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Ecological aspects of algal infectious diseases

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Abstract

This study reports some epidemiological aspects of the infections of *Mazzaella laminarioides* by *Endophyton* sp. and *Pleurocapsa* sp., the organisms associated with the green patch and deformative diseases respectively.

Infections affected an important segment of the host population and persisted throughout the year. The main infecting organism was *Endophyton* sp. Frequency, density and intensity index showed seasonal variations, with lower values in winter. It is suggested that tissue weakening and changes in the biomechanical properties of the infected individuals could be the responsible for this seasonal pattern of variation.

This study demonstrates that, at the host population level, the two life history stages of *M. laminarioides* are susceptible to the pathogens. We also detected an association between reproduction of the host and infection, although the basis for it are unknown.

The two pathogens showed different intra-frond distribution, with *Endophyton* sp. affecting preferentially the base of the frond. The spatial distribution within the beach was different for each pathogen. The main impact of *Pleurocapsa* sp. was recorded at the center, more protected sector of the beach.

Introduction

The study of infectious algal diseases may involve, on theoretical grounds at least, various complementary stages, and each of them may require different approaches, with specific protocols that will lead to answer questions at different levels of resolution.

There is a first, mainly descriptive stage, characterized by field and laboratory observations. The main objective of this stage is to individualize the potential pathogens associated with a given lesion and to characterize the damage caused to the host. Some basic knowledge about the biology of the host organism is extremely important at this stage, so differences in any morphological or physiological character between normal and diseased individuals are not confused with the normal variation within the species. The theoretical considerations regarding this aspect in the study of algal diseases are beyond the scope of this paper and have been discussed in detail by Andrews & Goff (1985). A number of researchers, particularly those responsible for the early studies, have not pursued their work beyond this first stage. Although important in its own right, information restricted to this stage is of little value in understanding the intimacy of any pathogenic association, and certainly is of no value at all to assess the potential impact of the suspected pathogen at a host population level.

The second stage, mainly in the laboratory, is characterized by an experimental approach whose main aim is to establish unequivocally causality. To accomplish this objective, it is required to fulfill the so called Koch's postulates. Andrews (1976, 1977) stressed the necessity to follow strict procedures, similar to those used by microbiologists, if significant progress in understanding algal diseases were to be realized. However, handling algae in the laboratory presents difficulties which sometimes work against a fully laboratory-based demonstration of Koch's postulates. In this context, Andrews & Goff (1985) indicated that some flexibility should be allowed, but without sacrificing the intent involved in each of the steps leading to establish causality.

Learning to manipulate algal hosts and their pathogens under laboratory conditions has also allowed significant improvements in our understanding of aspects such as host-specificity (Kazama, 1979; Correa & McLachlan, 1991; Müller & Parodi, 1993) mechanisms of infection and spread of the disease (Kazama & Fuller, 1970; Andrews, 1977; Molina *et al.*, 1988; Apt & Gibor, 1989; Ishikawa & Saga, 1989; Fujita, 1990; Correa & McLachlan, 1994; Weinberger *et al.*, 1994), and effects on physiological responses by the host (Wu *et al.*, 1983; Correa & McLachlan, 1992; Friedlander & Gunkel, 1992; Robledo *et al.*, 1994). This information has been critical in developing strategies for preventing or eliminate the pathogens in algal farms (Craigie & Shacklock, 1989; Craigie, 1990; Craigie & Correa, 1995).

The third stage is considered in the context of assessing the ecological meaning of a given disease, whose etiology has been established and its direct effects on individual hosts has been characterized. It must be realized at this point, that death of individual hosts may have no effects at population level, if it occurs before the point where their numbers are regulated in a density-dependent fashion (Harper, 1990).

Epidemiology is the discipline which quantifies the importance of a given disease at the host's population level (Agrios, 1988), and includes aspects such as: (a) incidence of the disease, (b) segment of the population being affected (i.e. young, old, or both), (c) differential susceptibility between life history phases, (d) severity of the disease, (e) spatial distribution and (f) seasonal variations.

This is the most overlooked aspect in the studies of pathogenic interactions in algae. In fact, with the exception of the limited information on some epidemiological features in the *Chondrus crispus* Stack.-*Acrochaete operculata* Correa et Nielsen pathosystem (Correa *et al.*, 1987), no report is currently available on this area.

Thus, the objective of this study is to characterize some epidemiological features of the two main infectious diseases affecting the red alga *Mazzaella laminarioides* (Bory) Fredericq (Correa *et al.*, 1993, 1994) in Central Chile.

Materials and methods

Matanzas (33°58′ S) is a fishermen's village, about 200 km south from Santiago. It is characterized by rocky platforms alternated with large boulders. During summer, sand covers most of the boulders as a result of wind and current regimes. A typical sandy beach prevails most of the summer and part of fall. During winter and early spring most of the sand is removed exposing the boulders.

The red alga *Mazzaella laminarioides* is the main occupant of primary space in the intertidal zone of Matanzas. To assess the epidemiology of the two main infectious diseases affecting this alga, samplings were done in January (Summer), May (autumn), August (winter) and November (spring). A section of the beach, 150 m long, was divided in 9 contiguous sectors, perpendicular to the sea border. Within each sector, 10 quadrants (25 cm^2) were randomly distributed, and the thalli of *M. laminarioides* were removed at the base of the fronds. Samples included all individuals larger than 5 mm, which were placed in labeled plastic bags, and were stored in a cooler with ice packs to maintain the temperature at 4–8 °C. The material was transported immediately to the laboratory in Santiago and deep-frozen for analysis.

A number of macroscopic and microscopic features were recorded from each frond. These included size, reproductive status, occurrence of the infections and infection severity. Each frond was divided arbitrarily in three segments (apical, central, basal) where the occurrence of the infecting pathogens and the severity of the infection was recorded. A qualitative scale to assess the severity of infection was chosen as the only possible way to analyze the large number of samples. It must be taken into consideration that the analysis of this parameter must be done under the dissecting microscope for each and whole frond. Detailed information regarding the macroscopic and microscopic changes in *M. laminarioides* by *Endophyton* sp. and *Pleurocapsa* sp. have been published elsewhere (Correa *et al.*, 1993, 1994) and therefore, will not be included here. *Endophyton* sp. and *Pleurocapsa* sp. are the causative agents of the green patch disease and deformative disease respectively in *M. laminarioides.* Data were expressed as frequency or density. Frequency is defined as the segment of the population, grouped seasonally, showing a particular feature. Density is defined as the number of individual thalli per unit of area.

An index to assess the intensity of the infection (I_i) was applied to pooled data from each sample:

$$I_i = \frac{(X_l)1 + (X_m)2 + (X_h)3}{3n_i}$$

where X_l, X_m, X_h represent the number of segments (3 per frond: apical, central, basal) in each sample, that display a low, medium and high values of infection severity respectively. The number 1, 2 and 3 in the numerator are constants included in the equation to give different weight to the qualitative values of severity. Thus, segments with 'high' values of severity have a stronger impact on the index than those with 'low' severity values. By doing that, we incorporated in the index an additional component to further discriminate the effect of different degrees of infection. The number 3 in the denominator represents the three segments into which the infected fronds (n_i) were divided.

Data were log transformed and parametric statistics were applied after assessment of mean-to-variance independence and homocedasticity (Sokal & Rohlf, 1981).

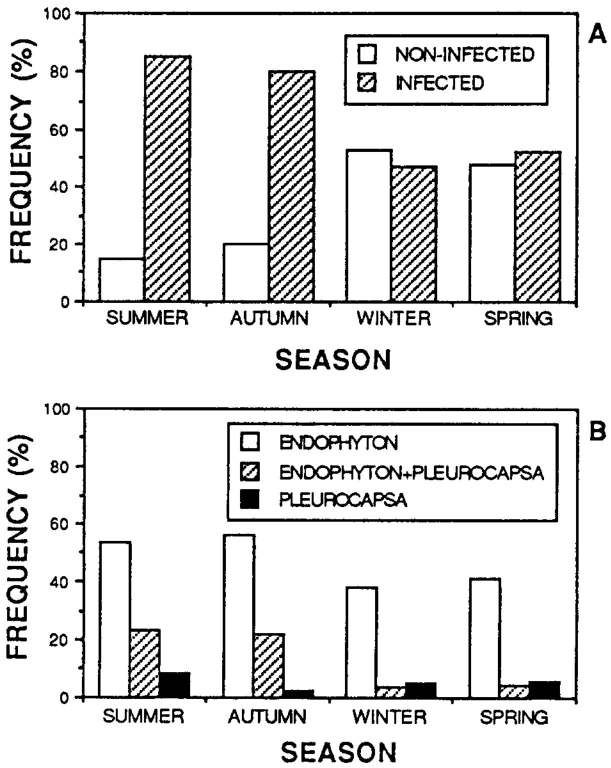

Figure 1. Incidence of infections in the wild population of *Mazzaella laminarioides* from Matanzas. A. Seasonal occurrence of infected fronds as a whole. B. The infected segment of the the population is separated in its three basic components.

Results

Infections as a whole varied from 45% to more than 80% of the examined fronds (Figure 1a). Frequency of infection was higher in summer-autumn than in winter-spring (Figure 1a). An important part of the population, 38–57%, was infected exclusively by *Endophyton* sp., whereas 3–9% of the individuals were infected exclusively by *Pleurocapsa* sp. (Figure 1b). Approximately 4–23% of the fronds were affected by the two pathogens at the same time (Figure 1b). Infections by *Endophyton* sp. showed consistently the highest incidence, with maximum values in autumn (Figure 1b). Infections by *Pleurocapsa* sp., on the other hand, affected a significantly lower proportion of the population, with a minimum in autumn (Figure 1b).

Density of infected fronds showed a clear seasonal fluctuation, where the high summer values decreased sharply toward autumn to reach a minimum during winter (Figure 2a). By comparison, non-infected fronds showed low and similar densities in summer and autumn, with a clear increase towards winter, reaching a maximum in spring (Figure 2a). The impact of each pathogen on the intensity index also showed a seasonal fluctuation, with higher values in summer, followed by a significant decline towards winter (Figure 2b).

Regarding the location of the infections within the fronds, *Endophyton* sp. clearly showed a preference for the basal segments of the thallus, with lower incidence in the central and apical segments (Figure 3). Infections by *Pleurocapsa* sp. on the other hand, affected mainly the central part of the fronds (Figure 3). The patterns of infection within the fronds did not change significantly throughout the year, with the exception of *Pleurocapsa* sp. in autumn, where the apical segments showed an infection incidence higher than the basal ones (Figure 3).

When fronds infected by *Pleurocapsa* sp. were grouped according to their reproductive status, the non-reproductive fraction was by far the most affected stage (Figure 4). This pattern was consistent throughout the year, although a decline in the percentage of infected non-reproductive fronds was observed in winter (Figure 4). A relatively low percentage of fronds infected by the tumor-causing *Pleurocapsa* sp. were either cystocarpic or tetrasporic, and that showed a slight increase in winter (Figure 4). Comparisons of

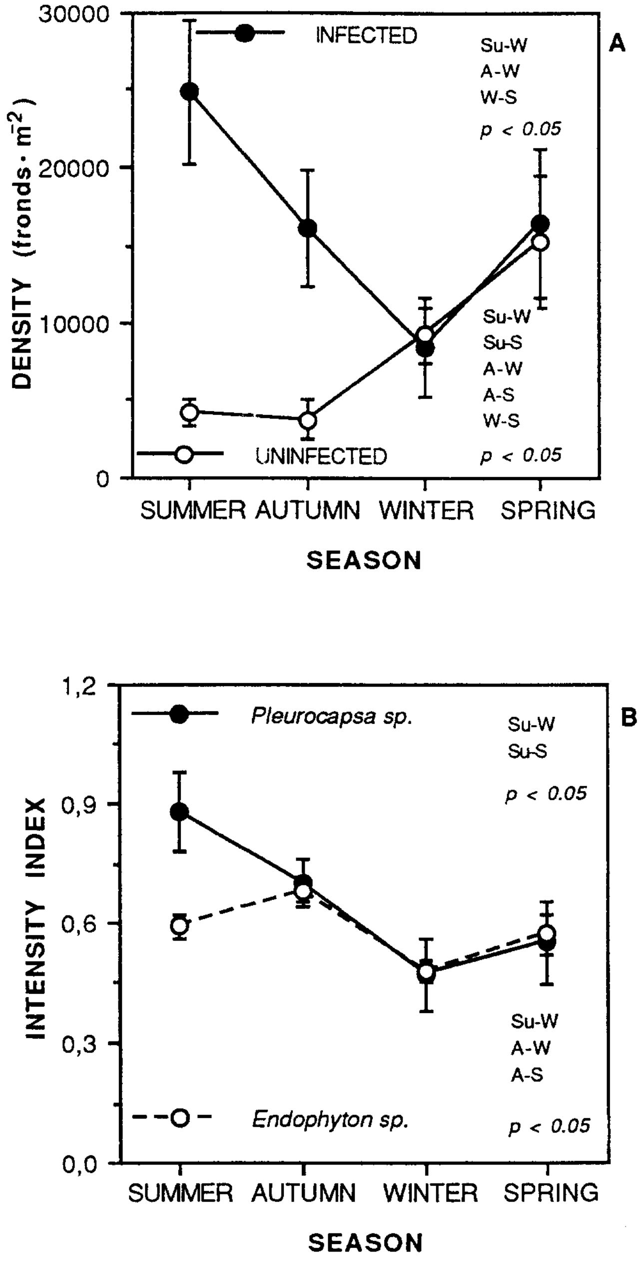

Figure 2. Seasonal fluctuations in density (A) and intensity index (B). Su= summer, A= autumn, W= winter, S= spring. The paired seasons are those whose mean are significantly different with a $p < 0.05$.

the I-C-T ratios between the infected and non-infected segments of the population (χ^2 test, $\alpha = 0.001$) showed that the proportions of reproductive (cystocarpic and tetrasporic) infected fronds were significantly different from the proportion of reproductive, non infected fronds. This indicated that there was an association between being reproductive and being infected by *Pleurocapsa* sp. (Figure 4), a trend which persisted throughout the year, with the exception of summer. Similar patterns were detected in the infections of *M. laminarioides* by *Endophyton* sp. (Figure 4).

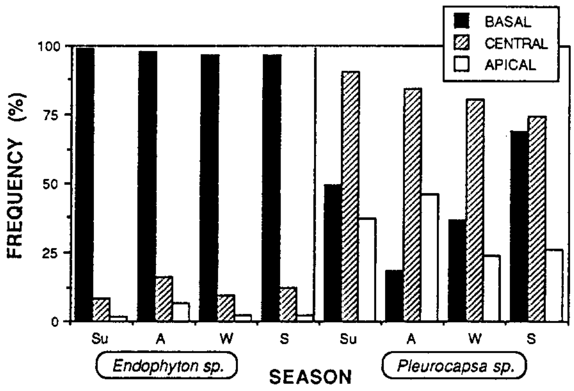

Figure 3. Spatial distribution of the infections by *Endophyton* sp and *Pleurocapsa* sp within the frond of *Mazzaella laminarioides*.

Considered on a yearly basis, the intensity index due to *Endophyton* sp. showed only minor fluctuations along the 150-m belt of *M. laminarioides* (Figure 5). Intensity index resulting from infections by *Pleurocapsa* sp., however, showed a clear increase in sectors 5 and 6 (Figure 5), the center and more protected section of the beach.

Discussion

Our results indicate that the infected status is common for individuals of *M. laminarioides* at Matanzas, and such a feature persists through the year. Furthermore it is important to consider that *Endophyton* sp. is the main pathogen responsible for the high infection rates. This pathogen, which causes the so called green patch disease, induces direct primary damage and also facilitates the entrance to secondary pathogens, like bacteria (Correa *et al.*, 1994). The degradative effects of the infection by *Endophyton* sp. are likely to debilitate the host tissues, making the fronds more susceptible to removal by wave action. The continuous wave impact on the weakened tissue may induce flaws on the thallus surface, an event that is quickly followed by fracture (Biedka et al.,1987; Denny, 1988; Denny *et al.*, 1989) and eventually results in the loss of the individual from the population. A similar argument was discussed regarding the association between *Acrochaete operculata* and *Chondrus crispus* (Correa & McLach-

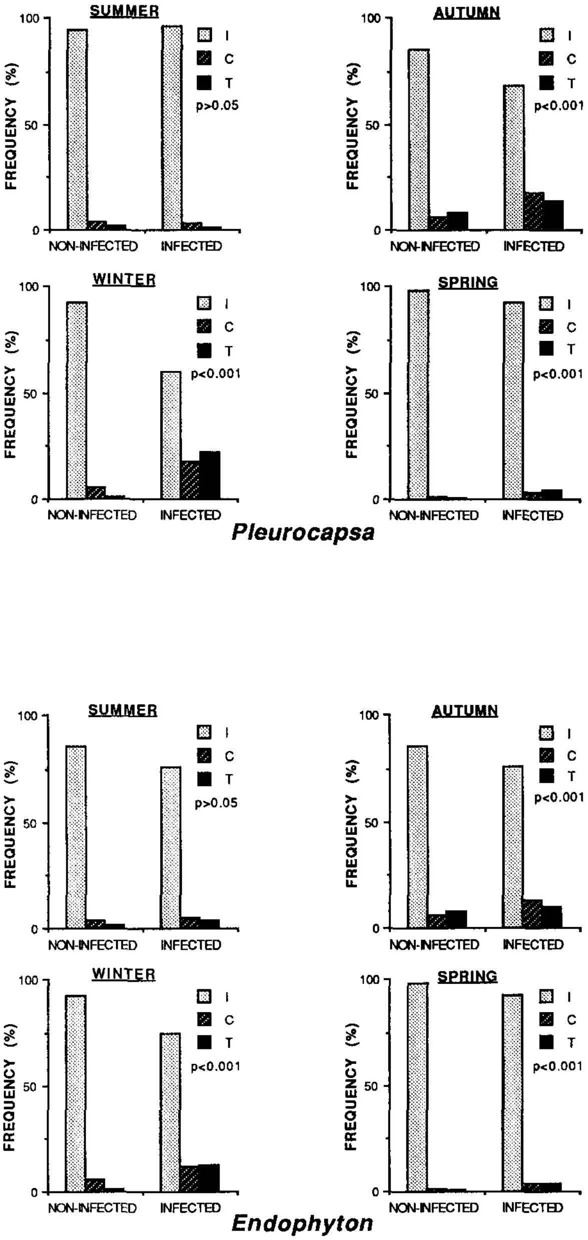

Figure 4. Reproductive status of the fronds in the infected and non-infected segments of the *Mazzaella laminarioides* population. I= non-reproductive, C= cystocarpic fronds, T= tetrasporic fronds. $p < 0.001$ indicates that the I-C-T ratios in the infected segment of the population is significantly different from the ratio in the non-infected segment.

lan, 1992). This pathogen causes damage to *C. crispus* (Correa & McLachlan, 1994) in an almost identical manner as *Endophyton* sp. does to *M. laminarioides* (Correa *et al.*, 1994). Field observations suggest that

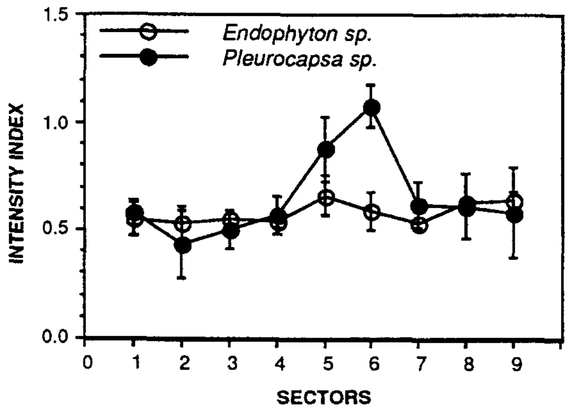

Figure 5. Infection intensities at the different sectors of the beach. Sectors are numbered from south to north.

the fracture of the fronds of *C. crispus* occurs at the central segment, where the infection is more frequent (Correa *et al.*, 1987), and not at the junction between stipe and holdfast which, according to McLachlan *et al.* (1989), is the weakest point. This is particularly relevant in the case of *M. laminarioides*, where *Endophyton* sp. clearly shows a preference by the basal part of the thallus which, in this algae, is the narrower and weakest point (Correa, pers. obs.).

The negative effect of the infections on *M. laminarioides* is further supported by the density data and by the intensity index. Infected fronds show a sharp and significant decline towards winter, which coincides with the time of the year when beaches are hit by winter storms. It seems clear that winter storms selectively remove the infected, weaker fronds because at the same time they are declining the non-infected component of the population begins its steady increase. Furthermore, the lowest intensity index during winter is the result of having individuals with overall low infection severity values, a situation which likely results from the removal of fronds with more severe infections. Preliminary experiments with tagged *M. laminarioides* showed that infected fronds were removed significantly faster than non-infected individuals (Correa *et al.*, unpublish.); these observations provide additional support to the above suggestions.

The deformative disease caused by *Pleurocasa* sp. is also present throughout the year. Its incidence, however, was minor in comparison with infections by *Endophyton* sp. The deformative disease results in severe alteration of the normal morphology and, as a result of the massive development of tumors, the smooth surface of the frond acquires a rough, sand paper-like texture (Correa *et al.*, 1992). Even though no tissue destruction was reported for this disease, tagging experiments similar to those performed with *Endophyton*-infected fronds suggest that tumor-deformed fronds of *M. laminarioides* are removed faster than normal fronds (Correa et al., unpublish.). Deformations and changes in the microtopography of the frond can be considered as features which could modify the biomechanical properties of any alga, particularly those inhabiting the intertidal zone (Koehl, 1986; Denny, 1988; Denny *et al.*, 1989; Carrington, 1990). The presence of papillae in *Mastocarpus papillatus* Kützing increased the drag values, although their relative importance in relation to other drag-modifying features remained unclear (Carrington, 1990). In the case of *M. laminarioides*, the potential direct negative effect of the tumors on hydrodynamics should be worsened by the deformations occurring in the frond as a whole. The lanceolate to fusiform shape of non-infected individuals contrasts with the stunted wrinkled and irregular morphology of the severely diseased individuals. Thus it is understandable that, as with *Endophyton* sp., the lowest frequency values were detected in winter, when drag forces are considerable higher, reaching up to 10–20 m s^{-1} (Denny, 1988). The lowest values of the intensity index in winter also suggest that the individuals with more severe infections, present in summer, are wiped-out during winter storms.

Although non-reproductive fronds are more frequently infected than reproductive ones, there are more diseased reproductive fronds than non-diseased reproductive fronds. This association between reproduction and infection is similar in the two diseases, but the meaning is not clear. One possibility is that spore release during reproduction of the host could expose the internal tissues, facilitating the entrance of the pathogens. However, *Endophyton* sp. and *Pleurocapsa* sp. are not found in direct spatial contact with either cystocarps or tetrasporangial sori (Correa *et al.*, 1993, 1994). An important aspect emerging from our data on the relationship between reproduction and infection is that both gametophytic and sporophytic fronds of *M. laminarioides* are susceptible to the infection by *Endophyton* sp and *Pleurocapsa* sp. This pattern differs from that reported for the *C. crispus-A. operculata* association, where the sporophytic phase was susceptible and severely damaged, whereas the gametophytic thallus was not (Correa & McLachlan, 1991, 1992, 1994). A direct effect of the infections on reproductive output has not being investigated, but qualitative observations suggest that full size, heavily diseased fronds (regardless of the pathogen involved), are rarely mature (Correa *et al.*, unpubl. obs.).

The spatial distribution of each pathogen within the population of *M. laminarioides* from Matanzas is different. Although both are presented along the whole 150-m beach, *Endophyton* sp. affects *M. laminarioides* more or less with the same intensity throughout the area. *Pleurocapsa* sp., on the other hand, affects mainly the individuals growing in the center of the beach. The reason for this spatial differential susceptibility is not known, although coincides with the part of the beach that is more protected from the direct wave action. This could be interpreted as two mutually exclusive alternatives. One is that genetic variability regarding susceptibility to diseases is expected within a population of any host (see Burdon & Leather, 1990) and therefore, a mosaic of susceptible and non-susceptible *M. laminarioides* may co-exist in the same area. The other is that susceptibility is the same throughout the population, and that in the center of the beach individuals last longer time because wave forces acting on them are less intense. Thus, the hosts would have more time to accumulate the effects (deformation, tissue destruction etc.) of the pathogen, which were detected by the intensity index. Transplant experiments, currently underway, will help us to elucidate this aspect of the relationship between *M. laminariodes* and its pathogens.

Mazzaella laminarioides is an economically valuable resource (Santelices & Norambuena, 1987; Avila & Seguel, 1993) with an additional ecological importance (Santelices, 1990; Gómez & Westermeier, 1991). Understanding the factors modulating reproduction, growth and mortality (among others) in this alga is an important challenge, not only to improve the management of exploited populations, but also for the future cultivation of this resource. In this context, understanding how infection diseases operate at a population level are the key for success. This is particularly true as the trend during cultivation is to generate artificial populations of genetically homogeneous organisms growing at high densities and, which is the ideal combination for pathogens to develop as epidemics (Correa & Craigie, 1991).

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