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Bryozoan-macroalgal interactions: do epibionts benefit?

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ABSTRACT: Many bryozoans, exemplified by species of *Membranipora*, are obligate epiphytes. We used laboratory and field experiments to ascertain whether colonies of *Membranipora isabelleana* benefit from contact with the fronds and exudates of *Lessonia trabeculata*, their natural substratum in central Chile. Type of substratum, presence or absence of microalgal food and of *L. trabeculata* fronds were the experimental factors, while colonial growth and percentage of non-degenerated zooids were the measured response variables. Colonies on *L. trabeculata* fronds did not grow faster than those attached to glass slides, either in the laboratory or in the field. Colonies grown for 1 mo on fronds, however, retained a significantly higher proportion of non-degenerated zooids than colonies grown on slides (88 and 73% respectively in the laboratory; 100 and 84% respectively in the field). When grown on slides, without microalgal food, colonies retained 79% of non-degenerated zooids in the presence of fronds but only 28% in their absence. These results suggest that colonies absorbed algal exudates when fronds were present, thus preventing the early degeneration of zooids. Even when fronds were separated from colonies by borosilicate membranes, allowing only the diffusion of molecules smaller than 1200 daltons, the above effect was still pronounced. In the field, colonies on fronds had a higher survival rate than those on slides. Association with an algal host therefore enhances at least 2 important life-history parameters in *M. isabelleana*: the percentage of non-degenerated zooids and colonial survivorship. Our results suggest that the trophic association with seaweeds is likely to be particularly important to epiphytic bryozoans under conditions of reduced particulate-food concentration.

KEY WORDS: *Membranipora isabelleana* · *Lessonia trabeculata* · Epibiosis · Seaweed exudates · Polypide degeneration · Bryozoa · Phaeophyta

INTRODUCTION

Many marine bryozoan species occur principally on macroalgae (Ryland 1962, Hayward 1980, Seed & O'Connor 1981, Cancino 1986). Such is the case within the cheilostome genus *Membranipora*, found almost exclusively on Phaeophyta and Rhodophyta (Ryland 1962, 1979, Moyano 1966, Moyano & Bustos 1974, Ryland & Hayward 1977). Numerous studies have addressed the population dynamics of bryozoans associated with seaweeds (Mawatari 1975, Bernstein & Jung 1979, Dixon et al. 1981, Yoshioka 1982, 1986, Cancino 1986), or the morphological adaptations and features of the life cycle that accompany the epiphytic habit (Ryland 1970, Seed & O'Connor 1981, Cancino 1986, Seed & Hughes 1992). Particularly important in this regard is the flexible and ephemeral nature of the substratum (Cancino 1986). Only limited information exists, however, on any benefits the epialgal bryozoans might derive directly from their hosts (De Burgh & Fankboner 1978, Oswald 1986, Oswald & Seed 1986, Williams & Seed 1992).

Bryozoans are modular (sensu Harper 1977), colonial organisms, in which basic feeding units or zooids comprise a polypide enclosed in the cystid (Ryland 1970). The former corresponds to the soft tissues, including the tentacular crown (lophophore) and all the structures

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related to the digestive tract (Ryland 1970). The polypide is a temporary structure which degenerates after a given period of active feeding Degeneration reduces the polypide to a mass of necrotic cells, the brown body (Gordon 1977). Brown body formation is known to be induced both by extrinsic and intrinsic cues, such as environmental deterioration and accumulation of excretory products in the gut cells (Gordon 1977). Fasting, also, should induce polypide degeneration due to energy which is insufficient to maintain the zooid.

Bryozoans are filter feeders which, depending on mouth size, consume particles 8 to 50 µm in diameter (Winston 1977). It has been suggested, however, that epiphytic bryozoans are also able to absorb dissolved organic matter (DOM) exuded by the host algae (De Burgh & Fankboner 1978, Oswald 1986, Oswald & Seed 1986, Williams & Seed 1992). DOM released by seaweeds includes proteins, lipids and carbohydrates (Velimirov 1986), but the nutritional significance to bryozoans of this potential resource has not previously been investigated.

In the present study, we experimentally investigated the effects of access to DOM from algal fronds on colonial growth, colonial survival and zooidal degeneration in *Membranipora isabelleana* (d'Orbigny, 1847), whose typical Chilean host is *Lessonia trabeculata* Villouta and Santelices, 1986.

MATERIALS AND METHODS

Fronds of the Phaeophyta *Lessonia trabeculata* with colonies of *Membranipora isabelleana* were collected by SCUBA diving at Punta de Tralca, central Chile (33° 24' S, 71° 42' W). In the laboratory, with the aid of a scalpel and binocular microscope, colonies of <5 zooids were carefully removed from the fronds. These colonies were gently pressed onto the experimental substrata by placing a cover slip over them. This preparation, when submersed for 24 h, allows the colonies to attach to any desired substratum (Cancino et al. 1991). The following sets of experiments were carried out:

Laboratory experiments. ***Effects of substratum type and feeding regime:*** During June–July 1988, 21 colonies were attached to 7 × 7 cm glass slides and another 14 were attached to small fronds of *Lessonia trabeculata* ranging from 12 to 15 cm in length and from 2.5 to 3.5 cm in width. The colonies were subjected to the following 5 experimental combinations of feeding regime and substratum type: (1) colonies on fronds, fed on *Isochrysis galbana*; (2) colonies on glass, fed on *I. galbana*; (3) colonies on fronds, without *I. galbana*; (4) colonies on glass, without *I. galbana* but with fronds present in the tank; and (5) colonies on glass, without *I. galbana* and without fronds.

There were 7 replicates per treatment, with 1 colony per replicate. Each replicate was kept in an 8 l tank, filled with 0.45 µm-filtered seawater at 11°C, photoperiod of 12:12 and photon-flux density of 40 mmol m^{-2} s^{-1}. The colonies in (1) and (2) were fed daily, while those in (4) had their frond changed once a week. In all experiments, the water was changed every 2 d. The amount of *Isochrysis galbana* given to the fed colonies was chosen according to the energetic requirements of the colonies, determined using an oxycaloric equivalent of 20.3 mJ ml^{-1} O_2 consumed (Widdows & Shick 1985). The metabolic rate per zooid per hour (M) was calculated as $M = 0.088\,X^{-0.356}$; X being the total number of non-degenerated zooids in the colony (M. C. Orellana & J. M. Cancino unpubl. data). The daily energy demand of the colony was obtained as $M \times X \times 24$, which in turn was divided by the caloric content of *I. galbana* (0.608 mJ $cell^{-1}$; Sprung 1984) to obtain the number of cells required daily.

Colonies were observed once a week under the binocular microscope and drawn with the aid of a camera lucida. We recorded the number of zooids which were degenerated or non-degenerated. From the drawing, the area of the colony was measured with a Numonics digitizing table, using Autocad software.

Effects of exudates: During June–July 1992, a further laboratory experiment was done to test the exclusive effects of algal exudates on zooids, free of the possible confounding effects of feeding on algal-tissue debris and associated microorganisms.

Colonies attached to glass slides were kept for 3 wk in a culturing apparatus located subtidally at Las Cruces, central Chile (33° 30' S, 71° 38' W). On transfer to the laboratory, 12 haphazardly selected colonies with 270 to 393 zooids were individually placed in 6 l containers divided into 2 compartments, connected through 2 holes 10 cm in diameter. The colonies were assigned to 4 treatments, representing all combinations of presence or absence of an algal frond in the neighbouring compartment and the presence or absence of borosilicate filter membranes (Micro Filtration Systems, GC50) across the holes between compartments. The filters prevented particles >1200 daltons (Da) diffusing from one compartment to the other. The 4 treatments were as follows: (1) colonies on glass, presence of borosilicate filter membranes and with fronds in the neighbouring compartment; (2) colonies on glass, presence of borosilicate filter membranes but without fronds in the neighbouring compartment; (3) colonies on glass, absence of borosilicate filter membranes and with fronds in the neighbouring compartment; and (4) colonies on glass, absence of borosilicate filter membranes and without fronds in the neighbouring compartment. Small fronds were used, as in the previous experiment.

The 0.45 µm-filtered seawater used in this experiment was changed every 2 d and the fronds weekly. In order to detect the exclusive effect of algal exudates, the colonies were not fed. Temperature was kept at 15°C, the photoperiod was 12:12 h light:dark and the light intensity 30 µmol m^{-2} s^{-1}. As in the previous experiment, colonies were drawn at weekly intervals to determine the number of degenerated and non-degenerated zooids.

Field experiments. In order to verify that the effects detected in the laboratory were also applicable to the field, 2 experimental trials were carried out subtidally at Las Cruces, central Chile. Small colonies of <5 zooids were used, as in the laboratory experiments.

In the first field experiment, August–September 1988, 15 colonies attached to fronds, plus 15 attached to 15 × 15 cm glass slides, were reared for 1 mo in an aluminium box located at 1 m depth, in a place where *Lessonia trabeculata* is common. The colony size and the number of zooids with a polypide were recorded every 2 wk by drawing with the aid of a camera lucida.

In the second experiment, April 1990, colonial survival was monitored in 55 colonies attached to 10 glass slides and 60 colonies attached to fronds.

General procedures. Due to natural deterioration of the outer layer of the fronds, all experiments described above lasted only for 1 mo.

Statistical differences among treatments for each of the response variables studied (colonial growth, colonial survivorship and percentage of non-degenerated zooids per colony) were analysed using an application of multivariate analysis of variance (MANOVA) known as profile analysis of repeated measures (PA). This type of analysis is appropriate where a set of p treatments is applied to 2 or more groups of subjects, provided that response variables for each group tested are measured on the same scale (Johnson & Wichern 1982, Tabachnick & Fidell 1989). The major question answered by PA is whether or not the profiles of the experimental groups differ on a set of measures throughout 3 different tests: (1) parallelism-of-profile test; (2) coincidence-of-profile test; and (3) flatness test. The parallelism test examines interactions, the null hypothesis (H_0) being accepted if treatments have the same (average) effect on different populations. If the profiles are parallel (parallelism H_0 accepted), the coincidence test determines if one treatment has, on average, a higher score than another. Finally, if the profiles are parallel and coincident (parallelism and coincidence H_0s accepted), the flatness test ascertains whether or not the mean responses in each group change over the period of measurement.

RESULTS

Effects of substratum type and feeding regime

In the laboratory, colonies fed on microalgae (Fig. 1A) grew an order of magnitude larger than those denied microalgae (Fig. 1B). In the PA for fed colonies, the parallelism H_0 was rejected (Table 1a). Sizes achieved by fed colonies therefore were significantly different in those attached to glass slides compared with those attached to fronds. For non-fed colonies, the parallelism and coincidence H_0 were accepted, but the flatness H_0 was rejected (Table 1a). Therefore, although the size of non-fed colonies increased throughout time, the size profiles were not significantly different among treatments.

Growth rate of colonies fed on *Isochrysis galbana* increased during the first 3 wk of the experiment (Fig. 2A), whereas in non-fed colonies it rapidly decreased to very low values (Fig. 2B). For fed colonies, the parallelism H_0 was rejected (Table 1b). Profiles of colonies fed on *I. galbana* therefore were significantly different between those attached to glass slides and those attached to fronds. From the third week onwards, the mean size of the colonies attached to glass slides was greater than that of colonies attached to algal fronds (Fig. 1A). The corresponding reduction in growth rate of colonies on algal fronds (Fig. 2A) was probably caused by the loss of frondal outer cell wall immediately surrounding the colonies, thus altering the normal growth of the colonial edge.

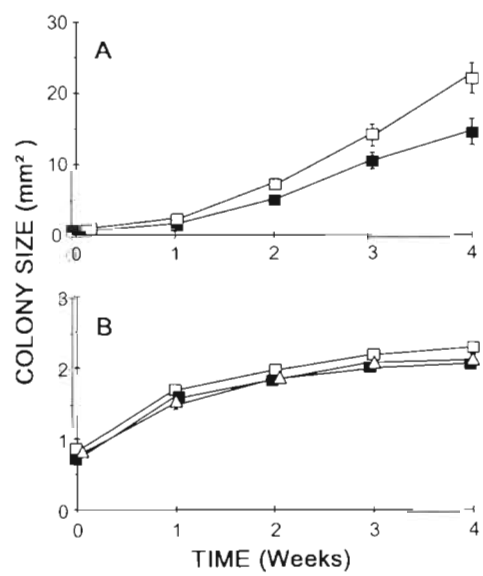

Fig. 1 *Membranipora isabelleana*. Size of colonies grown in the laboratory. (A) Colonies fed on *Isochrysis galbana*, (B) colonies lacking *I. galbana*; (■) colonies attached to fronds of *Lessonia trabeculata*, (□) colonies attached to glass slides, (▵) colonies attached to glass slides but kept in tanks with fronds of *L. trabeculata*. Data are means ± 1 SE, N = 7

Table 1 *Membranipora isabelleana*. Profile analysis conducted to test the effect of feeding regime and substratum type on: (a) colony size, (b) colony growth and (c) the percentage of zooids with a polypide under laboratory conditions. Critical values used to test the null hypotheses of parallelism, coincidence and flatness were calculated with $F_{1,12}$ and t_{12}. FCOF: fed colonies on fronds; FCOGS: fed colonies on glass slides; NFCOF: non-fed colonies on fronds; NFCOGS: non-fed colonies on glass slides; (F): presence of fronds in the tank. *$p < 0.05$; NS: not significant

Treatment	Parallelism	Coincidence	Flatness
(a) Colony size			
FCOF-FCOGS	12.60*	2.36	170.72
NFCOF-NFCOGS	1.50 NS	2.03 NS	859.20*
NFCOF-NFCOGS(F)	10.23 NS	0.67 NS	442.27*
NFCOGS-NFCOGS(F)	2.30 NS	1.33 NS	627.84*
(b) Colony growth			
FCOF-FCOGS	11.18*	2.57	174.49
NFCOF-NFCOGS	3.68 NS	1.79 NS	218.22*
NFCOF-NFCOGS(F)	8.30 NS	1.47 NS	243.71*
NFCOGS-NFCOGS(F)	2.19 NS	0.35 NS	679.12*
(c) Percentage of zooids with a polypide			
FCOF-FCOGS	6.82 NS	1.57 NS	25.20*
NFCOF-NFCOGS	18.97*	10.56	128.53
NFCOF-NFCOGS(F)	1.57 NS	0.39 NS	44.57*
NFCOGS-NFCOGS(F)	13.37*	9.92	140.51

In colonies denied *Isochrysis galbana*, growth rate remained at very low levels throughout the experiment (Fig. 2A, B). For these non-fed colonies, the parallelism and coincidence H_0 were accepted, but the flatness H_0 was rejected for all treatments (Table 1b). Therefore, although the growth rate of non-fed colonies changed throughout time, the growth rate profiles were not significantly different among treatments.

We observed no regeneration of polypides in any of the treatments; therefore, the percentage of zooids lacking a polypide could be used as an accurate index of cumulative degeneration. By the end of the experiment, the treatment effects on the percentage of non-degenerated zooids were ranked as follows: colonies fed on *Isochrysis galbana* and attached to fronds (88%); colonies denied *I. galbana* and attached to fronds (79%); colonies denied *I. galbana* and attached to glass in presence of fronds (79%); colonies fed *I. galbana* and attached to glass slides (73%); and colonies denied *I. galbana* and attached to glass in the absence of fronds (28%) (Fig. 3).

For the percentage of non-degenerated zooids in fed colonies, the parallelism and coincidence H_0 were accepted, but the flatness H_0 was rejected (Table 1c). Therefore, although the percentage of non-degenerated zooids in fed colonies changed throughout time, the profiles were not significantly different among treatments (Fig. 3A).

The timing of polypide degeneration was affected by food and presence of seaweeds. Colonies fed on *Isochrysis galbana* (Fig. 3A) showed no degeneration up to the second week of the experiment. Thereafter, a small percentage of polypides degenerated. In the absence of microalgae, degeneration began during the second week of the experiment (Fig. 3B). Colonies kept on glass slides in the absence of fronds of *Lessonia trabeculata* and of microalgae showed a much

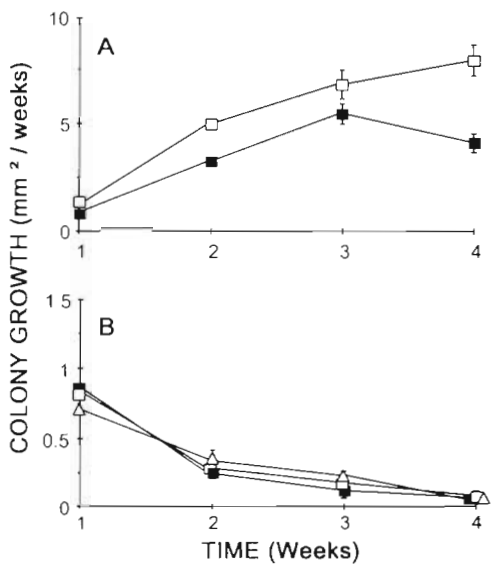

Fig. 2. *Membranipora isabelleana*. Growth rates of colonies grown in the laboratory. (A) Colonies fed on *Isochrysis galbana*, (B) colonies lacking *I. galbana*. Symbols are as for Fig. 1. Data are means ± 1 SE, N = 7

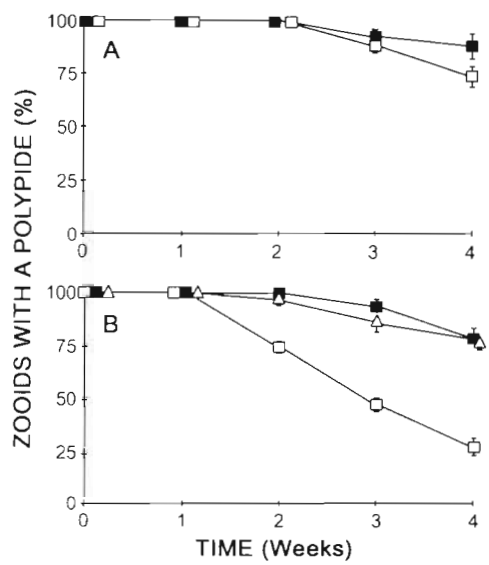

Fig. 3. *Membranipora isabelleana*. Percentage of zooids with a polypide (non-degenerated zooids) in colonies grown in the laboratory. (A) Colonies fed on *Isochrysis galbana*, (B) colonies lacking *I. galbana*. Symbols are as for Fig. 1. Data are means ± 1 SE, N = 7

steeper increase in the percentage of degenerated polypides than those on fronds or on glass slides but in the presence of fronds (Fig. 3B). Accordingly, for the percentage of non-degenerated zooids of non-fed colonies, the parallelism and coincidence H_0 were accepted, but the flatness H_0 was rejected (Table 1c). Therefore, although the percentage of non-degenerated zooids in these non-fed colonies changed throughout time, the profiles were not significantly different among treatments (Fig. 3B). However, in comparing non-fed colonies on fronds with those on glass slides, the parallelism H_0 was rejected (Table 1c). Therefore, throughout the period of measurement, the percentage of non-degenerated zooids was significantly higher in colonies grown on fronds, or on glass slides with fronds present, than in colonies grown on glass slides in the absence of fronds.

Effects of the exudates

In the absence of microalgae, a significant reduction in the percentage of non-degenerated zooids occurred from the second week onwards, this being more pronounced in colonies kept in the absence of fronds than in those kept with a frond in the neighbouring compartment (Fig. 4). For Treatments 1 and 2, with borosilicate filter membranes between the neighbouring compartments (Fig. 4A), the parallelism H_0 was rejected (Table 2), indicating that the presence of fronds had a significant effect on the percentage of non-degenerated zooids. By the end of the experiment, 57% of zooids were non-degenerated in Treatment 1 whereas none contained a polypide in Treatment 2. For Treatments 3 and 4, lacking filter membranes, the parallelism H_0 was rejected (Table 2), again indicating that the presence of fronds had a significant effect on the percentage of non-degenerated zooids. By the end of the experiment, 67% of zooids were non-degenerated in Treatment 3 whereas none contained a polypide in Treatment 4 (Fig. 4B).

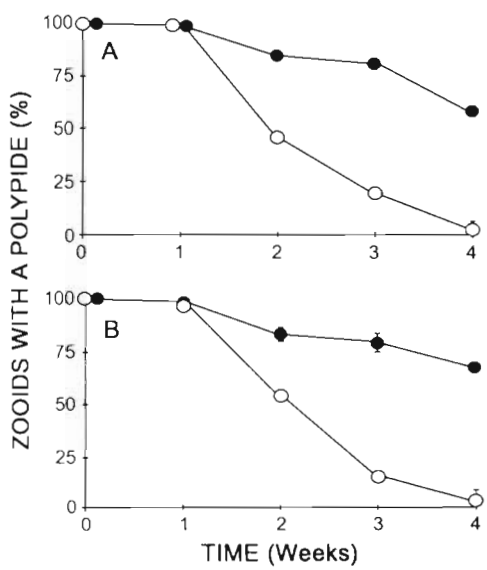

Fig. 4. *Membranipora isabelleana*. Percentage of zooids with a polypide (non-degenerated zooids) in colonies reared in the laboratory in tanks divided into 2 compartments interconnected by two 10 cm diameter holes. (A) Treatment with filter membranes across the interconnection holes. (B) Treatment without filter membranes. (●) Colonies kept with an algal frond in the neighbouring compartment of the rearing tank, (○) colonies in the absence of fronds. Data are means ± 1 SD, N = 4

Table 2. *Membranipora isabelleana*. Profile analysis conducted to test the effect of exudates on the percentage of zooids with a polypide under different laboratory treatment. Critical values used to test the null hypotheses of parallelism, coincidence and flatness were calculated with $F_{1,4}$ and t_4. COGS: colonies on glass slides; (FM): presence of borosilicate filter membranes between the neighbouring compartments of the rearing tank; (F): presence of fronds in the neighbouring compartment. $^*p < 0.05$; NS: not significant

Treatment	Parallelism	Coincidence	Flatness
COGS(FM)(F)-COGS(FM)	606.28*	17.73	1.45×10^3
COGS(F)-COGS	4.72×10^5*	19.50	2.19×10^6
COGS(FM)(F)-COGS(F)	134.63 NS	0.63 NS	2.67×10^{-3}*
COGS(FM) (F)-COGS	374.46*	15.0	1.51×10^4

When comparing treatments with and without filter membranes, the parallelism and coincidence H_0 were accepted, but the flatness H_0 was rejected (Table 2). Thus, although there was a significant change in the percentage of non-degenerated zooids during the course of the experiment, the presence of borosilicate filter membranes had no significant effect on the percentage of non-degenerated zooids (Fig. 4). This result suggests that the substances responsible for preventing degeneration of zooids diffused through the filter membranes and therefore were no more than 1200 Da in molecular mass.

Field experiments

The first experiment showed that substratum had no effect on the final size or on the growth rates of the colonies (Fig. 5). Colony size after 1 mo was approximately 40 mm^2 (Fig. 5), twice the size of the colonies grown in the laboratory on glass slides and fed on *Isochrysis galbana* (Fig. 1A). The parallelism and coincidence H_0 were accepted, but the flatness H_0 was rejected (Table 3a). Therefore, although colony size changed significantly during the period of measurements, the profiles were not significantly different

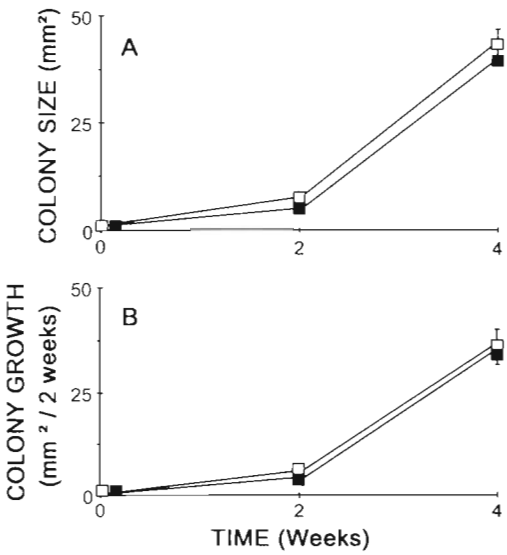

Fig. 5. *Membranipora isabelleana*. (A) Size and (B) growth rates in colonies grown in the field. (■) Colonies on fronds of *Lessonia trabeculata*, (□) colonies on glass slides. Data are means ± 1 SD, N = 15

between colonies growing on glass slides or on fronds. Similarly, for colonial growth rate, the parallelism and coincidence H_0 were accepted, whereas the flatness H_0 was rejected (Table 3b). Therefore, colonial growth rate changed significantly during the experiment, but colonies kept on fronds or glass slides did not grow at significantly different rates.

By the end of the experiment the proportion of non-degenerated zooids was 100% for colonies kept on fronds and 84% for colonies kept on glass slides (Fig. 6A). The parallelism, coincidence and flatness H_0 were accepted (Table 3c). In the field, therefore, the percentage of non-degenerated zooids was not significantly different between colonies kept on fronds or on glass slides.

Table 3. *Membranipora isabelleana*. Profile analysis conducted to test the effect of the exudates on: (a) colony size, (b) colony growth, and (c) the percentage of zooids with a polypide under field condition. Critical values used to test the null hypotheses of parallelism, coincidence and flatness were calculated with $F_{1,28}$ and t_{28}. COGS: colonies on glass slides; COF: colonies on fronds. $^{*}p < 0.05$; NS: not significant

Treatment	Parallelism	Coincidence	Flatness
(a) Colony size			
COGS-COF	29.03 NS	4.40 NS	5.69×10^{3}*
(b) Colony growth			
COGS-COF	28.18 NS	3.38 NS	5.72×10^{3}*
(c) Percentage of zooids with a polypide			
COGS-COF	0 NS	4.98 NS	0

Table 4. *Membranipora isabelleana*. Profile analysis conducted to test the effect of the exudates on the colony survival under field conditions. Critical values used to test the null hypothesis of parallelism, coincidence and flatness were calculated with $F_{1,113}$ and t_{113}. COGS: colonies on glass slides; COF: colonies on fronds. $^{*}p < 0.05$; NS: not significant

Treatment	Parallelism	Coincidence	Flatness
Colony survival			
COGS-COF	1.19×10^{3}*	1.98	1.02×10^{4}

In the second experiment, on colonial survival, the parallelism H_0 was rejected (Table 4). Therefore, in the field, the history of survival was significantly different between colonies on fronds and those on glass slides. By the end of the experiment, the survivorship of colonies on fronds and glass slides was 50 and 0% respectively (Fig. 6B).

DISCUSSION

Although previous studies have discussed the possibility that algal exudates are nutritionally beneficial to epialgal invertebrates (see review by Williams & Seed 1992), the present study provides the first experimental evidence of this. Thus, colonies of *Membranipora isabelleana* were less likely to undergo zooidal degenera-

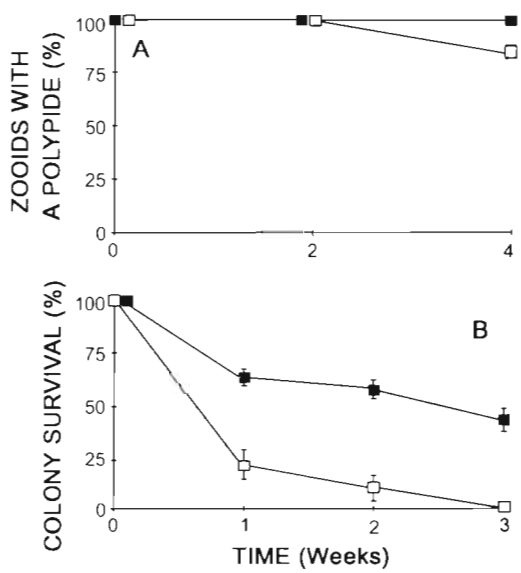

Fig. 6. *Membranipora isabelleana*. (A) Percentage of zooids with a polypide and (B) percentage survival of colonies in the field. (■) Colonies on fronds of *Lessonia trabeculata*, (□) colonies on glass slides. Data in (A) are means ± 1 SD (initial N = 15 and 15 for ■ and □ respectively). Data in (B) are means ± 1 SD (initial N = 60 and 55 for ■ and □ respectively)

tion when in direct contact with, or in close proximity to, their natural substratum, fronds of the Phaeophyta *Lessonia trabeculata*, than when isolated from fronds. Prevention of polypide degeneration by fronds separated from the colonies by a filter strongly suggests that the active fraction of algal exudates is characterized by a molecular mass of less than 1200 Da. Seaweed exudates include proteins, lipids (Velimirov 1986), carbohydrates (De Burgh & Fankboner 1978, Velimirov 1986), tannin-like substances (Al-Ogily et al. 1977) and antimicrobial compounds (Hornsey & Hide 1974), but further work is needed to identify the components used by bryozoans.

In our field experiments, DOM might have been available even to those colonies grown on glass slides, since macroalgae were abundant in the area. However, the lower percentage of non-degenerated zooids in colonies on fronds indicates that close proximity to fronds has a detectable physiological effect above background levels. Oswald (1986) has shown that bryozoans can absorb labelled photosynthates (photosynthetic compounds) directly through the base of the colony. It would be interesting to know if such products are responsible for the higher percentage of non-degenerated zooids obtained in the present study. Energy supply cannot be the only important factor, however, since degeneration of zooids in colonies on fronds was delayed relative to colonies on glass even in our field experiment, where other potential food sources were present.

The degeneration of polypides in bryozoans is a complex phenomenon, resulting from extrinsic and intrinsic causes (Gordon 1977, Bayer et al. 1994, Hunter et al. 1996). Although ultimately inevitable, degeneration may be accelerated or delayed by different factors such as unfavourable environmental conditions (e.g. lack of oxygen, food supply, extremes of temperatures, pH, and salinity) reproductive activity, the position of the polypide within the colony, accumulation of insoluble products or residual material in stomach cells, and possibly is a natural effect of senescence in the polypide (Ryland 1970, Gordon 1977, Muñoz et al. 1990). Our results show that degeneration is accelerated by the absence of food, probably through insufficient energy to keep the zooids active. Muñoz & Cancino (1989) found that the respiration rate of colonies of *Cauloramphus spiniferum* with everted zooids was an order of magnitude higher than when the polypides were withdrawn into the cystid. Although data on their energetic demands are lacking, degenerated zooids may be dormant (Cummings 1975). Degeneration therefore may be a mechanism for conserving energy and, if so, it may be predicted that starving zooids will degenerate once their energy reserves become depleted. The results shown in Figs. 2B, 3B & 4 support this interpretation, but see Bayer et al. (1994) for an alternative view.

In our experiments, the positive effects of the algal fronds on the percentage of non-degenerated zooids were more pronounced when other food sources were absent, suggesting that the host alga alone provided enough energy to prevent the extensive degeneration of polypides. This energy source seems insufficient to support production, however, since colonies growing on fronds did not grow faster than those on glass slides. In the laboratory, colonies on glass slides eventually grew faster than those on fronds, but this might have been due to the loss of substratum through deterioration of frondal epidermis. Loss of frondal epidermis has been reported in 2 species of *Lessonia* from Chilean shores (including *L. trabeculata*) and may be a mechanism for limiting colonisation by epiphytes (Martínez & Correa 1993).

Fitness in colonial modular organisms, such as bryozoans, depends on the performance of the modules that make up the colony. Moreover, in these organisms, life-history events are more dependent on size than on age of the colonies (Hughes & Jackson 1980, 1985, Jackson 1985, Jackson & Hughes 1985). Since food is captured only by zooids possessing a polypide, it may be highly advantageous to the colony to minimize zooidal degeneration. Such a strategy would maximize feeding inputs, growth and sexual reproductive outputs. Therefore, it is interesting to verify that seaweed fronds can function not only as a substratum for epialgal invertebrates but also as a food source. We have also shown that, in the field, survivorship of colonies on fronds is higher than on glass slides. The mechanism(s) responsible for this difference are not obvious, but may have involved differences in attachment efficiency or in vulnerability to predation (Manríquez & Cancino 1992).

The association of *Membranipora* with Phaeophyta is well documented for many localities world-wide (Moyano 1966, 1974, Moyano & Bustos 1974, Ryland 1974, 1976, Bernstein & Jung 1979, Dixon et al. 1981, Yoshioka 1982, 1986, Muñoz & Moyano 1988). It has been suggested that fast-growing kelps offer their epibionts the advantage of a competitor-free substratum produced in a seasonally predictable manner (Seed & O'Connor 1981, Cancino 1986). The present study provides experimental evidence that the association could also be favoured by a trophic relationship advantageous to the bryozoan.

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