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INFECTIOUS DISEASES OF *MAZZAELLA LAMINARIOIDES* (RHODOPHYTA): CHANGES IN INFECTION PREVALENCE AND DISEASE EXPRESSION ASSOCIATED WITH SEASON, LOCALITY, AND WITHIN-SITE LOCATION[1]

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ABSTRACT

This study addresses the issues of infection prevalence and disease expression in two wild populations of the red algal host Mazzaella laminarioides *and their variability associated with locality, season, and spatial location of the host in the intertidal zone. Our results demonstrated that* Endophyton ramosum *is the most frequent infective pathogen affecting* M. laminarioides *in Matanzas and Pucatrihue. This situation prevailed through the year and across the high-to-low intertidal gradient. Although there was a general trend for lower levels of infection in late winter and early spring, only in a few cases was well-defined seasonality detected. Furthermore, clear seasonal patterns, as displayed by deformative disease in the high intertidal zone of Pucatrihue, were attenuated in the middle and lower intertidal zones. Differences in levels of infection in* M. laminarioides *between the high intertidal zones of Matanzas and Pucatrihue diminished toward the low intertidal zone. Thus, effects of seasonality and locality on infection prevalence may be influenced, at least in part, by the position of the hosts in the intertidal zone.*

Spatial distribution of the diseased individuals also varied along the beach. This pattern was consistent between the two sites and seemed related to wave exposure and the specific pathogen. Comparisons of the size distribution of noninfected fronds with their infected counterparts showed that infections by Endophyton ramosum *and* Pleurocapsa *sp. more frequently affected medium-and large-sized fronds. This pattern was consistent temporally and similar in the two localities. Finally, a clear association between maturity and prevalence of infection was detected. This association resulted in most fronds of the noninfected segment of the host population being immature, whereas most mature fronds were infected. In conclusion, infectious diseases affecting the red alga* Mazzaella laminarioides *are a persistent phenomenon in wild populations of the host, although only a small segment of the infected populations displays the full expression of the disease. In spite of the suggested role of factors such as season, latitude, and spatial location of the host on disease prevalence and expression, additional studies are needed to understand fully the dynamics of infectious diseases in wild populations of algal hosts.*

Key index words: infectious disease; Mazzaella; *prevalence.*

Several studies (i.e. Littler and Littler 1995, Correa 1996, Correa and Sánchez 1996) have indicated that information on ecological aspects of algal diseases in marine environments is scarce. Most prior studies have focused on the identification of the pathogens and characterization of the anatomical and physiological effects on their hosts. Examples of physiological studies include the reports on malformations of young sporophytes of *Laminaria japonica* Aresch. caused by H_2S-producing bacteria (Wu et al. 1983), diminished growth rates of *Chondrus crispus* Stackh. caused by endophytic algae (Correa and McLachlan 1992), bleaching and thallus decay associated with diminished growth rates in species of *Gracilaria* infected by pathogenic bacteria (Friedlander and Gunkel 1992, Weinberger et al. 1994), and detrimental effects on photosynthesis in *Feldmannia irregularis* (Kützing) Hamel and *F. simplex* (P. et H. Crouan) Hamel infected by virus (Robledo et al. 1994). The most recent reports on cellular and tissue changes in algae induced by invasive pathogens include the degradative lesions in *C. crispus* and *Mazzaella laminarioides* (Bory) Fredericq (formerly *Iridaea laminarioides* Bory) caused by algal endophytes (Correa and McLachlan 1994, Correa et al. 1994) and the severe digestion of *Gracilaria chilensis* Bird, McLachlan, & de Oliveira following invasion of the thallus by an endophytic amoeba (Correa and Flores 1995). A nondegradative disease characterized by frond deformation has been reported in wild populations of *M. laminarioides* infected by endophytic cyanobacteria (Correa et al. 1993). Earlier literature has been reviewed elsewhere (Andrews 1976, Goff 1983, Correa and Craigie 1992).

Even though the brief preceding information represents the traditional approach for studying infectious diseases, it seems unlikely that such informa-

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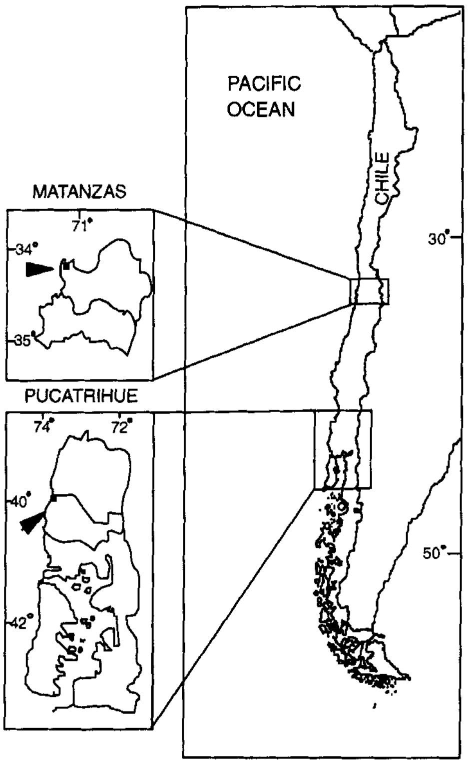

FIG. 1. Map of Chile with the geographical location of the study sites.

tion can be used to elucidate the role of pathogens on wild populations of algal hosts. In this context, information on epidemiological aspects of the diseases is a necessary first step in this process (Correa 1996, Correa and Sánchez 1996). However, epidemiological information regarding infectious diseases of algae is, today, almost nonexistent.

The objective of this study was to characterize the levels of infection, including temporal, spatial, and latitudinal fluctuations, of the two most common diseases affecting wild populations of the red algal host *Mazzaella laminarioides.* The deformative disease is caused by *Pleurocapsa* sp. (Cyanophyta), and it is characterized by the development of tumors, mainly in the central portion of the frond, which induce severe changes in the normal morphology (Correa et al. 1993). The green patch disease is caused by *Endophyton ramosum* Gardner (Chlorophyta), and it is characterized by a dark-green pigmentation of the basal part of the frond, accompanied by tissue softening in advanced infections. The green pigmentation results from massive proliferation of the endophyte within the tissues of the host (Correa et al. 1994).

METHODS

Study sites. Matanzas (Fig. 1; 33°58'S) is a small village located about 200 km southwest of Santiago. Although most of the beach is sandy, the southern part is characterized by rocky platforms and large boulders that are invaded seasonally by sand. During summer and early autumn, boulders tend to be covered by sand driven by wind and currents. Our observations indicate, however, that invasion by sand may vary greatly in intensity from year to year. Topographically, the rocky portion of the beach (ca. 150 m long) is naturally divided into three sections by rock formations oriented perpendicularly to the coastline and extending for about 20 m into the water. This topography leaves the central section more protected from the direct wave impact than the southern and northern sections.

The main intertidal algal species is *Mazzaella laminarioides,* which coexists with *Nothogenia fastigiata* (Bory) Parkinson, a red alga with a marked seasonal fluctuation in abundance. Other species, including *Gymnogongrus furcellatus* (C. Agardh) J. Agardh, *Gelidium lingulatum* Kützing, and *Ahnfeltia durvillaei* (Bory) J. Agardh appear only in the lower intertidal zone. None of these species have been recorded to develop the diseases that affect *M. laminarioides.*

Pucatrihue (Fig. 1; 40°33'S), the second study site, is located about 1000 km south of Santiago. It is a 200-m wave-exposed rocky beach characterized by platforms and ridges (75% of the beach length) and boulders (25% of the beach length). The platform area is exposed to strong wave action, particularly during winter storms, whereas the remaining section is more protected and typically contains coarse sand among the boulders. *Mazzaella laminarioides* monopolizes the primary space, although there are sectors where the rhodophycean *Trematocarpus dichotomus* Kützing and the chlorophycean *Ulva rigida* C. Agardh are also abundant.

Sampling. The *Mazzaella laminarioides* belt extends from 0.4 to 2.2 m above zero level (mean tide chart datum). The fringe occupied by *M. laminarioides* in each of the three beach sections in Matanzas was divided into high (1.6–2.2 m), middle (0.8–1.6 m), and low (0.4–0.8 m) subsections. Thus, Matanzas was divided into a grid of 9 sampling blocks (3 heights × 3 sections) covering an area of 1800 m^2. Within each block, 10 haphazardly placed quadrats of 25 cm^2 were used to remove all *Mazzaella laminarioides* fronds larger than 5 mm. Because of the characteristics of the symptoms, this approach did not induce a bias during the location of the quadrats. Samples from each quadrat were kept in individual, labeled plastic bags, taken to the laboratory within 4 h, and frozen at −20° C until microscopic analysis. For the analysis, 40 randomly chosen fronds were selected from each quadrat, and size, reproductive status, presence or absence of infections, position of the pathogen within the fronds, and severity of the infections were recorded.

A qualitative scale was used to assess severity of the infections. In the present analysis, a visual categorization of severity was done under the dissection microscope and restricted to the areas of the thallus known to manifest preferentially the symptoms of each disease (i.e. target areas): the narrow stipe in the case of infections by *Endophyton ramosum* and the lamina in infections by *Pleurocapsa* sp. A low severity of infection was considered to be cases when 10% or less of the target area was occupied by either *E. ramosum* or *Pleurocapsa* sp. At this low level, only initial stages of infection by the two pathogens were recognized. An intermediate level of infection was scored when individuals displayed 10–70% of any target area colonized by either pathogen. Usually, the typical symptoms of each disease (full disease expression; see Correa et al. 1993, 1994) were seen at this level of infection, particularly when the surface of the host tissue that was colonized by the pathogens approached the upper limit. A high level of infection was scored when 70% or more of the surface of the target area consisted of heavily diseased tissue.

The sampling procedure in Pucatrihue was identical to that in Matanzas. However, the former beach is longer (ca. 200 m) than Matanzas, resulting in the division of the beach into four sections and a grid of 12 sampling blocks (4 sections × 3 tidal heights). As in Matanzas, the limits of each section coincided with high rock formations oriented toward the sea.

The sampling period extended from March 1994 to March 1995. Each site was visited bimonthly with simultaneous sampling at Matanzas and Pucatrihue. Each visit resulted in the analysis of 3600 fronds from Matanzas and 4800 from Pucatrihue, with a total of 25,200 and 33,600 fronds, respectively, for the entire sampling period.

Statistics. All data were tested for an appropriate fulfillment of

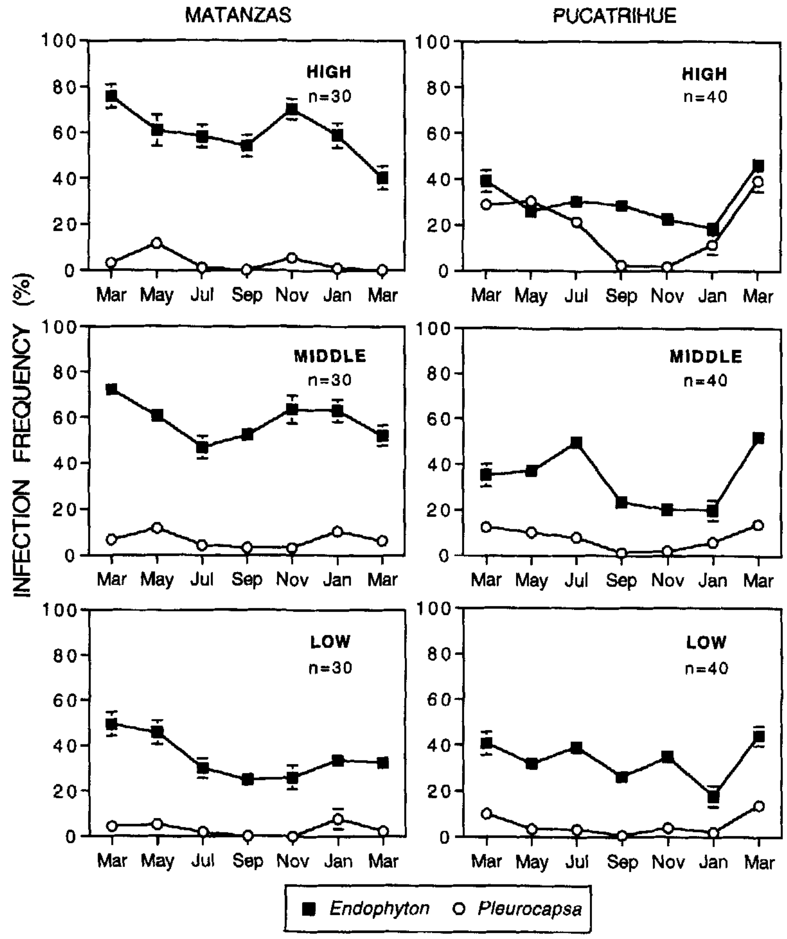

FIG. 2. Infection levels (mean ± 1 SE) of the two most common pathogens of *Mazzaella laminarioides* in Pucatrihue and Matanzas. Mean values represent the average of 30 and 40 quadrats (i.e. 10 in each section of the beach) from Matanzas and Pucatrihue, respectively. High, middle, and low indicate the relative position of the sampling blocks across the intertidal zone.

the requirements for ANOVA, and arcsin transformations were made when needed. Analyses included one- and two-way ANOVAs with Tukey HSD *a posteriori* multiple comparisons, the nonparametric Kolmogorov-Smirnov test for size–infection relationships, and chi-square for reproductive status–infection relationships (Sokal and Rohlf 1981). Computations were done in SYSTAT version 5.2 for Macintosh.

RESULTS

Infections by *Endophyton ramosum* were most frequent within the population of *Mazzaella laminarioides* from Matanzas (Fig. 2). This pattern was consistent throughout the year and various intertidal heights, and interaction between the two factors was not significant (Table 1). Intertidal height had a significant effect (Table 1) on the infection frequency by *E. ramosum*, which ranged from 40 to 75% in the high intertidal zone to 31 to 50% in the lower intertidal zone (Fig. 2). Frequency of infection decreased significantly toward July–September (late winter–early spring), although the persistence of lower levels of infection by *E. ramosum* varied according to the tidal height. The levels of infection during March 1994 varied from 75% in the high intertidal zone to 50% in the lower intertidal zone, whereas during March 1995 values fluctuated from 40% in the high intertidal zone to 31% in the low intertidal zone (Fig. 2).

In Pucatrihue, infections by *Endophyton ramosum* were also more common than those by *Pleurocapsa* sp. (Fig. 2). The frequency of infection by *E. ramosum* at this site was not significantly affected by intertidal height, and November–January showed lower levels of infection (Fig. 2, Table 1). Interaction between time of the year and intertidal height was significant (Table 1), indicating that infection frequency differed from one month to the other depending on elevation.

The frequency of infection by *Pleurocapsa* sp. in the population of *Mazzaella laminarioides* from Matanzas was significantly influenced by both intertidal height and time of the year (Fig. 2, Table 1). Whereas *Pleurocapsa* infections remained detectable throughout the year in the middle intertidal zone, they became rare at various times in the high and low intertidal zones (Fig. 2). Regardless of the above fluctuations, infections by *Pleurocapsa* sp. were much more restricted than those by *Endophyton ramosum*,

TABLE 1. *Effects of the relative spatial position (i.e. elevation) of the fronds in a tidal gradient (high, middle, and low) and time of year, on frequency of infection by* Endophyton ramosum *and* Pleurocapsa *sp.*

		Endophyton				*Pleurocapsa*			
		Matanzas		Pucatrihue		Matanzas		Pucatrihue	
Source	df	F	P	F	P	F	P	F	P
Elevation	2	61.1	$0.9 \cdot 10^{-15}$	0.33	0.72	7.7	$0.5 \cdot 10^{-3}$	89.3	$0.9 \cdot 10^{-15}$
Time	6	8.7	$0.4 \cdot 10^{-8}$	38.2	$0.99 \cdot 10^{-15}$	7.2	$0.2 \cdot 10^{-6}$	42.6	$0.9 \cdot 10^{-15}$
Elevation × time	12	1.7	$0.6 \cdot 10^{-1}$	5.1	$0.3 \cdot 10^{-7}$	1.3	$2 \cdot 10^{-1}$	8.2	$0.8 \cdot 10^{-14}$

with estimated mean values never higher than 18% of the host population (Fig. 2). Infections by the same pathogen in Pucatrihue were also affected significantly by time and tidal height (Fig. 2, Table 1). Furthermore, the interaction between tidal height and time of the year was statistically significant, indicating that monthly variations in infection frequency were modified by elevation. Seasonality was clear in the high intertidal zone of Pucatrihue, with the lowest values occurring during September and November (Fig. 2). This pattern became attenuated toward the middle and lower intertidal zones (Fig. 2).

Within the infected segment of the host population from Matanzas, the severity of the infections by *Endophyton ramosum* was low (Fig. 3). This pattern was consistent throughout the year and at the different intertidal heights. Terminal infections (i.e. high severity) were found in only a minor portion of the infected population, although they were present all year. With the exception of May (high intertidal zone) and January (low intertidal zone), *Pleurocapsa* sp. infections in most fronds were of low severity (Fig. 3). The frequency of fronds highly infected by *Pleurocapsa* varied erratically through the year and among tidal heights. The situation in Pucatrihue was similar for both diseases, although highly infected fronds were rare, regardless of the infecting organism (Fig. 3).

The spatial distribution of the diseased fronds varied depending on the pathogen and the site under consideration (Fig. 4, Table 2). For example, considering the annual mean values of infection for each section of the beach, the central section of Matanzas had a significantly higher frequency of infections by *Pleurocapsa* sp. than the southern and northern sections for the same pathogen (Fig. 4). In the same site, however, no significant differences among sections were found in fronds affected by the green patch disease (Fig. 4). In Pucatrihue, annual mean values of infection by *Pleurocapsa* sp. did not vary significantly among sections 1, 2 and 3, but decreased significantly in section 4 (Fig. 4, Table 2). *Endophyton ramosum,* however, infected significantly fewer fronds in section 3 than in the others (Table 2).

Most of the noninfected *Mazzaella laminarioides* fronds (usually 70% or more) were 4 cm or smaller

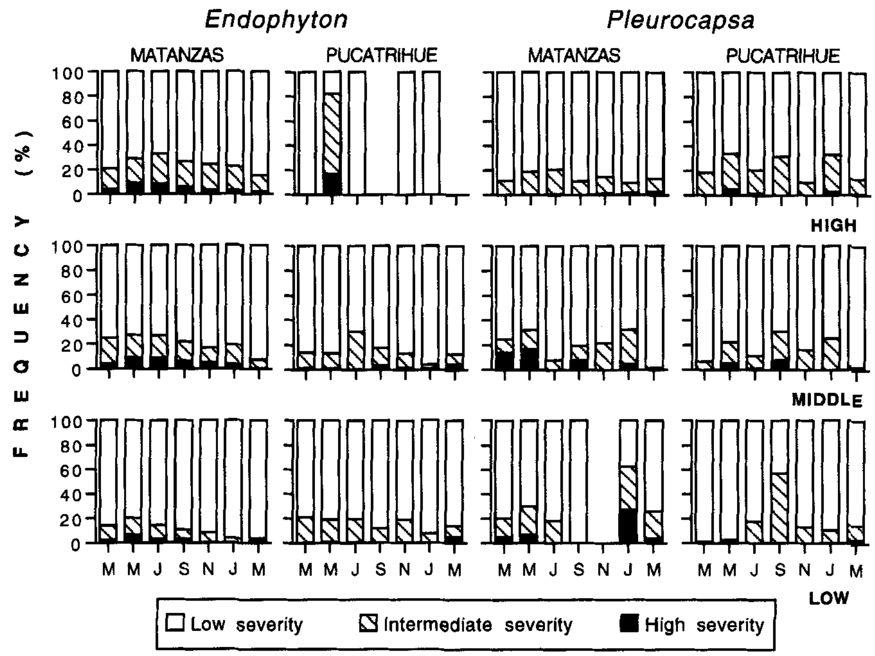

FIG. 3. Disease severity in *Mazzaella laminarioides* from Matanzas and Pucatrihue, expressed as frequency of each category within the infected segment of the two host populations.

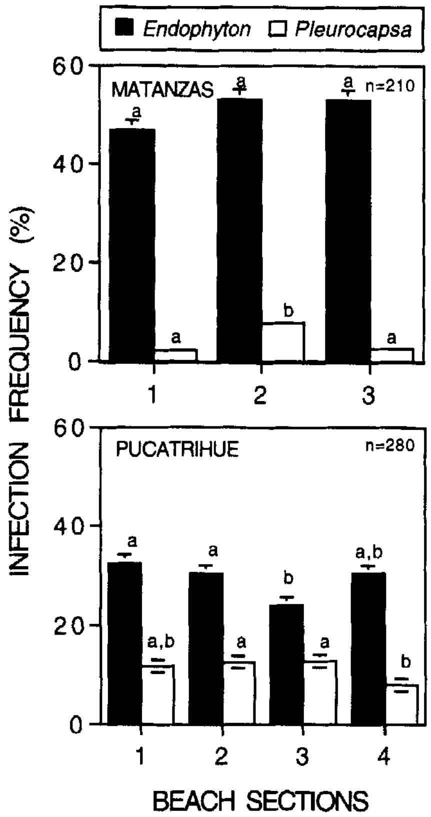

FIG. 4. Spatial distribution of *Endophyton ramosum* and *Pleurocapsa* sp. Sections 2 (Matanzas) and 1–3 (Pucatrihue) are protected areas. Different small letters on the bars indicate statistically significant differences (Tukey, $P \leq 0.05$). All heights and times within each beach section were pooled; no significant interactions between beach sections and tidal heights were found.

(Fig. 5). This pattern was consistent throughout the year in Matanzas and Pucatrihue (Fig. 5). The size distribution of diseased fronds, on the other hand, varied in shape according to site, time of the year, and the species of pathogen involved (Fig. 5). These differences between the noninfected and infected segments of each host population were all significant, regardless of the time of the year, pathogen, or site (Fig. 5; Kolmogorov-Smirnov test, $\alpha = 0.05$). In general, both the green patch disease and deformative disease appeared to affect medium- and large-size fronds preferentially. This trend was more evident in infections by *Pleurocapsa* sp., particularly in *M. laminarioides* from Pucatrihue. Whereas most infections by *Endophyton ramosum* at Pucatrihue were in the 2–8-cm segment, they were concentrated in the 0–4-cm segment of the population at Matanzas (Fig. 5). Size classes of *M. laminarioides* $\geq$4 cm were composed mainly of infected individuals.

Immature fronds of *Mazzaella laminarioides* from both Matanzas and Pucatrihue most frequently lacked infection (Fig. 6). The same pattern was observed in the segments of the two populations infected by either *Endophyton ramosum* or *Pleurocapsa* sp. (Fig. 6). However, the ratio of immature to mature fronds decreased significantly in the infected portion of both populations (Table 3), indicating an association between infection and maturity. The highest values for mature, infected fronds were detected from July to November in Matanzas and Pucatrihue (Fig. 6).

DISCUSSION

This study demonstrates that infections by pathogenic organisms are a persistent phenomenon in wild populations of *Mazzaella laminarioides*; infections by either *Endophyton ramosum* or *Pleurocapsa* sp. affect at least 40% of the host population at Matanzas and 20% at Pucatrihue. Maximum values, on the other hand, exceeded 60 and 40% of the populations at Matanzas and Pucatrihue, respectively. With the exception of a recent report by Littler and Littler (1995) and previous reports from our laboratory (Correa et al. 1993, Correa and Sánchez 1996), no epidemiological information on any algal disease is available, making comparative analyses impossible.

Correa et al. (1993) characterized the macro- and microscopic features of the deformative disease of

TABLE 2. *Effect of the beach sections on the frequency of infection by* Endophyton ramosum *and* Pleurocapsa *sp.* F *values from one-way ANOVA are followed by a matrix of pairwise comparison probabilities (Tukey HSD multiple comparison test).*

Endophyton				*Pleurocapsa*			
Matanzas		Pucatrihue		Matanzas		Pucatrihue	
F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
2.7	0.067	4.2	0.006	21.8	0.001	4.2	0.006

Tukey HDS multiple comparison test

	Endophyton Pucatrihue section				*Pleurocapsa* Matanzas section			*Pleurocapsa* Pucatrihue section			
Section	1	2	3	4	1	2	3	1	2	3	4
1	—				—			—			
2	0.958	—			$0.21 \cdot 10^{-4}$	—		0.999	—		
3	0.006	0.029	—		0.751	$0.22 \cdot 10^{-4}$	—	0.824	0.887	—	
4	0.751	0.960	0.106	—				0.066	0.046	0.004	—

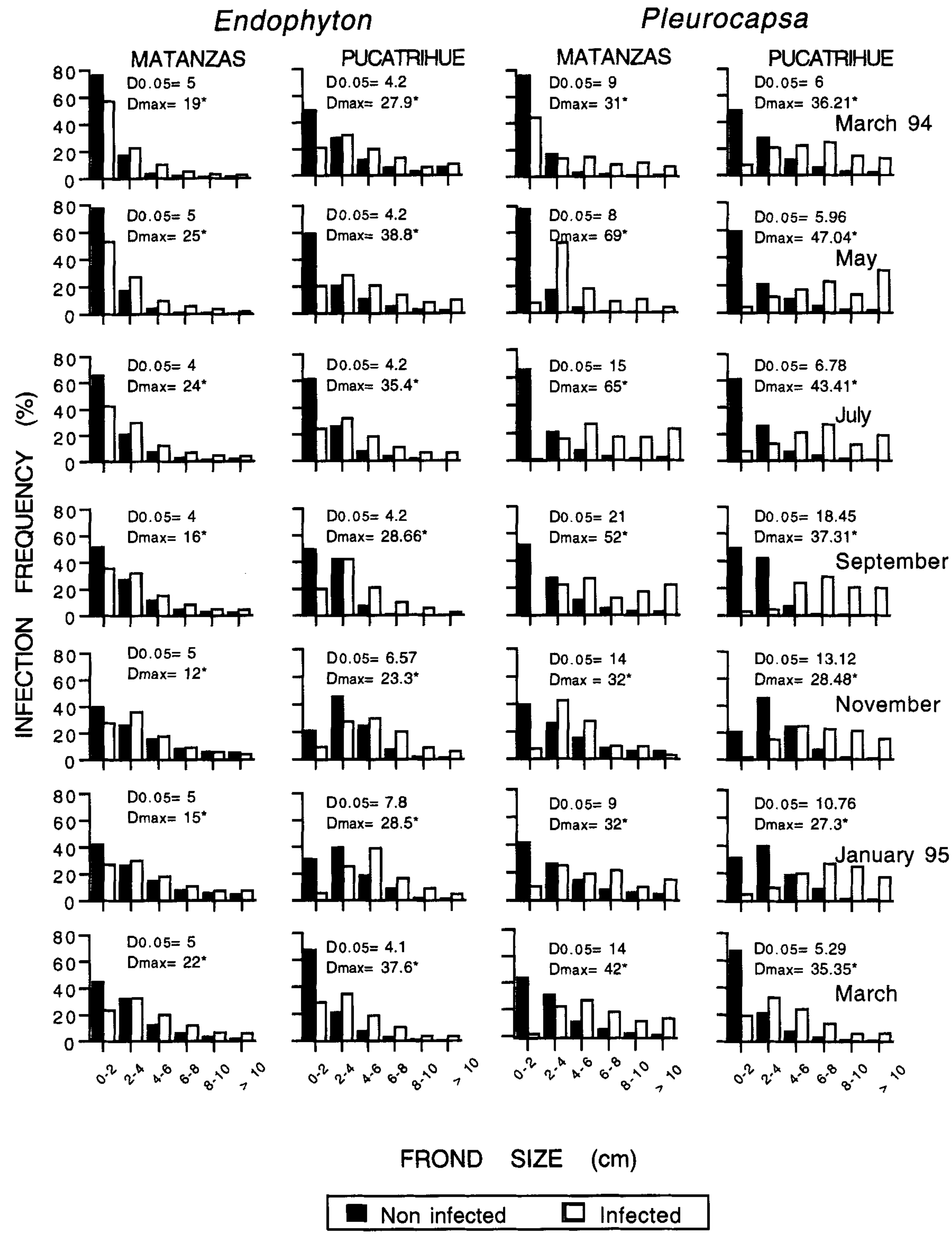

FIG. 5. Size distribution of infected and uninfected fronds of *Mazzaella laminarioides*. $D_{0.05}$ and D_{max} represent the critical difference (α = 0.05) and maximum unsigned difference for the Kolmogorov-Smirnov test, respectively.

Mazzaella laminarioides, providing the first quantitative account on ecological aspects of an infectious algal disease. Those results were part of a 1-year (1992) monitoring program restricted to the host population at Matanzas. It did not include information on the green patch disease, a much more common pathology affecting *M. laminarioides* throughout its geographic distribution (Correa et al. 1994). More recently, epidemiological information for the two diseases, even though restricted to Matanzas, was integrated by Correa and Sánchez (1996), who used the 1992 data base to characterize

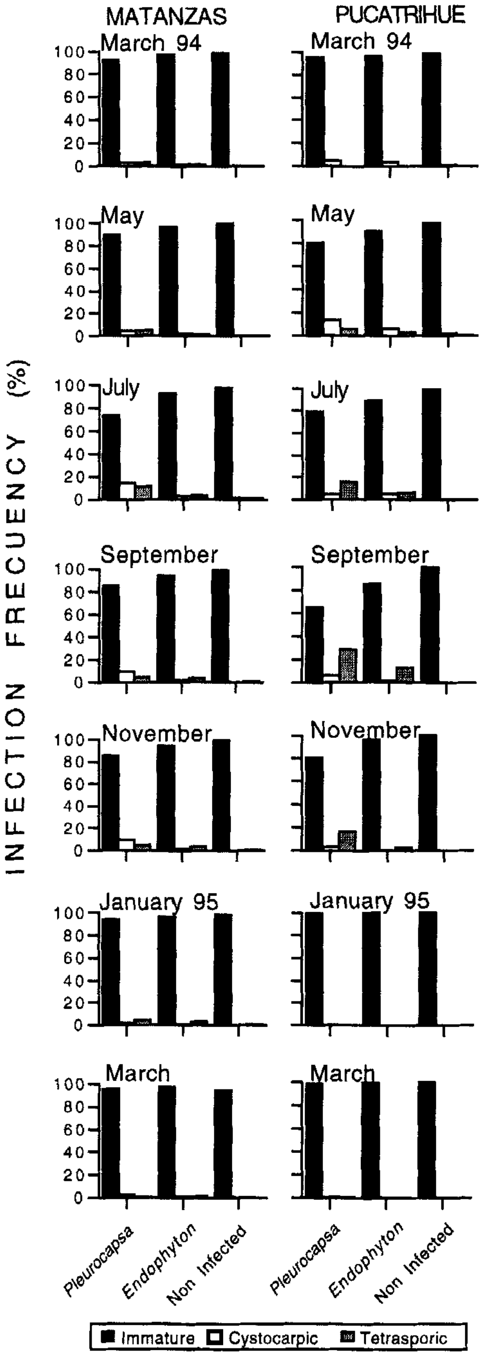

FIG. 6. Infection frequency vs. reproductive status of *Mazzaella laminarioides.*

disease seasonality, location of the lesions within the host, and the relationship between host reproductive status and infection.

Comparisons between results of the 1992 (Correa and Sánchez 1996) and the 1994–1995 (this study) monitoring programs revealed the persistence of some epidemiological features in the host population at Matanzas. Similarities between these monitoring periods include the high prevalence of infections by *Endophyton ramosum* throughout the year

TABLE 3. *Chi-square analysis designed to test the hypothesis that mature fronds have an incidence of infection higher than expected at random, given their frequency in the population. Values represent calculated* χ^2*s values for the differences in immature-to-mature ratios between infected and noninfected segments of the* Mazzaella laminarioides *from Matanzas and Pucatrihue.* *P ≤ 0.05.

	Endophyton		*Pleurocapsa*	
	Matanzas	Pucatrihue	Matanzas	Pucatrihue
March 94	76*	62*	399*	53*
May	749*	717*	7599*	11,016*
July	303*	2732*	6257*	11,685*
September	812*	115,610*	19,276*	846,088*
November	20*	4555*	331*	145,292*
January 95	114*	26*	312*	1029*
March	185*	7*	270*	14,575*

and the relatively low prevalence of *Pleurocapsa* infections, which tend to be even less prevalent during winter. The more or less homogeneous pattern of spatial distribution of hosts infected by *E. ramosum* and the highly localized distribution of thalli infected by *Pleurocapsa* sp. (features first reported for the 1992 monitoring program [Correa and Sánchez 1996]) were also evident in the present study. Finally, the association between host maturity and infection appeared as yet another persistent characteristic of the infectious diseases of *Mazzaella laminarioides.*

Endophyton ramosum, the causative agent of the green patch disease, remains the main infective organism of *Mazzaella laminarioides.* This was consistent not only for Matanzas during the two monitoring periods but also for Pucatrihue. However, the clear seasonality displayed by *E. ramosum* in 1992 (Correa and Sánchez 1996) was not apparent in the present study, suggesting that infection prevalence varies from year to year. This observation is further supported by our own results showing that levels of infections by *E. ramosum* in Matanzas during March 1994 were consistently higher (i.e. at high, middle, and low intertidal) than those recorded during March 1995. Similar erratic responses have been detected in terrestrial plant pathosystems, where results indicate that environmental stochasticity may lead to considerable fluctuations in disease frequency among years (Kaltz and Schmid 1995).

In spite of the high prevalence of infection in wild populations of the host, only a small percentage of the infected individuals appeared to be terminally diseased. Combined prevalence of infection and expression of disease have not been directly included in the few epidemiological studies on algal diseases (see Correa and Sánchez 1996), even though such an approach may shed some light on the dynamics of the diseases at the host population level. According to the classification system used in this study, intermediate and high levels of disease were characterized by a full disease expression; they differed only in the extent to which the host was affected. Theoretically (see Harper 1990), a low frequency of individuals with full disease expression may result from a long-standing relationship that has evolved a balance characterized by a low virulence of the pathogens (i.e. low progression rate from initial infection to full expression of symptoms). This condition would allow the co-existence of host and pathogens in such a way that only a minor segment of the host population is terminally diseased. The genetic constraints involved in such a relationship have been discussed in the context of plant (Harper 1990) and algal (Correa 1996) pathology. An alternative explanation is that pathogens are highly virulent and a full expression of the disease modifies the overall performance of the affected individuals such that they are lost from the population (i.e. by wave action) much faster than individuals with low levels of infection. Although the resulting prevalences may be similar, the impact on the host population is quite different. In the first case the number of individuals lost due to the disease is low, whereas in the second case the number is likely to be large. Algal thalli with terminal symptoms like tissue softening and decay in the green patch disease of *M. laminarioides* (Correa et al. 1994) and in the degradative disease of *Chondrus crispus* (Correa and McLachlan 1992, 1994), as well as frond deformations caused by *Pleurocapsa* sp. (Correa et al. 1993), represent individuals that are particularly susceptible to dislodgment by wave action. Modifications of the biomechanical properties of the normal algal tissues (i.e. elasticity, strength, and drag, among others; see Denny 1988) caused by either necrosis or deformations may trigger dislodgment of the thallus. Our recent experimental studies show that full expression of a disease decreases host survivorship (unpubl. data), and they support the hypothesis of faster and selective removal of those individuals from the population. In spite of the preceding, there is a need for more research to understand the dynamics of disease at the population level in *M. laminarioides*.

Latitude may have important effects on infection prevalence and disease expression in the two pathologies affecting *Mazzaella laminarioides*. Short-term fluctuations in infections by *Endophyton ramosum*, expected in association with seasonal changes in physical parameters, appeared to be influenced by latitude. In Matanzas the lowest values were recorded in early spring, whereas in Pucatrihue equivalent values appeared during summer (January). These fluctuations are likely to be the result of extended wintery climatic conditions, characteristic of the southern part of the country. Regarding disease expression, even though fronds displaying terminal symptoms (i.e. high infection severity status) caused by *E. ramosum* infections represented a low proportion of the infected population at Matanzas, they persisted throughout the year. Furthermore, the other two infection categories were also present year-round. In Pucatrihue, on the other hand, terminally diseased individuals were exceedingly rare regardless of the time of the year and, at times, individuals belonging to the low and intermediate categories of infection occurred at frequencies too low to be detected. The typically low, overall prevalence displayed by *Pleurocapsa* infections also may be partially related to latitude. In Matanzas prevalence was rarely more than 10% of the host population, whereas in the high intertidal zone of Pucatrihue the *Pleurocapsa*-infected fronds surpassed 20% from March to July 1994 and March 1995. As with *E. ramosum*, the frequency of severely diseased individuals (i.e. those with terminal symptoms) was clearly lower in Pucatrihue than in Matanzas. In spite of the preceding, the effects of latitude on disease prevalence should be considered a hypothesis, as only two localities were included in the present study. That the Pucatrihue population is less susceptible to the diseases caused by *E. ramosum* and *Pleurocapsa* sp. cannot be fully ruled out. However, it seems unrealistic as transplant experiments (unpubl. data) have shown that susceptibility is similar in the two populations. Furthermore, susceptibility was mainly related to the spatial location of the host within the beach.

The concentration of *Pleurocapsa*-infected fronds in the central section of Matanzas was noted during the 1992 program (Correa and Sánchez 1996) and was confirmed by the present study. Similarly, this pathogen was concentrated in sections 1–3 in Pucatrihue. Although the actual causes of this particular pattern of spatial distribution remain to be elucidated, protection from direct wave impact appears as the common factor at both Matanzas and Pucatrihue. It is interesting that in a period of 2.5 years no significant changes occurred in the patterns of within-site spatial distribution of diseased individuals. This information suggests that the deformative disease is not expanding in Matanzas, in spite of the apparently high rate of infection by *Pleurocapsa* in field experiments (unpubl. data), where several hundred noninfected thalli transplanted to the central section of the beach became visually infected in 1–2 months and fully diseased in 4–6 months. A clear case of an expanding infectious disease in the Great Astrolabe Reef (Fiji) was reported recently by Littler and Littler (1995), who showed how the lethal coralline orange disease increased from 0% in 1992 to 100% in 1993.

The infection pattern in the different size segments of *Mazzaella laminarioides* varied between the two sites and with the species of pathogen involved. Whereas most fronds infected by *Endophyton ramosum* in Matanzas were small, the profile in Pucatrihue was skewed toward larger sizes. A similar pattern was observed with *Pleurocapsa* sp., although in this case there was a higher proportion of large fronds infected by *Pleurocapsa* sp. than by *E. ramosum*. This aspect of the host–pathogen interaction was not discussed in our previous studies (Correa et al. 1993, Correa and Sánchez 1996). The preceding information, however, indicates that the infected segment of the population develops as the result of spore colonization of the host, as suggested by Correa et al. (1993), and not by regeneration of infected thalli.

The association between infection and frond maturity was also a persistent feature in the two host populations, and it did not vary from that found in 1992 (Correa and Sánchez 1996). Given the patterns of development of the disease within the frond and the impact upon their target tissues (Correa et al. 1993, 1994), it is unlikely that the association between maturity and infection is directly facilitated by reproductive events in the host. Neither the initial invasion by the pathogens nor the subsequent lesions of the two diseases are in direct spatial contact with cystocarps and tetrasporangial sori. Age, considered as the permanence of individuals in the system, accompanied by a possible overall physiological weakening due to energy investments in reproduction, is an alternative explanation for the preceding relationship.

In conclusion, infectious diseases affecting the red alga *Mazzaella laminarioides* are a persistent phenomenon in wild populations of the host, although only a small segment of the infected populations display the full expression of the disease. Fully diseased fronds are usually medium to large in size. Seasonality in disease prevalence, although slightly erratic through time, is also influenced by location of the host within each site and possibly by latitude. Mature fronds are associated with higher frequencies of infection, although no cause–effect relationship has been established. Both diseases displayed a different spatial distribution within the beach (i.e. patchy vs. evenly distributed; see also Correa and Sánchez 1996), suggesting differential responses to the various microenvironments within each site.

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Andrews, J. H. 1976. The pathology of marine algae. *Biol. Rev.* 51:211–53.

Correa, J. A. 1997. Infectious diseases of marine algae: current knowledge and approaches. *In* Round, F. E. & Chapman, D. J. [Eds.] *Progress in Phycological Research,* Biopress Ltd., Bristol, Vol. 12 (in press).

Correa, J. A. & Craigie, J. S. 1991. Algal pathology. *In* García-Reina, G. & Pedersén, M. [Eds.] *Proceedings of the COST-48 Workshop. Seaweed Cellular Biotechnology, Physiology and Intensive Cultivation.* Universidad de Las Palmas de Gran Canaria, Las Palmas, pp. 67–82.

Correa, J. A. & Flores, V. 1995. Whitening thallus decay and fragmentation in *Gracilaria chilensis* associated with an endophytic amoeba. *J. Appl. Phycol.* 7:421–5.

Correa, J. A., Flores, V. & Garrido, J. 1994. Green patch disease in *Iridaea laminarioides* (Rhodophyta) caused by *Endophyton* sp. (Chlorophyta). *Dis. Aquat. Org.* 19:203–13.

Correa, J. A., Flores, V. & Sánchez, P. 1993. Deformative disease in *Iridaea laminarioides* (Rhodophyta): gall development associated with an endophytic cyanobacterium. *J. Phycol.* 29: 853–60.

Correa, J. A. & McLachlan, J. L. 1992. Endophytic algae of *Chondrus crispus* (Rhodophyta). IV. Effects on the host following infections by *Acrochaete operculata* and *A. heteroclada* (Chlorophyta). *Mar. Ecol. Prog. Ser.* 81:73–87.

——— 1994. Endophytic algae of *Chondrus crispus* (Rhodophyta). V. Fine structure of the infection by *Acrochaete operculata* (Chlorophyta). *Eur. J. Phycol.* 29:33–47.

Correa, J. A. & Sánchez, P. 1996. Ecological aspects of algal infectious diseases. *Hydrobiologia* 326/327:89–95.

Denny, M. W. 1988. *Biology and the Mechanics of the Wave-Swept Environment.* Princeton University Press, New Jersey, 329 pp.

Friedlander, M. & Gunkel, W. 1992. Factors leading to thallus disintegration and the control of these factors in *Gracilaria* sp. *In* Moav, B., Hilge, V. & Rosenthal, H. [Eds.] *Proceedings of the 4th German–Israeli Status Seminar,* EAS Special Publication, pp. 221–43.

Goff, L. J. 1983. Marine algal interactions: epibiosis, endobiosis, parasitism and diseases. *In* Tseng, C. K. [Ed.] *Proceedings of the Joint China–U.S. Phycology Symposium.* Science Press, Beijing, pp. 221–74.

Harper, J. L. 1990. Pests, pathogens and plant communities: an introduction. *In* Burdon J. J. & Leather S. R. [Eds.] *Pests, pathogens and plant communities.* Blackwell Scientific Publications, Oxford, pp. 3–14.

Kaltz, O. & Schmid, B. 1995. Plant venereal disease: a model for integrating genetics, ecology and epidemiology. *Trends Ecol. Evol.* 10:221–2.

Littler, M. & Littler, D. 1995. Impact of CLOD pathogen on Pacific coral reefs. *Science* 267:1356–60.

Robledo, D. R., Sosa, P. A., García-Reina, G. & Müller, D. G. 1994. Photosynthetic performance of healthy and virus-infected *Feldmannia irregularis* and *F. simplex* (Phaeophyceae). *Eur. J. Phycol.* 29:247–51.

Sánchez, P., Correa, J. A. & García-Reina, G. 1996. Host-specificity of *Endophyton ramosum* (Chlorophyta), the causative agent of the green patch disease in *Mazzaella laminarioides* (Rhodophyta). *Eur. J. Phycol.* 31:173–9.

Sokal, R. R. & Rohlf, F. J. 1981. *Biometry,* 2nd ed. W. H. Freeman, New York, 859 pp.

Weinberger, F., Friedlander, M. & Gunkel, W. 1994. A bacterial facultative parasite of *Gracilaria conferta. Dis. Aquat. Org.* 18: 135–41.

Wu, C. Y., Chen, D. & Li, J. 1983. On the diseases of cultivated *Laminaria japonica. In* Tseng, C. K. [Ed.] *Proceedings of the Joint China–U.S. Phycology Symposium.* Science Press, Beijing, pp. 211–20.