater possibilities of re-infestation of the same colony by the progeny).

3.1.3 Distribution over the colonies. — The graphs (fig. 6) represent the frequency distributions of the parasite densities over the colonies, arranged in four depth classes. None of them corresponds to the normal distribution, with possible exception of the colonies from 3-5 m, the number of observations being too small to be decisive. Anyway, all distributions are skewed to the right: many with zero or few, relatively very few with the average density of the depth class concerned, and a considerable number with a relatively high density.

The ratio between the number of colonies without parasites and the ones with one or more parasites can serve as an indicator for the chance of a primary infestation from the water. Because of the low infestation rate on the N.E. coast and also because of the large yolk-rich eggs, we may assume that the larva of *Corallonoxia longicauda* is a highly developed one, without or with a very short pelagic stage. It will therefore settle in the vicinity of the colony where it originated from, or perhaps even in its own colony. If this assumption is true, the chance of a primary infestation will depend on: (1) the density of *Meandrina meandrites* on the spot, (2) the magnitude of the local parasite population, determining the amount of larvae that are released into the water, (3) colony size, in view of the chance to be "hit" by a larva, (4) possible other factors facilitating or hampering the settling of a larva, e.g. the water movement, or the behavior of the larvae. As far as these factors are known they can be arranged in tabular form as given in table V.

TABLE V

Density of *Meandrina meandrites* and *Corallonoxia longicauda*, and average superficies of coral colonies at different depths at station 1.

depth (m)	% of coverage of *Meandrina*	average density of *Corallonoxia* per colony	average colony surface in cm²
3-5	19.9	49.2	163.2
10-12	6.4	323.4	159.3
15-22	3.8	21.2	168.1
27-33	3.9	15.4	155.9

On account of the figures in table V we can formulate the following expectations:

(A) 3-5 m compared to 10-12 m: indecisive. The density of the host is higher at 3-5 m, the parasite population, on the other hand, is smaller.

(B) 3-5 m compared to 15-22 m and 27-33 m: more infested colonies in the shallow waters, because both the host population and the parasite population are larger.

(C) 10-12 m compared to 15-22 m and 27-33 m: more infested colonies at 10-12 m for the same reasons.

(D) 15-22 m compared to 27-33 m: no difference.

In the next tabulation, concerning the numbers of infested and uninfested colonies at several depths (table VI) the figures are derived from table III. The differences between the groups in table VI are in accordance with the expectations given above. The significance of these differences can be tested with Fisher's test. With a confidence of 95% can be stated that the difference between 3-5 m and 15-22 m and the difference between 3-5 m and 27-33 m are significant indeed, the differences between the other groups are not. Apparently the factor "density of the host" is a very important one.

TABLE VI

Numbers of infested and uninfested colonies, and percentage of infested colonies at station 1.

depth (m)	*N* colonies uninfested	*N* colonies infested	% infested
3-5	0	9	100
10-12	7	20	74.1
15-22	8	10	55.6
27-33	7	12	63.2

Now the form of the distribution of the parasites is partially elucidated. Still the frequency of heavily infested colonies and the absence of a middle group (with average infestation rate) remain to be explained. Especially at 10-12 m we find exceedingly high densities. This suggests a mechanism by means of which an existing parasite population supplies its own colony with new progeny. There may exist a reproduction cycle completely inside the host; an alternative possibility is a situation whereby initially the larvae are released into the seawater, but are caught back partially by their own colony. This second possibility offers an explanation for the apparent fact that this mechanism is not equally effective everywhere on the reefs.

Whatever the nature of the mechanism, the self-support will only start functioning after the parasite population has reached a certain threshold value. Until that moment the size of the population will largely depend on the supply from the surrounding water and the life span of the parasites. As soon as the threshold is reached, the demographic determinants become different: the factor "birth", in case of a cycle entirely inside the coral, is dependent on the number of fertile females and the presence of a sufficient number of males per 100 cm² coral; in case of larvae being released and partially caught back it is, in addition, dependent on factors facilitating or impeding the catch-back, like the size and shape of the colony, the water movement and the behavior of the larvae.

The figures in the next table (table VII) are derived from table III. The chosen density of 20 parasites per 100 cm² is somewhat arbitrary, but must be "above the threshold" I believe, owing to the shape of the frequency distribution of the densities. Furthermore, we only consider *infested* colonies here, because the aim is to examine the effectivity of the "self-supporting mechanism" at different depths.

TABLE VII

Infested coral colonies: colonies with more and colonies with less than 20 parasites per 100 cm² coral, at station 1.

depth (m)	colonies with less than 20 parasites per 100 cm²	colonies with more than 20 parasites per 100 cm²
3-5	4	5
10-12	2	18
15-22	6	4
27-33	10	2

According to Fisher's test (95% confidence) the group of 10-12 m has significantly more colonies with 20 parasites or more per 100 cm² than the deeper categories. Compared to 3-5 m the difference is not significant (but it is, if we compare the number of colonies with 40 parasites

or more per 100 cm^2). The efficiency of the mechanism is highest at 10-12 m, below 15 m most colonies probably do not reach the threshold, as the chances on a primary infestation are relatively small. At 3-5 m this cannot be the case, for the chance on a primary infestation here is probably the same or even better than at 10-12 m. Presumably the failure of the catch-back is due to the water movement, which is rather violent at this depth because of the surf action, so the larvae are washed away quickly from their own colony.

3.2 Transplantations

Table VIII records the rate of infestation, the living colony surface as well as the part of the colony that died since the transplantation six months before.

TABLE VIII

Transplantations executed at station 1, results after six months. The column "dead surface" records the coral surface that has died after the transplantation.

N Corallonoxia	living surface (cm^2)	dead surface (cm^2)	parasites per 100 cm^2 coral
from 10 m transplanted to 30 m:			
0	74.9	0	0
0	84.1	11.4	0
6	103.2	0	5.8
12	190.4	0	6.3
37	125.7	1.7	29.4
45	99.7	12.5	45.1
51	82.3	0	62.0
80	103.7	24.5	77.1
152	120.3	10.7	126.4
209	60.4	0	346.0
222	188.4	2.2	117.8
632	55.1	112.0	1147.0
985	137.7	37.9	715.3
mean 187.0	*109.7*		*200.1*
from 30 m transplanted to 10 m:			
0	214.4	0	0
0	190.8	0	0
0	124.3	0	0
0	122.3	0	0
0	114.0	0	0
0	103.0	0	0
0	75.3	0	0
3	116.7	0	2.6
5	133.4	0	3.7
17	73.1	0	23.3
47	114.4	0	41.1
70	101.7	0	68.8
85	139.1	0	61.1
194	118.8	0	163.3
mean 32.4	*124.4*		*26.0*

The corals that were transplanted to shallower waters reacted very favorably to their new environment. At the end of the six months' period they were all very healthy, they seemed to have grown and no trace was left of the small damages at the edges that had served to mark their orientation. The corals transplanted to the deep did not so well. A few weeks after the transplantation some of them started to show white spots. The more convex their shape, the more they suffered. Some of them died off along the edges and at the end of the six months' period 3 of the 30 had completely died and many had died off partially.

Considering the infestation rate no difference can be demonstrated between the corals transplanted from 10 to 30 m and the corals permanently growing at 10-12 m (table III), neither in percentage infested nor in density of the parasites. The group transplanted from 30 to 10 m did not show a difference in infestation percentage with the control group growing at 27-33 m. But the transplanted colonies did have significantly more colonies with 20 parasites or more per 100 cm^2. This is an indication that somehow the catch-back works more effectively at 10 m, in that case the difference in parasite density between the corals from 10-12 m and 27-33 m is not entirely due to the fact that at 10-12 m it is easier to reach the threshold value for self-support.

Furthermore the results suggest that the parasites, after settling in the colony, have a fairly long life. One would expect that the group transplanted to shallower waters would count more infested colonies after six months. Apparently, even at 10 m the chance on a primary infestation is small, which implies that the life span of the parasite must be fairly long in order for the population as a whole to be maintained. Also the fact that the parasite density in the colonies transplanted to the deep did not drop steeply despite the deterioration of the host, is an indication of a long life span.

3.3 Infestation rate in very young colonies

Very young colonies composed of one to four polyps were examined for the presence of parasites. With the aid of data collected by Bak & Engel (preliminary results, in preparation) con-

cerning the growth rate of *Meandrina meandrites* of this format, the age of the corals in question was estimated. The results are summarized in table IX.

TABLE IX

Infestation rate and age of young colonies of *Meandrina meandrites* at station 1.

diameter (cm)	estimated age (months)	*N* parasites ♀♀	♂♂	juvs.	depth (m)
1.8	12-28	—	—	—	18
1.0	5-12	—	—	—	15-20
1.7	11-26	—	—	—	15-20
1.4	8-20	—	—	—	15-20
1.6	10-24	—	—	—	15-20
1.9	13-30	—	—	—	15-20
1.4	8-20	—	—	—	12
1.0	5-12	—	7	—	12
1.0	5-12	—	—	—	12
1.0	5-12	—	—	—	8
1.0	5-12	—	—	—	8
0.7	3-8	—	—	—	8

It is clear that these young colonies usually do not have parasites, so there must exist something like a distribution capacity of the parasite, to cause the higher infestation rate in older colonies.

Remarkable is the finding of seven males in one of these small corals; perhaps the larvae (or eggs) attach to the planula of *Meandrina*, the latter being considerably larger than the *Corallonoxia*-eggs (planula 2-3 mm, eggs 0.4-0.7 mm), thus it could be possible that in some cases a coral is born with its parasites.

3.4 Ratio males, females and juveniles

In a number of colonies the males, females and juveniles were separately counted, these numbers and the percentages are given in table X. At all depths we found two to three times as many males as females. Assuming that the animals and especially the females are not very mobile within the colony, this could be functional.

The small number of juveniles in the samples suggests either a short duration of the juvenile stage, or a low birth rate. We do have reason to believe that all adult females in a colony will procreate simultaneously (see § 2.4), in other words one can expect to find in a colony either none or very few juveniles (those that came from the surrounding water), or a complete new generation produced from own stock. The highest percentage found was 20% juveniles, that is 1.17 descendants per female. Considering the number

TABLE X

Numbers and percentages of males, females and juveniles at station 1.

depth (m)	parasites per 100 cm² coral	*N* ♂♂	*N* ♀♀	*N* juvs.	% ♂♂	% ♀♀	% juvs.
3-5	2.6	0	3	0	0	100	0
	10.9	15	2	0	88.2	11.8	0
	11.5	17	3	1	81.0	14.2	4.8
	13.7	12	2	0	85.7	14.3	0
	21.4	22	6	7	62.9	17.1	20
	26.3	52	15	0	77.6	22.4	0
	29.6	24	10	1	68.6	28.6	0
	61.6	72	62	0	53.7	46.3	0
	73.2	68	47	2	58.1	40.2	1.7
	mean				*63.7*	*33.9*	*2.5*
	total	*282*	*150*	*11*			
10-12	5.3	4	0	4	50	0	50
	58.6	100	24	0	80.6	19.4	0
	90.4	98	40	1	70.5	28.8	0.7
	140.6	341	64	0	84.2	15.8	0
	166.2	238	97	74	58.2	23.7	18.1
	845.9	685	664	62	48.5	47.1	4.4
	874.2	1146	231	46	80.5	16.2	3.2
	1058.1	1696	430	114	75.7	19.2	5.2
	mean				*69.9*	*25.2*	*4.9*
	total	*4308*	*1550*	*301*			
15-22	0.3	1	0	0	100	0	0
	1.2	2	0	0	100	0	0
	1.9	3	1	0	75	25	0
	2.9	4	2	0	66.7	33.3	0
	15.5	14	3	0	82.4	17.6	0
	15.6	13	5	0	72.2	27.8	0
	19.8	24	23	1	50	47.9	2.1
	21.2	37	1	0	97.4	2.6	0
	57.0	73	6	4	88.0	7.2	4.8
	166.8	145	17	2	88.4	10.4	1.2
	mean				*82.9*	*15.2*	*1.8*
	total	*316*	*58*	*7*			
27-33	2.1	1	3	0	25	75	0
	2.4	2	2	0	50	50	0
	4.3	6	2	1	66.7	22.2	11.1
	6.4	6	5	0	54.5	45.5	0
	6.6	7	2	0	77.8	22.2	0
	11.0	9	2	0	81.8	18.2	0
	12.9	9	9	2	45	45	10
	18.8	21	4	2	77.7	14.8	7.4
	28.9	50	12	2	74.6	17.9	3.0
	mean				*69.8*	*25.8*	*4.4*
	total	*111*	*41*	*7*			

of eggs per female (40 to 80), this is not very much. Apparently the rest leaves the colony or does not develop.

4. *Spatial distribution within the colony*

After examination of different cubes cut from the same colony, some cubes appeared to have strikingly more parasites than other ones. In order to find out if this was some systematic phenomenon, each cube was numbered according to its place in the colony. According to the null hypothesis, any cube, regardless of its place, will have the same parasite density. As long as the expected number of parasites per cube is not smaller than 5, the discrepancy between expected and observed frequencies can be tested with a χ^2-test. From the 18 colonies fulfilling the above condition, 14 had a distribution differing significantly from a random distribution with a confidence of 95% or more, the remaining four were not significant. The latter were either colonies with rather few parasites or colonies sawed into four or less pieces. Some colonies have been diagrammatically pictured in fig. 7. The +, + +, 0, — and — — indicate the magnitude and direction of the deviations of the average.

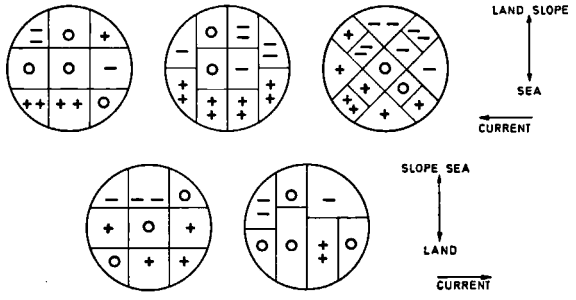

Fig. 7. Colonies of *Meandrina meandrites*, diagrammatically represented, showing the spatial distribution of its parasites: 0 = more or less average; + = distinctly above average; + + = far above average; — = distinctly below average; — — = far below average. Top row: colonies from station 1; bottom row: colonies from station 2.

Most colonies had a cluster of parasites at one side of the colony. From 13 colonies the orientation is known: in 8 colonies the greatest concentration of parasites is at the side away from the slope and downstream, 3 more colonies have most parasites at the off-slope side but not definitely downstream. This pattern is absent (a) in colonies where there are not too many parasites; in this case we do not find overdispersion either; (b) in colonies from the reef plateau, where both light conditions and water movement differ from those on the reef slope. Here we do find overdispersion, but no regular pattern (more than one cluster and no special side of preference).

The colonies from station 2 originate from a reef slope which lies, compared to station 1, opposite to the current. The two colonies that contained a sufficient number of parasites show the parasites' preference for the off-slope and downstream side of the colony as well (fig. 7, below). In the samples from the N.E. coast, likewise from a differently oriented reef, the number of parasites present was too small to allow for a check on their orientation.

A few night dives were made to see if the corals at nighttime, when the polyps are expanded, would show some particularities that could explain the observed asymmetry in the distribution of the parasites. Nothing was found.

As overdispersion appears to be correlated with large densities, it is suggestive that there might be a connection with the self-supporting mechanism, to the effect that this mechanism also causes the remarkable spatial pattern in the distribution of the parasites in the colony. If this is true, we have to decide in favor of a mechanism whereby the larvae (or eggs) leave the colony and are caught back partially, and not for a reproductive cycle taking place entirely within the colony. As the greatest concentration of parasites is off-slope, we may assume that the larvae (or eggs) deliberately move in that direction. Either the light attracts them, or the zone with the greatest water movement. The latter seems more probable, for one would expect an animal that is going to creep inside a coral to be more or less photophobic. The slowest swimmers then are carried away only a very short distance with the current and land downstream of their parents in the same colony.

On the reef plateau, especially in the shallower part, the water movement is more vehement and irregular than on the reef slope. Presumably the larvae are here washed away easily from their own colony, but they have more chance to hit a neighbouring colony, because the density of *Meandrina*

is so high. The phenomenon of clustering at these depths is explained by the fact that the entire surface of a colony most probably will not have an equal chance of being hit and there may be certain areas where the larvae easily wash up.

5. *Infestation rate and biomass*

Table XI gives gross tissue weight (ash-free dry weight in mg), that is the total biomass, composed of coral tissue, *Corallonoxia* and possible other parasites. In addition the table includes the density of *Corallonoxia* in the corals in question and their tribute to the total biomass, computed from the number of males and females found in these corals and their average weight per sex, viz. 86.6×10^{-3} mg for the female and 22.9×10^{-3} mg for the male.

TABLE XI

Biomass and parasites per cm^2 coral at station 1.

depth in m	gross tissue weight in mg/cm^2	*N Corallonoxia* (observed) per cm^2 coral	parasite weight (computed) in mg/cm^2
12-15	32.5	0	0
	31.3	2.31	0.107
	22.7	1.46	0.051
	22.6	3.47	0.077
	19.2	2.27	0.079
	17.8	0	0
	14.7	0	0
	14.7	2.14	0.069
27-33	33.1	0	0
	23.9	0.86	0.036
	23.6	0	0
	23.5	0	0
	21.0	0	0
	19.5	3.22	0.162
	11.1	0.65	0.037
	10.8	0.41	0.023
	10.1	0.04	0.001
	8.8	0	0

Even in heavily infested colonies, containing for instance 10 parasites per cm^2, the parasite weight will be no more than about 0.5 mg per cm^2. That is not a very significant portion (1.5 to 5.7%) of the total biomass, which means that the CO_2 production of the parasites cannot play a rôle of any importance in the calcification of the coral.

Neither is there any correlation between tissue weight and parasite weight in these corals. If the parasites eat tissue, it seems that they do so quite moderately. Another point is that the gross tissue weight per cm^2 proves to vary considerably. This is not beyond expectation, for there are notable differences in the size and form of the septae, which are left out of account in the measure "projected surface".

6. *Infestation rate of "bleached" corals*

It is a well-known fact that some corals, including *Meandrina*, under stress expell their zooxanthellae, and thus gain a white aspect. On the Curaçao reef one can observe sometimes white corals amongst non-bleached congeners. The reason why these corals did expell their zooxanthelles remains a matter of discussion. Could, in the case of *Meandrina meandrites* in Curaçao, *Corallonoxia* be a major cause? Table XII lists a few of such white

TABLE XII

Parasite density in white corals at station 1.

parasites per 100 cm^2 coral, at 10-12 m depth	parasites per 100 cm^2 coral, at 15-22 m depth
0	0
0	0
0	0
322.5	15.6
845.9	166.8
1176.0	

corals and their density of *Corallonoxia longicauda*. It is clear that some of the white corals do have quite a few parasites, but in most of the white corals examined, *Corallonoxia* could not be blamed for the bleaching. Besides, I found some perfectly normal-looking colonies containing similar numbers of parasites.

CONCLUSION

The suggested model for the parasites' way of propagation (diagrammatically represented in fig. 8), together with some subsidiary assumptions concerning the larvae, explains both the spatial distribution of the parasites within the colony and the distribution of densities over the colonies. One implication is that the parents, as compared to the speed with which their offspring populates the colony, do not move over a considerable distance

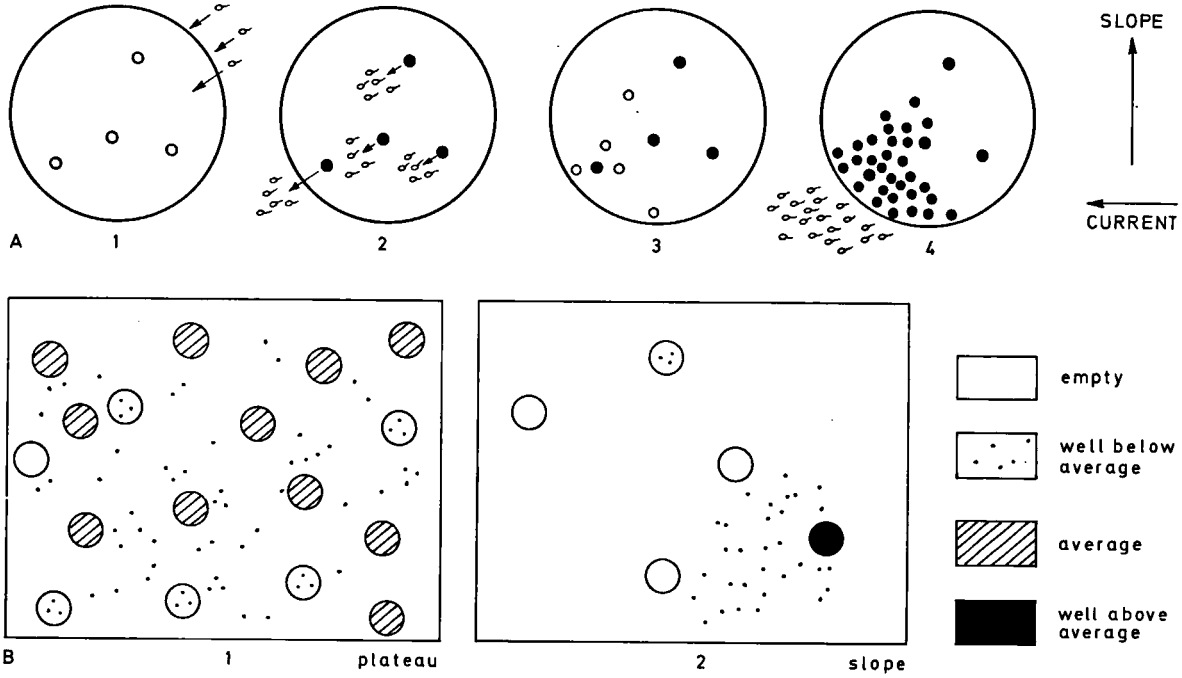

Fig. 8. Suggested model for the parasite's way of propagation. A, Development of a spatial pattern through self-infestation. (1) Infestation from the surrounding water. Few parasites, randomly distributed. (2) Procreation starts, larvae are released and move in downstream and off-slope direction. (3) Part of the larvae are caught back and settle in the same colony. (4) Many parasites, clustered together at one side of the colony, producing large quantities of larvae.
B, Distribution of coral colonies, parasites and larvae at the plateau and on the slope. (1) Situation at the plateau. A high density of *Meandrina*, many infested, larvae-producing colonies. Self-infestation is hampered by the strong and irregular water movement (but probably still takes place), infestation from the surrounding water is facilitated by the high host density. The available data are indecisive as to which process prevails. (2) Situation at the slope. A comparatively low density of the host and an accordingly lower infestation from the surrounding water, resulting in a relatively large number of colonies without or with very few parasites. Self-infestation works particularly well, resulting in exceedingly high densities in relatively few colonies.

inside the coral host. The question arises whether they are able to move at all. I would say they are, for from the discrepancy between the number of corals with 20 or more parasites per 100 cm² and the less densely infested corals, one can conclude that propagation starts to function at densities well below 20 parasites per 100 cm², which, considering also the ratio males/females appears to point to a certain mobility in order to assure fertilization.

The number of descendants is small, the fraction contributing to their own population growth inside the colony is even smaller. Still, after a time, this growth will by far exceed the growth of the host. The danger that the host will die under heavy parasitic pressure is coped with by several mechanisms. In the first place the coral can harbour an amazingly great number of parasites without obvious suffering; secondly the parasites are not distributed evenly over the colony. The most heavily parasitized part will die off first, so that at least a part of the colony will survive. Thirdly, the offspring of every new generation is produced closer to the edge of the colony and will have less chance to settle in the same colony. This is of course favorable for the dispersal of the species.

The overall picture shows a parasite very well adapted to its host, in harmfulness as well as in life span and speed of reproduction. Even in places where the density of the host is not so high, it is possible for the species to survive, as long as there are a few coral colonies of such shape and location that a rich parasite population can be built up, producing large quantities of larvae during a long period.

SUMMARY

Corallonoxia longicauda has been found along a large part of the S.W. coast of Curaçao from Santa Marta to Cornelis Baai. Probably it occurs along the entire S.W. coast. On the N.E. coast it has thus far only been found at Sint Joris.

Near Piscadera Baai it is most abundant at 10-12 m. The percentage of infested corals is highest at 3-5 m, where its host, *Meandrina meandrites*, is most abundant, the greater abundance of *C. longicauda* at 10-12 m being due to the higher average parasite density in the colonies infested.

The first infestation of the corals is brought about by eggs or larvae from the surrounding water. The chance for a colony to be hit by such a larva is small, but once settled in the colony the parasites live very long.

Their spatial distribution inside the colony is not random, in some places the density is higher than expected, in other places lower. In corals growing on the reef slope there is even a distinct pattern: most parasites are to be found at the off-slope and downstream side of the colony, in the other directions the concentration slopes down gradually.

The copepods are capable of various kinds of movements, especially the males, but it is not clear if they are able to move around inside the coral colony. Most coral colonies contain two to three times as many males as females, on the other hand the female weighs about three times as much as the male. There are not many juveniles, pointing to a long life span.

Compared to the host's, the parasite's biomass is very small. Overburdening of the coral by its parasites, even in very heavily infested colonies, could not be established incontestably.

The female produces relatively few eggs. The efficiency of the propagation does not depend on the number of eggs, but on the reproductive strategy: through self-infestation a colony can become so full of parasites that many larvae can be produced. Most probably the larvae are highly developed, without a pelagic stage, they will move swimming or creeping along the substratum.

In view of the frequency distribution of the parasites over the different colonies it is probable that the reproduction cycle does not take place entirely inside the coral, but that some of the eggs or larvae released are caught back by their own colony. This mechanism can very well be responsible for the spatial distribution of the parasites within the colony and the difference in average parasite density of the colonies living at 3-5 m and 10-12 m. We will have to assume then, that the larva moves actively in the direction with the greatest water movement, away from the slope. The stronger the current or water movement, the more larvae or eggs will be taken along, although some of them manage to stay in their own colony.

ACKNOWLEDGEMENTS

This research has been made possible by grants from the Instituut voor Taxonomische Zoölogie (ITZ), Amsterdam, the WSO Foundation, The Hague, and the Treub Maatschappij, Utrecht, The Netherlands.

Furthermore, the cooperation of the Caribbean Marine Biological Institute and its director, Dr. I. Kristensen, for housing, laboratory accomodation, equipment and diving facilities is acknowledged. The author is indebted to Prof. Dr. J. H. Stock, Dr. R. P. M. Bak and Drs. J. Dieleman for help and advice. Diving assistance was rendered mostly by Mr. Lionel Maria, Mr. Humphrey de Windt, Mr. Oscar Frank, Mr. Frank Isabella and Mr. Aubrey Tiel. Thanks are due to Mr. Carol Cardose for assistance in technical questions and to the entire staff as well as visitors of the Caribbean Marine Biological Institute for many other services during the period of the author's stay in Curaçao.

REFERENCES

BAK, R. P. M., 1973. Coral weight increment in situ. A new method to determine coral growth. Mar. Biol., Berlin, **20**: 45-57.

——, 1975. Ecological aspects of the distribution of reef corals in the Netherlands Antilles. Bijdr. Dierk., **45** (2): 181-190.

JOHANNES, R. E. & W. J. WIEBE, 1970. A method for the determination of coral tissue biomass and composition. Limnol. Oceanogr., **15**: 822-824.

STOCK, J. H., 1975. Corallovexiidae, a new family of transformed copepods endoparasitic in reef corals. Stud. Fauna Curaçao, **47** (155): 1-45.

Received: 16 June 1978