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Infestation, population dynamics, growth and reproductive cycle of *Myzostoma cirriferum* (Myzostomida), an obligate symbiont of the comatulid crinoid *Antedon bifida* (Crinoidea, Echinodermata).

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Abstract: The population dynamics of the symbiont *Myzostoma cirriferum* and the dynamics of infestation of its host *Antedon bifida* were investigated at Morgat (Brittany, France) over a 5-year period. The larger the host, the greater the infestation. The infestation varies according to the season: it is maximum in winter, decreases in spring, and becomes stabilized at a low level from summer to the next winter. The huge infestation in winter is due to the recruitment of young individuals into the population of *M. cirriferum*. That recruitment is independent of myzostome reproductive activity (ovarian maturity, spermatophoral emissions, and egg layings are steady throughout the year), but may be linked to an increase in the comatulid feeding activity: in feeding more, comatulids can catch more infestive-stage myzostome larvae. In spring, the infestation falls, which may be due to both the myzostomes' natural mortality and the appearance of amphipods on the hosts which may act as predators. From summer to the next winter, infestation stays stable, which can be explained by the equilibrium existing between the natural mortality of the myzostomes and their continuous reproduction. The longevity of *M. cirriferum* is estimated to be *ca* 6 months.

Résumé : *Infestation, dynamique de population, croissance et cycle de reproduction de* Myzostoma cirriferum *(Myzostomida), un symbiote obligatoire de la comatule* Antedon bifida *(Crinoidea, Echinodermata).*
La dynamique de population du symbiote *Myzostoma cirriferum* et la dynamique d'infestation de son hôte *Antedon bifida* ont été étudiées à Morgat (Bretagne, France) durant une période de cinq ans. Plus l'hôte est grand, plus l'infestation est importante. L'infestation varie avec la saison : elle est maximale en hiver et diminue au printemps pour atteindre un minimum en été et rester stable jusqu'à l'hiver suivant. Le pic d'infestation hivernal est dû à un recrutement important de jeunes *M. cirriferum* à cette période. Ce recrutement, indépendant de l'activité sexuelle des myzostomes qui reste stable tout au long de l'année, semble plutôt lié à une augmentation de l'activité alimentaire des comatules : ces dernières s'infesteraient massivement en s'alimentant davantage. La diminution de l'infestation observée au printemps serait due à la mortalité naturelle des myzostomes ainsi qu'à l'apparition, dans la population de comatules, d'amphipodes prédateurs. La stabilité de l'infestation observée de l'été à l'hiver suivant peut être expliquée par l'équilibre existant entre la mortalité naturelle des myzostomes et leur reproduction continue. La longévité de *M. cirriferum* est estimée à six mois.

Keywords : Crinoidea, Myzostomida, Infestation, Population dynamics.

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Introduction

Echinoderms are often subject to intensive infestation by various symbionts (Clark, 1921; Jangoux, 1990).

Myzostomes are among the most peculiar of these symbionts. They are obligate associates of echinoderms and live mainly with crinoids (Graff, 1877, 1884, 1887; Eeckhaut, 1995). Investigations carried out on fossil crinoids suggest that they form a very old taxon, which has evolved intimately with their hosts (Graff, 1885; Brett, 1978; Arendt, 1985).

Until now, information on myzostome ecology has remained anecdotal in the literature, the only relevant works being those of Woodham (1992) and Eeckhaut & Jangoux (1993). Woodham (1992) described the structure of the population of *Myzostoma cirriferum* Leuckart, 1836, in a Scottish sea loch and suggested some hypotheses concerning its dynamics. Eeckhaut & Jangoux (1993) deciphered the life cycle of *M. cirriferum* and explained how the infestation occurs: the host, the comatulid *Antedon bifida* (Pennant, 1777), catches infestive larvae through the use of its feeding system.

This work results from a 5-years survey of a dense population of *Antedon bifida* subject to myzostomidan infestations. It aims at understand the infestation, the growth rate and the reproductive cycle of the symbiont, *Myzostoma cirriferum.*

Material and methods

Sampling

Individuals of *Antedon bifida* and their symbiotic myzostomes, *Myzostoma cirriferum* were hand-collected by SCUBA diving at Morgat (Douarnenez Bay, Brittany, France). The sampling site consists of a pile of concrete blocks about 100 m from the shoreline. The pile extends over *ca* 200 m^2 (20 m long by 10 m wide), its base and top lying respectively at 10 and 3 m depth at high tide. The comatulids live attached to the blocks and colonize the lowest 2 m of the pile.

Samples were taken over a 59-month period, from October 1988 to August 1993 (Table 1). Once detached from the substrate, the comatulids (and their associated myzostomes) were put in a collecting net, transferred to an aerated tank, and transported to the laboratory. In order to be sure that no myzostomes were lost during transportation, some comatulids were picked up in separate watertight plastic containers during dives. No difference in the host infestation rate was found whatever the mode of sampling. The crinoids and their symbionts were kept in open-circuit marine aquaria at the Observatoire Océanologique of Roscoff until needed.

Infestation Study

At each sampling, some tens of uninjured host individuals were put separately in flasks and fixed in Bouin's fluid for 24 h, rinsed with distilled water, and stored in 70% ethanol (special care was taken not to loose any myzostomes). The length of the largest non-regenerating arm of each host was measured (referred to as the host size hereafter) and the associated *M. cirriferum* were located under a binocular microscope (most of them still remained attached to their host, a few were found on the bottom of the flasks), separated from their host, and measured (length). Counts of pinnular individuals (*i. e.* young myzostomes attached inside host pinnular grooves) and vagile individuals (*i. e.* older myzostomes moving outside host pinnular grooves) were also made (see Eeckhaut & Jangoux (1993) for a detailed account of these stages in *M. cirriferum).*

Table 1. Sampling dates for *Antedon bifida* and *Myzostoma cirriferum*
Tableau 1. Dates d'échantillonnage des *Antedon bifida* et des *Myzostoma cirriferum*

1988	1989	1990	1991	1992	1993
October 30	March 02	January 04	February 28	February 27	January 16
December 15	May 15	March 01	June 11	May 26	April 13
	September 15	May 22	October 21	November 06	June 03
		August 21			August 24
		November 20			

To investigate the infestation by *M. cirriferum*, we focused on (1) the frequency of infestation, F_i (*i. e.* the percentage of infested hosts); (2) the rate of infestation, R_i (*i. e.* the mean number of *M. cirriferum* observed per infested comatulid); and (3) the population structure of the infesting symbionts (*i. e.* size-frequency distributions). These three parameters were studied in relation to the host size, the season of the year, and the site where infested hosts originated in their population.

Growth Study

Growth in *M. cirriferum* was estimated by measuring the increase of the mean body length of a sample of 52 myzostomes as a function of time. Myzostomes chosen for this experiment were the smallest vagile individuals found on *A. bifida* in March 1991. They were located on their hosts under a binocular microscope, picked up using a Pasteur pipette, placed in Petri dishes in ten groups (9 groups of 5 individuals and 1 of 7 individuals), and replaced on 10 uninfested comatulids. The experimentally infested hosts were transferred from the Observatoire Océanologique of Roscoff to the Station Marine of Wimereux (Pas-de-Calais) where they were maintained in life in an open-circuit marine aquarium (the temperature and salinity in the aquaria of Roscoff and Wimereux are quite similar). For 16 weeks, the lengths of the myzostomes were measured approximately every 3 weeks.

Reproduction Study

The reproductive cycle of *M. cirriferum* was investigated by (1) determining whether individuals have mature ovaries,

(2) determining whether they are able to undergo the process of spermatophoral transfer (see Eeckhaut & Jangoux, 1991 for an explanation of the reproduction process in *M. cirriferum)*, and (3) counting the number of eggs laid by individuals. These three parameters were considered according to the myzostome size and season of the year.

Ovarian maturity was determined based on histological sections (see Eeckhaut, 1995 for a detailed description of the ovaries of *M. cirriferum*). Some of the Bouin's-fixed individuals were dehydrated with graded concentrations of ethanol, embedded in Paraplast Plus, cut into 7 µm thick sections, and stained with a Masson's trichrome (Gabe, 1968). Two classes of female germinal cells were taken into account: the first were previtellogenic oocytes (class-A germinal cells), and the second included both vitellogenic oocytes and fertilized eggs (class-B germinal cells). The total number (from all sections) of germinal cells of the two classes was determined for each of the investigated myzostomes (only germinal cells with a visible nucleolus were counted).

Spermatophoral emission is the process during which one myzostome emits its spermatophore onto the integument of another individual (see Eeckhaut & Jangoux, 1991). An attempt to detect attached spermatophores on living myzostomes was made on each sampling occasion while observing the symbionts on their hosts under a binocular microscope. An assessment of the size at which a myzostome is able to emit a spermatophore and the size at which it is able to receive one was also made by separating living individuals from their hosts, placing them in Petri dishes, and provoking contacts between pairs of individuals. Ninety-six myzostomes were used for these experiments. A test was considered positive if the transfer of a spermatophore occurred during the 30 min following contact.

The rate of egg laying by myzostomes was studied by separating individuals from their hosts, placing them in Petri dishes (the myzostomes laid eggs spontaneously), and counting the number of eggs emitted during a 24 h period.

Results

Infestation of Antedon bifida *by* Myzostoma cirriferum

Myzostoma cirriferum is the only obligate symbiont observed all the year round on *Antedon bifida* at Morgat. Additional facultative symbionts were seen during the spring (May and June), *viz.* three amphipod species (*Talitrus saltator* (Montagu), *Corophium volutator* (Pallas), and *Caprella linearis* (Linné)) and one pycnogonid species (*Nymphon gracile* Leach). Among these species *C. volutator* and *C. linearis* were the most abundant (F_i = 20% for each species), while *T. saltator* and *N. gracile* were only found occasionally (F_i<5% for each species).

In June 1991, three samples were made randomly at three different sites in the *A. bifida* population in order to determine whether the *M. cirriferum* infestation was homogeneous or not (the sites were 10 m apart). The results are shown in Table 2 and Figure 1. At each site, from 32 to 36 comatulids of the same size were sampled (size equivalence of individuals in the three samples was checked by ANOVA; p>0.05). From 70 to 92 myzostomes infested comatulids of each sample. Frequencies (Chi-Square, p>0.05) and rates of infestation (ANOVA; p>0.05) did not differ significantly at the three sites. Myzostomes from 0.2 to 2.2 mm long were observed in the three comatulid samples, and the mean sizes of the myzostomes were similar in the three samples, about 1.1 mm (p>0.05; ANOVA) (Table 2). The ratio of pinnular individuals to vagile individuals observed in all samples was about 1:10, and the samples did not differ significantly from each other (p>0.05; Chi-Square) (Table 2).

Table 2. Characteristics of individuals of *Antedon bifida* and their infesting *Myzostoma cirriferum* sampled at 3 different sites within the host population.
Tableau 2. Caractéristiques des *Antedon bifida* et des *Myzostoma cirriferum* échantillonnés en trois endroits de la population de comatules.

	Site A	Site B	Site C
Number of hosts sampled	33	32	36
Mean comatulid arm length ± SD (cm)	26.6 ± 6.5	25.5 ± 6.5	26.0 ± 6.7
Number of *M. cirriferum* at the pinnular stage*	8	8	8
Number of *M. cirriferum* at the vagile stage*	82	62	84
Mean myzostome size ± SD (µm)	1080 ± 490	1130 ± 510	1240 ± 510

* For the life cycle and life-stages of *M. cirriferum*, see Eeckhaut & Jangoux (1993).

Only the post-pentacrinoidian comatulids (*i. e.*, those over the stalked juvenile stage) were infested. Observations done on 475 comatulids collected on 15 occasions from November 1988 to August 1993 showed that the smallest comatulid infested had an arm length of 6 mm. The frequency and rate of infestation observed in 5 size classes (each of an amplitude of 10 mm) are illustrated on figure 2, and the characteristics of the samples are given in Table 3. Both the frequency and rate of infestation were very low for the smallest comatulids (*i.e.*, those having an arm length <10 mm). Ninety percent of the largest crinoids (*i.e.*, those having an arm length>40 mm) were infested with an average of about 21 myzostomes per individual.

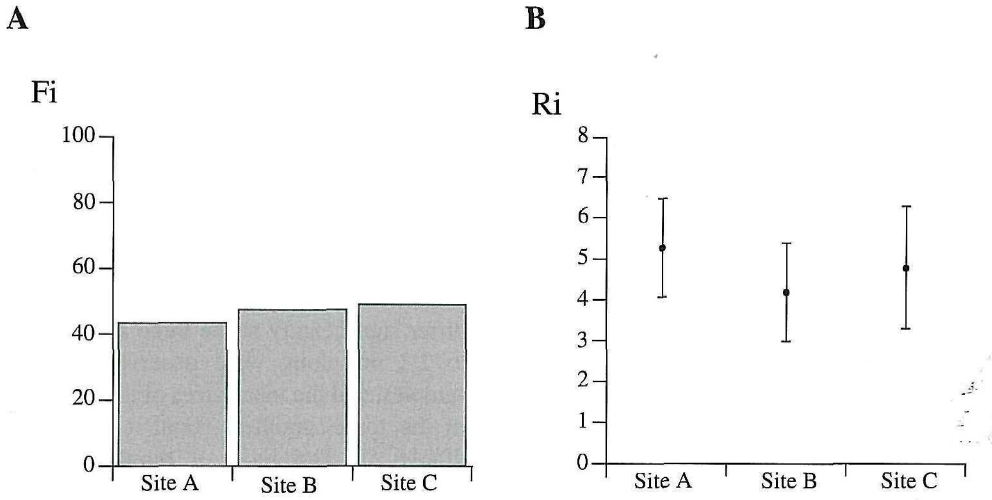

Figure 1. Frequencies (A) and rates (B) of infestation of *Antedon bifida* by *Myzostoma cirriferum* at three different sites within the host population. Bars in figure B indicate 95% confidence intervals.

Figure 1. Fréquences (A) et taux (B) d'infestation d'*Antedon bifida* par *Myzostoma cirriferum* observés à trois endroits de la population de comatules. Les barres d'erreur de la figure B indiquent les intervalles de confiance à 95 %.

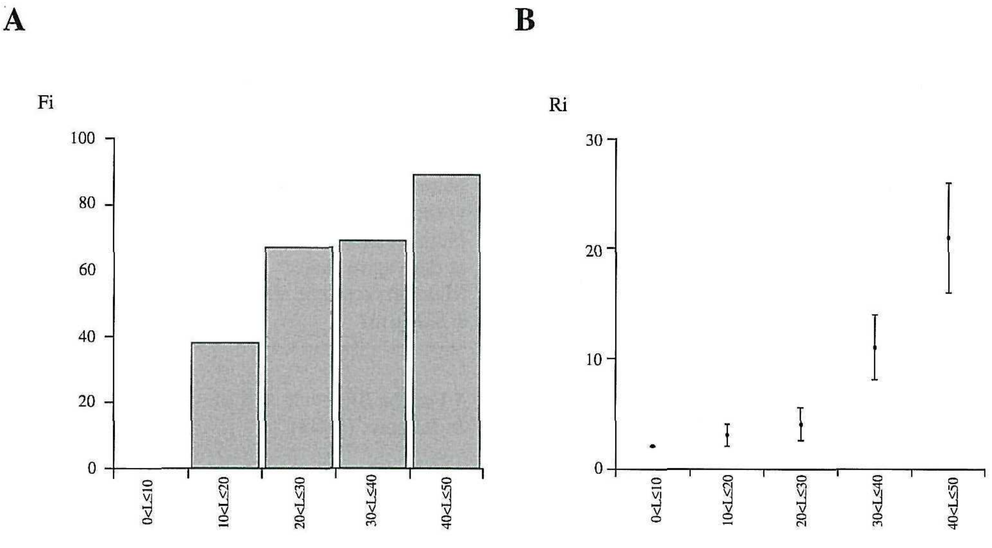

Figure 2. Frequencies (A) and rates (B) of infestation observed in five size classes of *Antedon bifida*. L: comatulid arm length (mm).

Figure 2. Fréquences (A) et taux (B) d'infestation observés dans cinq classes de taille d'*Antedon bifida*. L : longueur des bras des comatules (mm).

Consequently, the larger the comatulid, the greater the infestation.

The characteristics of the samples are shown in Table 3. The population structure of *M. cirriferum* does not vary with the size of *A. bifida*: the mean length of the myzostomes is about 750 µm and does not differ significantly in the 5 size classes of infested comatulids ($p>0.05$; ANOVA). Again, the proportions of pinnular and vagile individuals are similar in the 4 samples of largest comatulids ($p>0.05$; Chi-Square).

The seasonal changes in both frequency and rate of infestation were studied on 10 occasions extending from

Table 3. Characteristics of the 5 size classes of *Antedon bifida* and of their infesting myzostomes
Table 3. Caractéristiques des cinq classes de tailles d'*Antedon bifida* échantillonnés et des myzostomes qui les infestaient

	0<L<10*	10≤L<20	20≤L<30	30≤L<40	40≤L<50
Number of *A. bifida*	88	171	121	65	50
Number of *M. cirriferum* at the pinnular stage	0	64	81	177	361
Number of *M. cirriferum* at the vagile stage	3	86	139	316	588
Mean myzostome size ± SD (µm)	770 ± 500	730 ± 390	730 ± 420	760 ± 410	760 ± 430

*L: length of the comatulid's arms (mm)

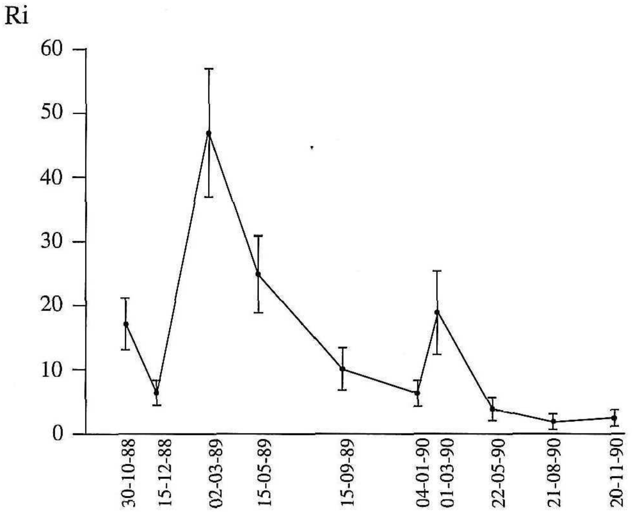

Figure 3. Seasonal change in the rate of infestation of *Antedon bifida* by *Myzostoma cirriferum*. Bars indicate 95% confidence intervals.

Figure 3. Evolution saisonnière du taux d'infestation d'*Antedon bifida* par *Myzostoma cirriferum*. Les barres d'erreur indiquent les intervalles de confiance à 95 %.

October 1988 to November 1990. Each time, the 10 largest comatulids were fixed in separate flasks. All individuals had an arm length of between 4 and 5 cm. The frequency of infestation in the samples did not vary with the period of the year: it was always 100%. On the other hand, the rate of infestation varied greatly: it reached a maximum at the end of winter 1989, a period during which 71 myzostomes were observed on one comatulid, and a minimum in August 1990 with at the most 5 myzostomes on one comatulid (Fig. 3). The shape of the graph in figure 3 suggests that the seasonal changes in the rate of infestation follow an annual cycle. Indeed, two cycles, both of a duration of about 12 months, are evident in the figure: the first cycle extended from October 1988 to September 1989, the second extended from September 1989 to November 1990. During each cycle, the rate of infestation followed a similar course, reaching a maximum at the end of winter and decreasing afterwards from spring to autumn.

Seasonal changes in the host's population structure were studied from May 1992 to August 1993, through 6 sampling intervals. At the same time, the frequency and rate of infestation of the comatulids sampled were taken into account. Figure 4 illustrates the host-size frequency distributions found in each sample. In May 1992, hosts of all lengths were present at Morgat, while in November only small ones (arm length<2.5 mm) were observed. These small individuals formed a cohort that grew up until June. From November to June, the mean arm length of the hosts changed from 12 mm to 27 mm. At the end of August, only small individuals (arm length<20 mm) of a new generation were present in the population. Both the frequency and rate of infestation evolved similarly: they decreased greatly from May to November when they reached their minima (Fi=4%; Ri=1), increased until January when they reached their maxima (Fi=98%; Ri=5.5) and decreased again to become very low in August (Fig. 5). The maximum frequency and rate of infestation followed the period when comatulids growth was the fastest, *i. e.* from November to January, when the mean arm length increased *ca* 90 µm per day.

Population dynamics and growth of Myzostoma cirriferum

The size frequency distributions of 15 successive samples of *M. cirriferum* found on comatulids are illustrated in figure 6. A total of 475 hosts was collected, on which

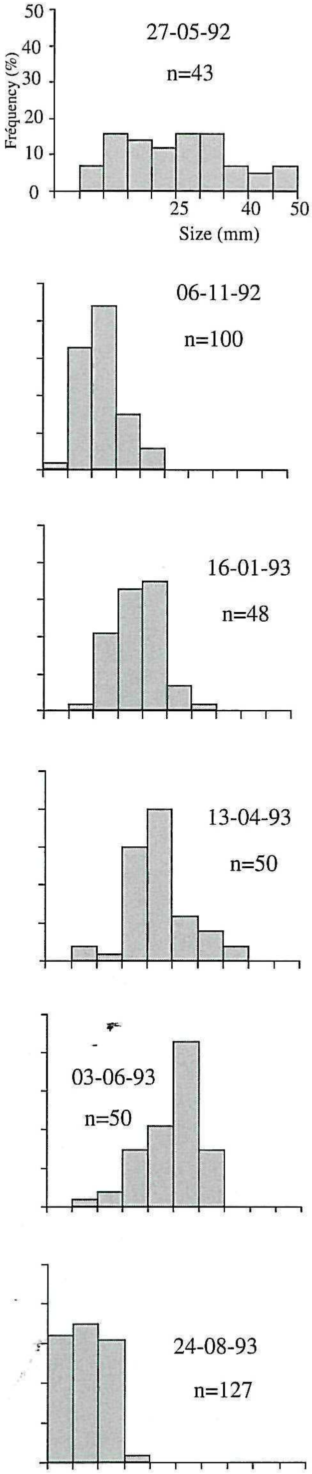

Figure 4. Size frequency distributions of *Antedon bifida* sampled on six occasions from May 1992 to August 1993. n indicates the number of comatulids collected.

Figure 4. Distributions des fréquences de taille des *Antedon bifida* échantillonnés au cours de six périodes de mai 1992 à août 1993. n indique le nombre de comatules échantillonnées.

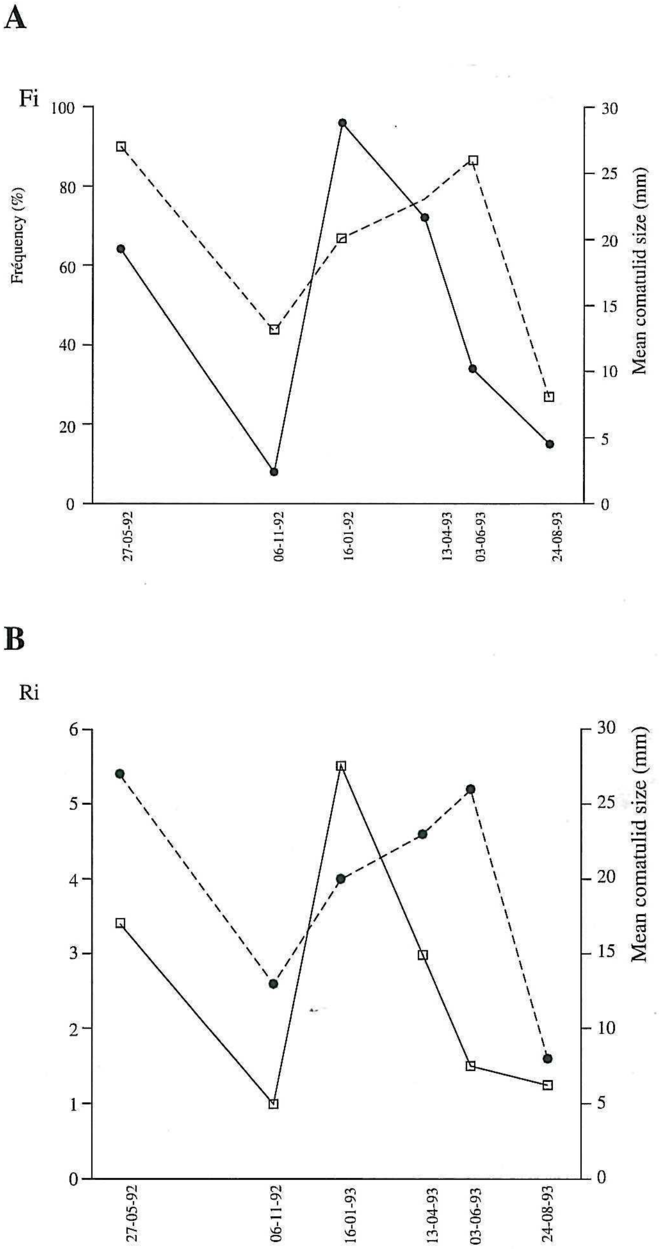

Figure 5. Seasonal changes in the frequency (A) and rate (B) of the infestation of *Antedon bifida* by *Myzostoma cirriferum* and their connection with the seasonal changes in the mean size of host on six occasions from May 1992 to August 1993. Solid lines: changes in the frequency (A) and rate (B) of infestation; dotted lines: changes in the mean length of the comatulid arms.

Figure 5. Evolutions saisonnières de la fréquence et du taux d'infestation d'*Antedon bifida* par *Myzostoma cirriferum* en regard de l'évolution saisonnière de la taille moyenne des *Antedon bifida*. Traits pleins : évolution de la fréquence (A) et du taux (B) d'infestation ; traits pointillés : évolution de la longueur moyenne du bras des comatules.

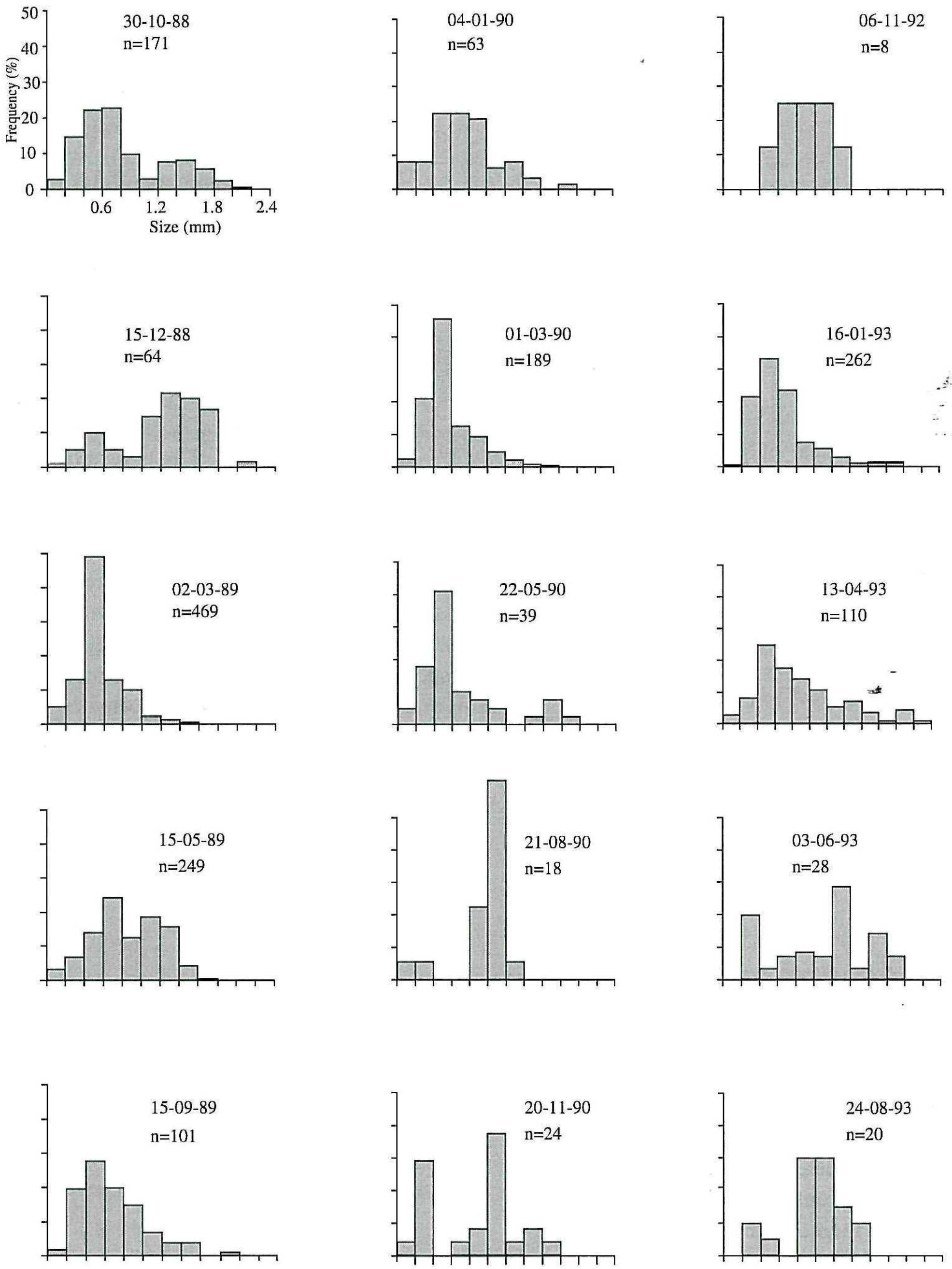

Figure 6. Size frequency distributions of *Myzostoma cirriferum* infesting crinoids sampled on fifteen occasions (n indicates the number of myzostomes observed).

Figure 6. Distributions des fréquences de taille des *Myzostoma cirriferum* infestant les crinoïdes échantillonnés au cours de quinze périodes (n indique le nombre de myzostomes observés).

1815 myzostomes were found. The largest myzostome observed was 2.3 mm long, the smallest 70 µm long. Except for periods when the myzostomes were scarce (*i. e.*, less than 60 specimens observed, see figure 6), individuals of lengths up to 1.6 mm were always present. They represented 90% of the total number of myzostomes sampled. In four of the 15 collections (*i. e.*, March 1989, March 1990, May 1990, January 1993), individuals smaller than 0.6 mm represented more than 50% of the myzostomes sampled.

Both pinnular and vagile myzostomes were observed in

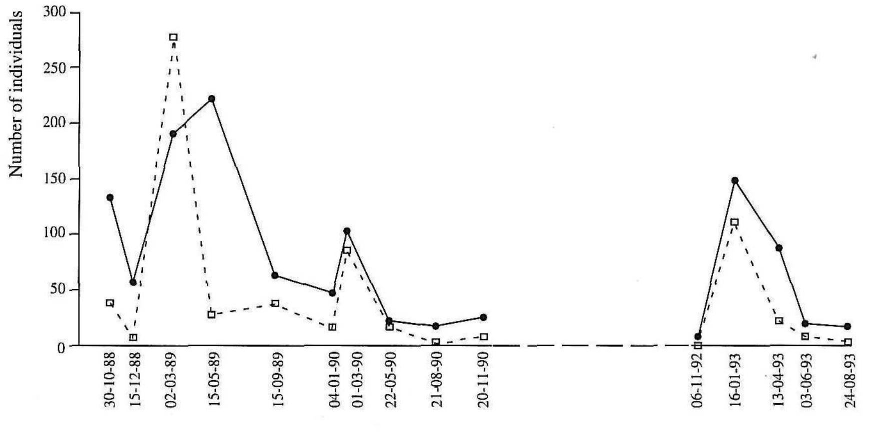

Figure 7. Changes in the number of pinnular (dotted line) and vagile (solid line) individuals of *Myzostoma cirriferum* infesting *Antedon bifida*.

Figure 7. Evolution du nombre de myzostomes fixés dans les sillons pinnulaires sur *Antedon bifida* et du nombre de myzostomes vagiles.

Table 4. Characteristics of the sample of *Myzostoma cirriferum* reared on *Antedon bifida*.
Table 4. Caractéristiques des échantillons de *Myzostoma cirriferum* élevés sur *Antedon bifida*.

Timetable	Number of individuals observed	Mean myzostome size (µm)
02-03-91	52	675
27-03-91	47	980
15-04-91	49	990
07-05-91	43	1160
02-06-91	29	1090
22-06-91	15	950

all samples (Fig. 7). The number of pinnular and vagile individuals evolved similarly except from March to May 1989 when the number of the former fell drastically, while that of the latter increased (Fig. 7). Pinnular and vagile individuals were each very abundant in 3 samples, although these samples were a bit different for the two life stages: pinnular individuals reached their maximum in March 1989, March 1990 and January 1993; vagile individuals in May 1989, March 1990, and January 1993. The least time between a period when pinnular individuals are very scarce and a period when they are highly abundant is 56 days (*i. e.*, from January 1990 to March 1990; Fig. 7). Most of these pinnular individuals are between 400 and 600 µm long (Fig. 6).

The sample of *M. cirriferum* experimentally infesting a set of 10 crinoids grew significantly ($p<0.001$; ANOVA) during the first 66 days of the experiment (Fig. 8), although after May, a lot of hosts with their myzostomes died resulting in a decreasing of the mean body length of the sample (Table 4). During the first 66 days, the mean body length increased from 675 µm to 1160 µm, corresponding to a mean growth of 7 µm per day (Fig. 8).

Reproductive cycle of Myzostoma cirriferum

The numbers of class A germinal cells (*i. e.*, previtellogenic oocytes) and class B germinal cells (*i. e.*, both vitellogenic oocytes and fertilized eggs) observed in the ovaries of a set of 39 myzostomes of different lengths are shown in figure 9. Individuals smaller than 600 µm long have no more than 20 class-A germinal cells and no class-B cells. The largest individuals have up to 4300 class-A germinal cells and up to 500 class-B cells.

A comparison of the ovarian maturity of 1.2 mm long myzostomes was made across six samples collected from May 1992 to August 1993. The total number of germinal cells of classes A and B of 3 such individuals was counted, and the results displayed in figure 10. At all periods, myzostomes with both types of germinal cells were present and had 250 to 1530 class-A germinal cells and 0 to 147 class-B germinal cells. Though the numbers of germinal cells of each class differed from

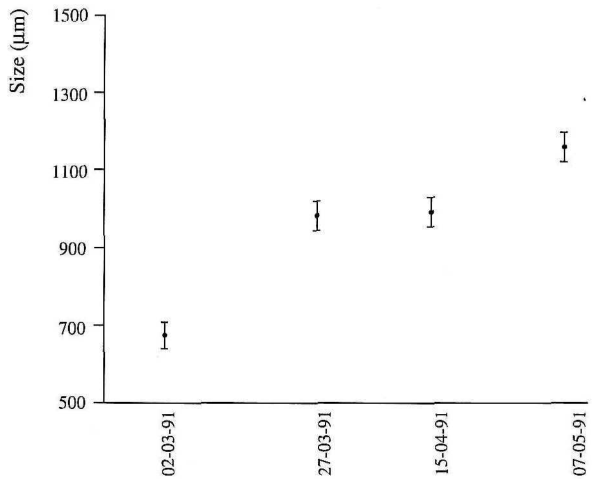

Figure 8. Growth of a sample of 52 *Myzostoma cirriferum* developing on experimentally infested hosts. Bars indicate 95% confidence intervals.

Figure 8. Evolution au cours du temps de la longueur moyenne d'un échantillon de 52 *Myzostoma cirriferum* élevés sur *Antedon bifida*. Les barres d'erreur indiquent les intervalles de confiance à 95 %.

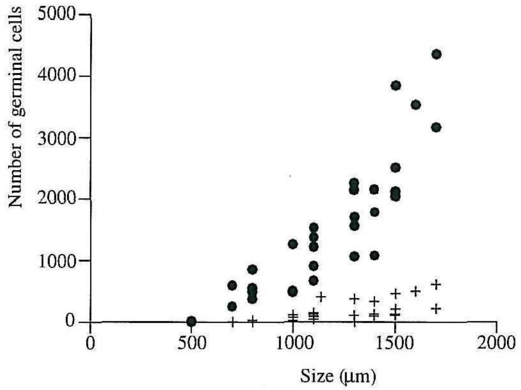

Figure 9. Relationship of germinal cells of classes A and B with the size of *Myzostoma cirriferum* (●: number of class-A germinal cells; + number of class-B germinal cells).

Figure 9. Relation entre le nombre de cellules germinales de classes A et B et la taille des *Myzostoma cirriferum* (● : nombre de cellules germinales de classe A ; + : nombre de cellules germinales de classe B).

one individual to another (that is showed by the importance of the standard deviations on figure 10), they did not differ significantly among the 6 samples (p>0.05; Kruskal-Wallis). The same kind of study was made on myzostomes 1.5 mm long over the same period. These myzostomes had from 1050 to 4350 class-A germinal cells and from 100 to 600 class-B germinal cells. Again, the numbers of germinal cells of each class were not significantly different among all the samples (p>0.05; Kruskal-Wallis).

Emissions of spermatophores were observed at each time we went to Roscoff (Table 1). Table 5 shows results of the tests assessing the sizes at which myzostomes are able to emit and receive spermatophores. No myzostome is able to emit a spermatophore before reaching a length of 1 mm. Fourteen individuals longer than 1 mm, out of 29 potential donors, successfully emitted spermatophores. On the other hand, whatever their size, myzostomes are able to receive spermatophores even if they are still at the pinnular stage. Twelve individuals, out of 20 potential receivers, received successfully spermatophores.

Individuals less than 0.7 mm long never laid eggs, while larger ones laid a few to several hundred of eggs (see Eeckhaut & Jangoux, 1993). The mean numbers of eggs laid by groups of 5 to 9 myzostomes, *ca* 1.2 mm long, and observed at 6 different times are shown in figure 11. They generally laid about 150 eggs during a 24h period, although 500 eggs were laid by one myzostome in April 1993. The smallest number of eggs laid by an individual was 25 (June 1993). The number of eggs laid by myzostomes of the same size did not differ significantly among the samples (p>0.05; Kruskal-Wallis).

Discussion

The infestation by *M. cirriferum* is homogeneous in the studied population of *A. bifida*. In a sample at a given time, the frequency and the rate of infestation by *M. cirriferum*, and the population structure of the symbiont, are similar everywhere in the host population. *M. cirriferum* only infests post-pentacrinoidean individuals. As already observed by Woodham (1992) on myzostomes infesting *A. bifida* in a Scottish loch, the larger the host, the greater the infestation. Eeckhaut & Jangoux (1993) showed that the infesting stage of the symbiont is the metatrochophora larvae. These are caught by host pinnular podia as any suspended particles. That large crinoids are much more heavily infested than small ones presumably results from the higher development of their feeding system : in the course of one year, the number of pinnules per arm of a single individual passes from 3 to more than 60 (Lahaye, 1987). On the other hand, the population structure of *M. cirriferum* remains unchanged whatever the size of the investigated host, which indicates that competent larvae may infest both small and large hosts.

In the Scottish population of *A. bifida* that Woodham (1992) studied, as well as in the one we investigated, the rate of infestation by *M. cirriferum* varied according to the season: it reached a maximum in winter, decreased in spring and remained low but stable from the summer to the next winter. In the two populations, the number of pinnular myzostomes was highest when the infestation was most intense (*i. e.* during winter). The occurrence of many young myzostomes between January and March (young myzostomes were abundant in February in the Scottish population; Woodham 1992) suggests that a massive recruitment occurs at the end of autumn or at the beginning of winter, depending on years. Woodham (1992) suggested that this recruitment is influenced by the availability of more infesting myzostome larvae in winter, itself depending of an intensification of the myzostome reproduction at that time even though she observed that the number of adult myzostomes reached a peak in June (more than 2000 adults infested a single host at that time). Unlike to Woodham's suggestion, our results show that such intensive recruitment is presumably not related to an increase in the production of myzostome larvae. Indeed, (1) spermatophoral emissions occurred throughout the year, (2) the number of oocytes and fertilized eggs in myzostomes of similar size remained unchanged whatever the period of the year and (3) the number of vagile individuals did not increase from summer to the following winter, which means that the number of myzostomes able to reproduce remained unchanged. We consequently hypothesize that the success of the recruitment is linked to the host biology. According to Lahaye *et al* (1990), the life span of most comatulids at Morgat is from 12 to 18 months. During that period they reproduce once

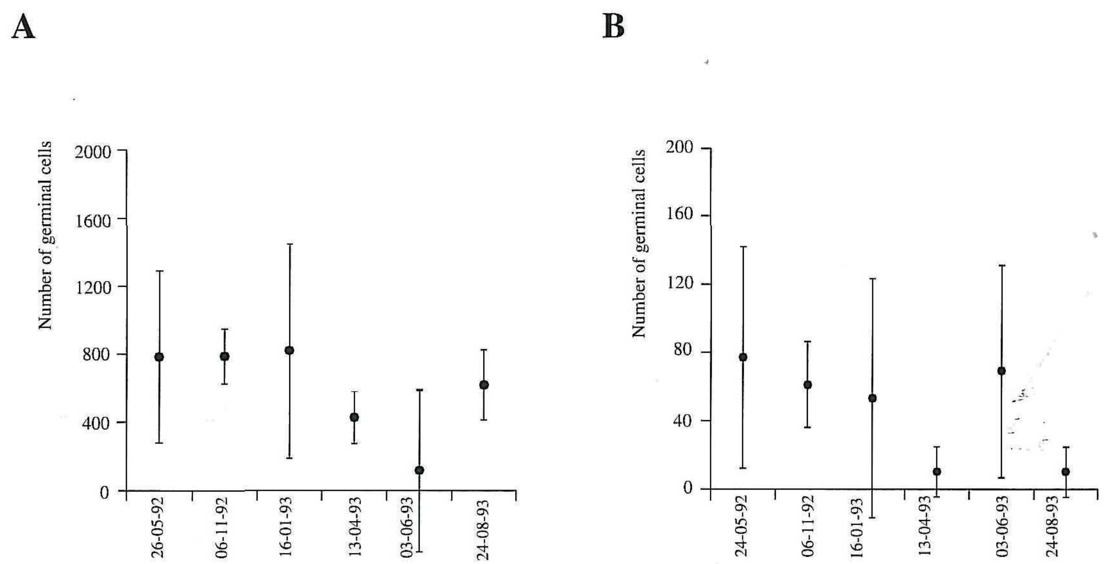

Figure 10. Mean numbers of germinal cells of classes A (A) and B (B) observed in the ovaries of six samples of *Myzostoma cirriferum* (all *ca* 1.2 mm long) on six occasions from May 1992 to August 1993. Bars indicate standard deviations.

Figure 10. Comparaison des nombres moyens des cellules germinales de classes A (A) et B (B) observés dans les ovaires de six échantillons de *Myzostoma cirriferum* (tous *ca* 1,2 mm de longueur) collectés au cours de six périodes de récolte, de mai 1992 à août 1993. Les barres d'erreur indiquent les déviations standard.

Table 5. Emission and reception of spermatophores. Results of the tests determining the length at which *Myzostoma cirriferum* is able to emit spermatophores and the length at which it is able to receive them.

Tableau 5. Emission et réception de spermatophores. Résultats des tests déterminant la taille à laquelle les *Myzostoma cirriferum* sont susceptibles d'émettre des spermatophores et la taille à laquelle ils sont susceptibles d'en accepter.

Myzostome length (in µm)	Number of potential donors tested	Number of individuals successfully emitting a spermatophore	Number of potential receivers tested	Number of individuals successfully receiving a spermatophore
400<L≤600	2	0	2	1
600<L≤800	4	0	2	1
800<L≤1000	5	0	2	1
1000<L≤1200	5	3	3	2
1200<L≤1400	4	4	4	2
1400<L≤1600	4	2	3	3
1600<L≤1800	3	3	2	1
1800<L≤2000	2	2	2	1

(between May and June), and then they die in the course of the six months following their reproduction. The winter recruitment of *M. cirriferum* thus occurs when the host population includes many growing comatulids and a few individuals of about 1 year old, the number of which varies from year to year (in 1992 and 1993, these latter were totally absent from the population). The growth of the comatulids is fastest at the end of autumn and during winter (Lahaye *et al,* 1990, present paper), which is also the period during which their gonads differenciate (Nichols, 1994). It is consequently highly probable that the comatulid feeding activity is higher in late autumn and winter than during the remaining periods of the year. An increase in host feeding activity surely would favour infestation by *M. cirriferum*

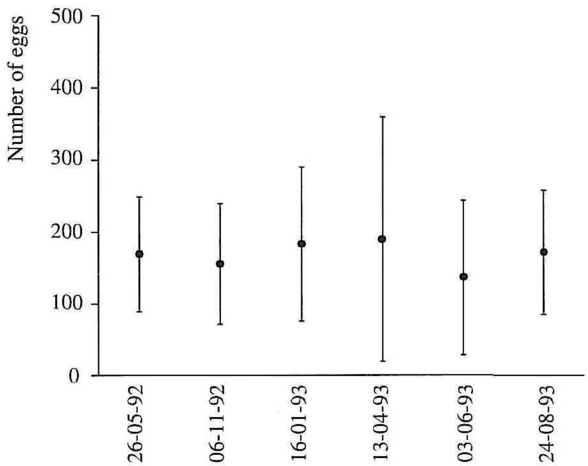

Figure 11. Mean numbers of eggs laid during a 24 h period by six samples of *Myzostoma cirriferum* on six occasions from May 1992 to August 1993. Bars indicate standard deviations.

Figure 11. Comparaison des nombres moyens d'œufs pondus durant 24 h par six échantillons de *Myzostoma cirriferum* collectés au cours de six périodes de récolte, de mai 1992 à août 1993. Les barres d'erreur indiquent les déviations standard.

larvae, since the latter are caught by the host's feeding system. Though such considerations are rather speculative and nothing is known about seasonal variations in the feeding of comatulids, one may note that seasonal variations in the feeding have been observed in non-crinoid echinoderms such as echinoids (Chiu 1984), ophiuroids (Thorson, 1955) and holothuroids (Coulon & Jangoux, 1993). In the last, the feeding activity increases ten times according to the season (Coulon & Jangoux, 1993). Also, seasonal variations in the feeding activity of the holothuroid *Stichopus californicus* were proposed to explain the seasonal variations in the population of its endosymbiotic turbellarian *Wahlia pulchella* (see Shinn, 1986).

The myzostome infestation decreases drastically after each winter recruitment, indicating that a high mortality occurs in the symbiont population. Such spring time mortality could be due to the appearence of a parasitic disease, to a predation, or to the natural death of individuals. Although some parasites were recorded in a few species of myzostomes (Nansen, 1885; Wheeler, 1896; Jägersten, 1941), none has been described in *M. cirriferum* nor observed during this study. On the other hand, some of the epibionts of comatulid observed from May to June (*i. e.* the amphipods *Caprella linearis* and *Corophium volutator*), being known predators of hydrozoans and polychaetes, might also act as predators of myzostomes. That would explain the sudden decrease in myzostomes in the spring. From summer to the beginning of winter, *viz.*, the next recruitment period, the population of myzostomes remains stable. This suggests that in the absence of predators (these amphipods disappear by the end of June), the natural mortality of myzostomes is counterbalanced by the fact that they reproduce continuously.

Our observations on the population of *M. cirriferum* show that the duration of the pinnular stage is no more than 55 days and that the size of vagile individuals increases about 7 µm per day. As 90% of the observed myzostomes are no more than 1.6 mm long, we suggest that most of them do not exceed that length by the end of their life. The duration of the vagile phase can thus be broadly estimated at about 135 days and consequently the entire life span of myzostomes is about 190 days. *Myzostoma cirriferum* is undoubtely a seasonal species with most of the individuals living about six months.

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