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Sinking rates and viability of spores from benthic algae in central Chile

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Abstract: Spore-sinking rates and viability were studied in 12 species of benthic macroalgae from the intertidal zone in central Chile: two Chlorophyta, *Enteromorpha intestinalis* (L.) Link and *Ulva rigida* C. Ag.; one Phaeophyta, *Lessonia nigrescens* Bory; nine Rhodophyta, *Ahnfeltia durvillaei* (Bory) J. Ag., *A. gigartinoides* J. Ag., *Gelidium chilense* (Mont.) Santelices et Montalva, *G. lingulatum* J. Ag., *Gymnogongrus furcellatus* (*C. Ag.*) J. Ag., *Iridaea ciliata* Kütz, *I. laminarioides* Bory, *Nothogenia fastigiata* (Bory) Park., and *Porphyra columbina* Mont. In still water, interspecific differences in sinking rates were found. Whereas *E. intestinalis* swarmers remained near the water surface, suggesting a low sinking rate, concentration of spores gradually decreased in all other species. After 2–5 h, the percentage of spores that remained near the surface, varied between 80% in *A. gigartinoides* and 20% in *I. ciliata*. The sinking rate of spores measuring <15 μm in diameter was significantly lower than that of spores >15 μm ($P<0.01$). Sinking rate of spores under continuous water stirring was tested for spore suspensions of *I. laminarioides* and *P. columbina*. Spores remained suspended near the water surface for >12 h but their concentration decreased to $<50\%$ of the initial value after 24 h. Differences in spore-germination capacity and viability were observed among species. *A. durvillaei*, *G. furcellatus*, *N. fastigiata*, and *P. columbina* seem to have seasonal fluctuations in germination capacity. Spores were viable from 4 to 11 days, depending on the species. Characteristics of the spores might influence their dispersal potential and, in some species, be related to the life-history strategies of the algae.

Key words: Dispersal; Germination; Intertidal; Seaweed; Sinking rate; Spore

INTRODUCTION

The distances at which spores of benthic macroalgae are dispersed away from parent plants depend on the water motion, the time spores remain in suspension before settling, and the time they remain viable (Hoffmann, 1987). Although algal spores are extremely small in relation to the magnitude of water movements, and it could be thought that they are stirred away by water, some evidences indicate that there are interspecific differences in dispersal that could be due to intrinsic properties of spores. It has been proposed that the rate at which spores sink, is related to their size, density, motility, and the presence of a mucilage sheath (Coon et al., 1972; Boney, 1975; Amsler & Searles, 1980; Norton, 1981; Okuda & Neushul, 1981; Waaland & Dickson, 1983). Sinking rates are different when spores are released singly or as aggregates (Pollock, 1969; Coon et al., 1972;

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Neushul, 1972; Moss, 1974; Oza, 1975; Boney, 1975) and sedimentation rates might be related to the life-history strategies of the species (Amsler & Searles, 1980; Hoffmann & Ugarte, 1985).

Spore viability is an important factor in algal dispersal. The scarce studies devoted to this subject indicate that spores usually survive only for a few days (Suto, 1950; Kain, 1964). It has been reported, however, that spores of *Enteromorpha* could survive up to 8 days (Jones & Babb, 1968).

The aim of this study was: (a) to determine the sedimentation patterns of benthic macroalgal spores; (b) to evaluate temporal changes in the germination capacity of spores and; (c) to relate these findings to spore size and motility, as well as to life-history strategies of the species.

Materials and Methods

Samples of 12 species of intertidal macroalgae were collected at several sites along the Chilean central coast (33°35′ to 33°56′ S) from 1986 through 1987 (see Table I). Samples were brought to the laboratory in plastic buckets. Fertile thalli were sorted, washed in tapwater and placed overnight in dishes filled with sterile seawater at 15 °C. On the next day, thalli were discarded and the spore suspension was diluted to 3000–5000 spores · ml^{-1} and divided into two parts, one for sedimentation-rate studies (Spore Suspension 1) and one for viability tests (Spore Suspension 2).

To determine sedimentation rates, Spore Suspensions 1 were placed in 800-ml beakers. Spore Suspensions 1 of *Iridaea laminarioides* and *Porphyra columbina* were divided into two parts. One was kept in still water and the other was kept under continuous stirring on a rotatory shaker (Junior Orbit Lab-Line) at 150 rpm. This speed was enough to prevent immediate and fast spore sedimentation. Spore Suspensions 1 of all other species tested were kept in still water. 15-ml samples were obtained near the surface of the spore suspensions kept in 800-ml beakers and the number of spores in each sample was determined with a Coulter counter (Model A). Five measurements were made on each sample. In spore suspensions kept in still water, samples were taken every 15 min. Samples were taken for 4–5 h in preliminary experiments but afterwards they were restricted to 2.5 h because differences in sinking rates became indistinct after that time. In spore suspensions that were stirred, samples were taken at 1-h intervals for 4 h in one experiment and once every 12 h in another experiment. Results were expressed as spore concentration (in percentage) as compared with the initial spore numbers. In *Lessonia nigrescens*, and occasionally in *I. laminarioides* and *P. columbina*, some spores were included in mucilage conglomerates. These mucilage masses had to be discarded so as not to affect the Coulter countings.

To evaluate the time spores remain viable, daily samples of Suspension 2 were taken during 5–11 days, depending on the presence of spores in the suspensions. In preliminary experiments, Suspensions 2 also were divided into two parts, one was kept under

continuous stirring with a magnetic agitator (Corning PC 353; speed at 4.5 rpm) and the other was kept in still water. Since results showed no differences in germination percentages at either condition, spore suspensions thereafter were maintained under stirring to prevent sedimentation. 5-ml samples of the Suspensions 2 were placed in each of two 60 × 20 Petri dishes added with 5 ml SWM_3 (McLachlan, 1973) and incubated in culture chambers (Lab-Line) at 15 °C, 12-h photoperiod, and a photon-flux density of 20–30 $\mu mol \cdot m^{-2} \cdot s^{-1}$. The number of spores that settled was counted in each culture dish after 5 days on 12 fields at random. Results were expressed as the number of settled spores $\cdot cm^{-2}$. Germination percentage was determined 5–10 days later by counting the number of germlings $\cdot cm^{-2}$. Cultures were examined every other day but no important mortality was detected. In any case, > 90% germination was recorded for several species, suggesting that spore mortality (which would result in underestimation of germination values) was negligible. Results were expressed as percentage of germinated spores in relation to the number of settled spores. Whenever feasible, experiments were repeated at least twice for each species and results represent average values.

To determine seasonal variations in spore germination, spore samples were periodically incubated under the same conditions described above. Spores were distributed in four to five Petri dishes that were considered as replicates. Germination percentages were established after 10 days and results were expressed as average values. Our data were complemented with those available in the current literature.

Calculations were done in a VAX 8600 computer. Results were tested by correlation analysis and a simple and factorial ANOVA, after arcsine transformation of the data. Interactions were tested using Tukey's a posteriori test (Sokal & Rohlf, 1981)

RESULTS

SIZE

Spores of 12 species of macroalgae were obtained: two chlorophytes, one phaeophyte and nine rhodophytes (Table I). Spore diameter ranged from 4 to 29 μm. Spores obtained from the red algal species were, in general, of smaller diameter than the size ranges reported by Ngan & Price (1979). The diameter of spores varied slightly within the same species and the greatest variations were found in spores of *Gelidium lingulatum* (Table I).

SINKING RATE

Concentration of spores near the surface remained almost constant through 4.5 h in spore suspensions of *I. laminarioides* and *P. columbina* kept under stirring (Fig. 1). Thereafter, the concentration of spores decreased until reaching values of ≈ 40% of the initial value after 24 h. After 108 h (4.5 days), spores of *I. laminarioides* almost had disappeared from the surface whereas ≈ 18% of *P. columbina* spores still were present (Fig. 2).

Spores tented to sink faster in still water but some interspecific differences were apparent. Whereas spores of *Enteromorpha intestinalis*, *Ahnfeltia gigartinoides*, *A. durvillaei*, *Ulva rigida*, *Nothogenia fastigiata*, *L. nigrescens*, and *P. columbina* remained initially near the water surface, those of *G. lingulatum*, *I. laminarioides*, and *I. ciliata* (carpospores and tetraspores) sank at faster rates. These differences in settling patterns were noticeable after the first 15 min and were clearly evident between 75 and 135 min (Fig. 3).

TABLE I

Species included in study. Spore type and diameter and life strategy of species. C, carpospores; S, swarmers; T, tetraspores; Z, zoospores. Values represent averages of 150–200 measurements. SE, standard error. Life-history strategies after Littler & Littler (1980) and Santelices et al. (1983).

Species	Spore type	Diameter (μm)	SE	Life-history strategy
Ahnfeltia durvillaei (Bory) J. Agardh	C	10.40	0.13	S
A. gigartinoides J. Agardh	C	11.75	0.15	S
Enteromorpha intestinalis (L.) Link	S	5.23	0.11	0
Gelidium chilense (Montagne) Santelices et Montalva	C	28.93	0.56	S
G. lingulatum J. Agardh	C	23.84	1.21	S
Gymnogongrus furcellatus (C. Agardh) J. Agardh	C	11.26	0.14	S
Iridaea ciliata Kützing	C	22.88	0.36	S
Iridaea ciliata Kützing	T	20.00	0.73	S
Iridaea laminarioides Bory	C	24.94	0.35	S
Lessonia nigrescens Bory	Z	5.74	0.09	S
Nothogenia fastigiata (Bory) Parkinson	C	4.14	0.19	S
Porphyra columbina Montague	C	10.96	0.12	0
Ulva rigida C. Agardh	Z	9.91	0.55	0

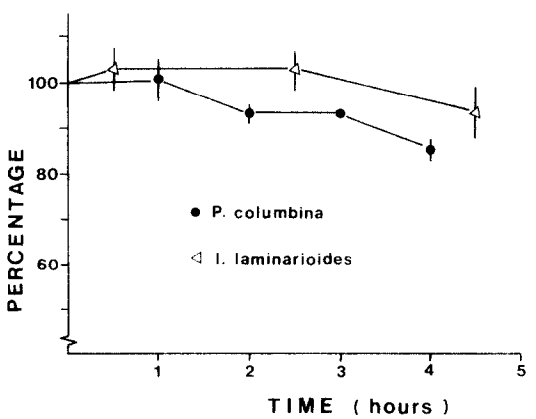

Fig. 1. Sedimentation of *I. laminarioides* and *P. columbina* spores in stirred suspensions through 4.5 h. Expressed are changes in spore concentration (in percentage) as compared with initial values. Each point corresponds to average of five measurements. Vertical bars represent 1 SE.

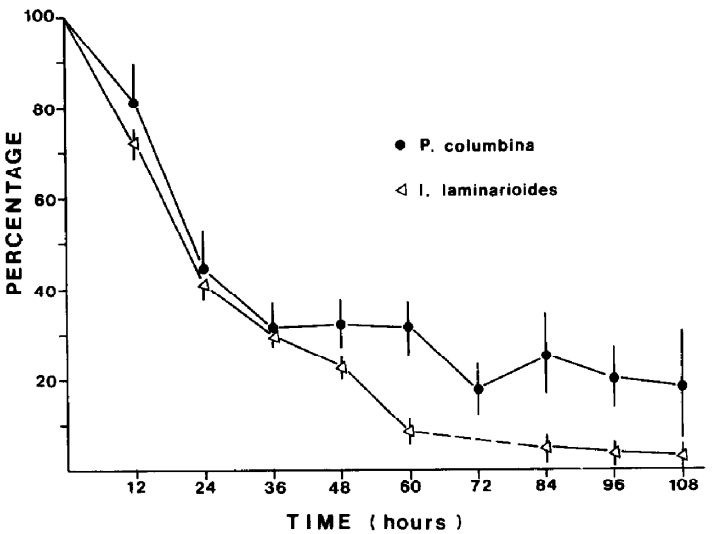

Fig. 2. Sedimentation curves of *I. laminarioides* and *P. columbina* spores in unstirred suspensions through 108 h. Each point same as in Fig. 1.

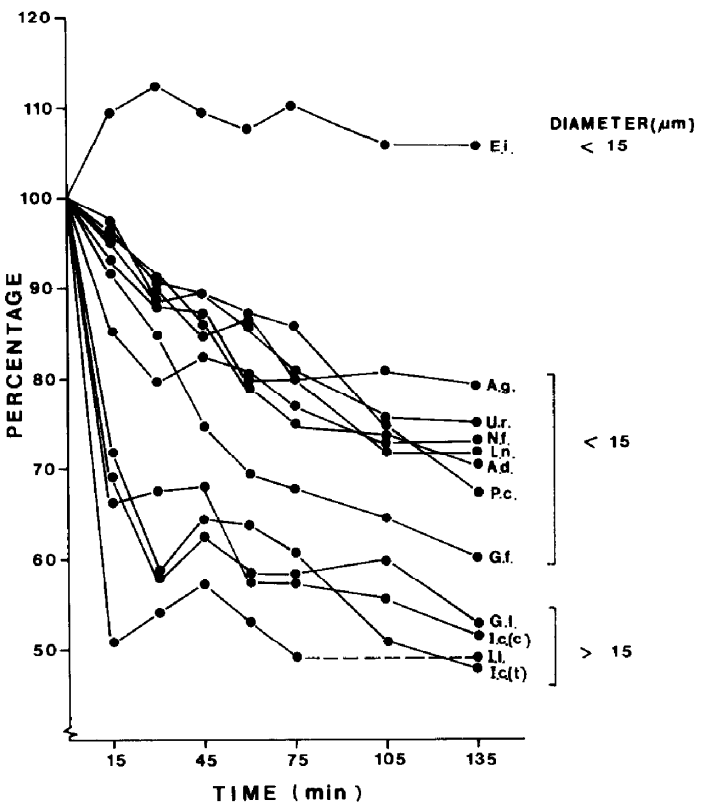

Fig. 3. Sedimentation curves of macroalgal spores in unstirred water. A.d., *A. durvillaei*; A.g., *A. gigartinoides*; E.i., *E. intestinalis*; G.l., *G. lingulatum*; G.f., *G. furcellatus*; I.c.(c), *I. ciliata* (carpospores); I.c.(t), *I. ciliata* (tetraspores); I.l., *I. laminarioides*; L.n., *N. nigrescens*; N.f., *N. fastigiata*, P.c., *P. columbina*; U.r., *U. rigida*. Each point same as in Fig. 1.

Spore diameter and sinking rate are apparently related: small spores tended to sink more slowly than larger spores, with a statistically significant correlation (Pearson $r = 0.82$, $P < 0.01$). Moreover, the sinking rate of spores < 15 μm in diameter was significantly lower than that of spores over that size ($P < 0.01$).

Motility also seemed to influence sinking rates although interspecific differences were apparent. Swarmers of *E. intestinalis* remained near the water surface throughout the experiment, the concentration of spores near the surface rose slightly over the initial values after the first 15 min and remained almost constant which suggested a very low sinking rate. In contrast, swarmers of *L. nigrescens* and *U. rigida* had higher sinking rates.

In all the other species, the concentration of spores at the surface gradually decreased. At the end of the experiment, the proportion of spores that remained near the surface of the water column, varied between 80% of the initial value, in *A. gigartinoides*, and $< 50\%$, in *I. ciliata*.

VIABILITY

Spore-germination capacity and time of survival were tested in 10 species of macroalgae. Initial germination varied according to species, from almost 100% in *Gymnogongrus furcellatus*, *L. nigrescens*, and *U. rigida*, to only 40% in *N. fastigiata* (Fig. 4).

Germination capacity of spores of all species decreased through successive days of the experiment (Fig. 4). In some species, $< 30\%$ of the spores germinated in samples taken 4 days after starting experiments. Such was the case in *E. intestinalis*, *A. durvillaei*, *G. furcellatus*, and *N. fastigiata*. No relation appeared to exist between initial germination and spore survival: while initial germination was almost 100% in *G. furcellatus*, it was 40–60% in *N. fastigiata* and *E. intestinalis* and only 30% in *A. durvillaei*.

In other species, $> 30\%$ of spores still germinated in samples taken > 4 days after starting the experiment. Although the proportions of viable spores gradually decreased, 60% of *U. rigida* spores were viable after 6 days and 10–20% of those of *G. chilense* and *P. columbina* still germinated in samples taken after 11 days.

Differences in germination percentages between the first and last day were significant in all species ($P < 0.001$). No differences were detected in the germination patterns of opportunistic and successional species and no relation could be established between viability, spore size and life history strategy.

On the other hand, the available data suggest that in several species, e.g., *A. durvillaei*, *G. furcellatus*, *N. fastigiata*, and *P. columbina*, germination capacity of spores undergoes seasonal fluctuations (Table II).

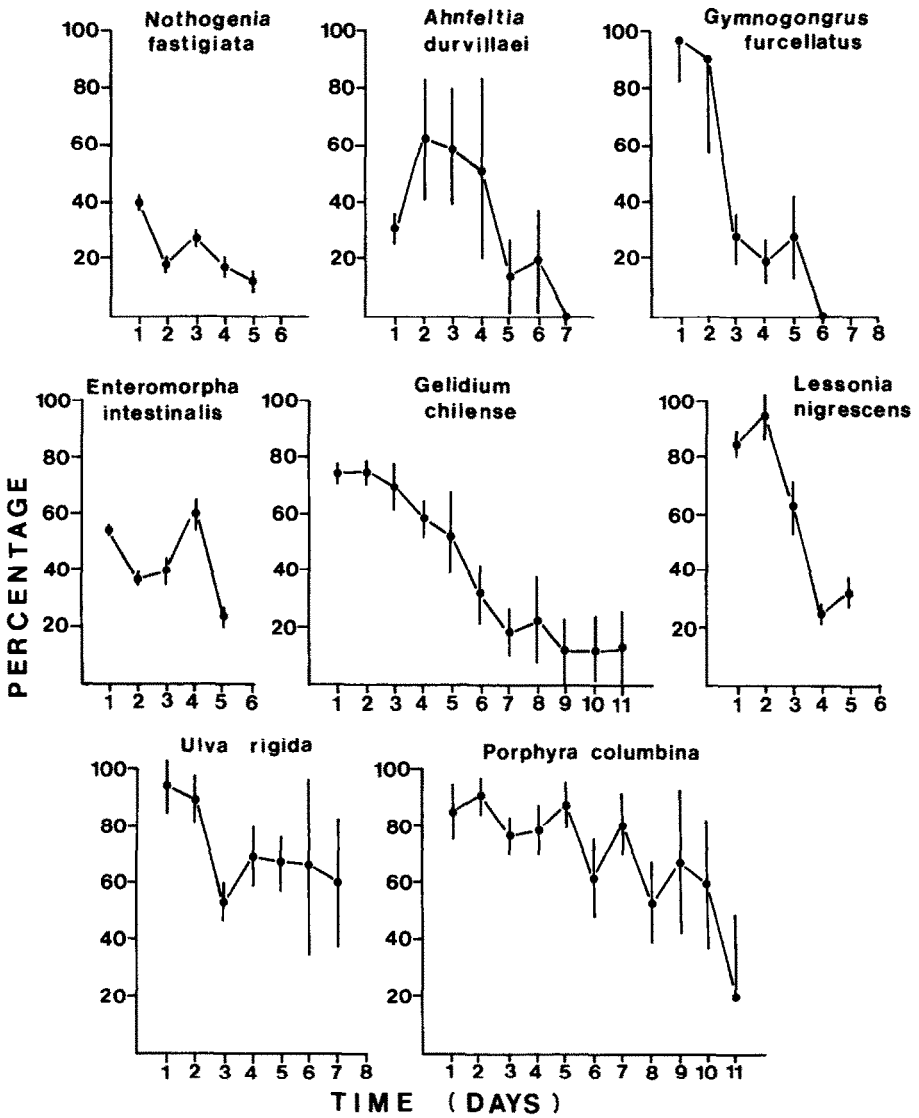

Fig. 4. Germination of spores of benthic algae. Daily samples of spore suspensions were taken. Values represent percentages of settled spores that germinated in each sample at Day 14.

TABLE II

Spore germination percentages and their seasonal variations. Values obtained during present study correspond to Day 1 samples, those marked with an asterisk are same as shown in Fig. 4. Remaining values were obtained from references in literature. C, carpospores; S, swarmers; T, tetraspores; Z, zoospores; SE, standard error.

Species	Spore type	Month	Germination (%)	SE	Source
Ahnfeltia durvillaei	C	July	51.2	8.0	This paper
Ahnfeltia durvillaei	C	May	*29.9	6.4	This paper
Enteromorpha intestinalis	S	July	*54.2	1.0	This paper
Gelidium chilense	C	July	*74.6	1.7	This paper
Gelidium chilense	T	July	50–70		Correa et al. (1985)
Gelidium chilense	T	November	50–70		Correa et al. (1985)
Gymnogongrus furcellatus	C	July	62.4	10.2	This paper
Gymnogongrus furcellatus	C	May	*96.6	15.6	This paper
Iridaea laminarioides	C & T	August	35		Luxoro (1987)
Iridaea laminarioides	C & T	March	90		Luxoro (1987)
Iridaea laminarioides	C & T	April	0		This paper
Lessonia nigrescens	Z	September	95		Hoffmann et al. (1984)
Lessonia nigrescens	Z	November	90		Avila et al. (1985)
Lessonia nigrescens	Z	April	*94.7	4.4	This paper
Nothogenia fastigiata	C	December	*38.8	2.2	This paper
Nothogenia fastigiata	C	April	90		Ramírez (unpubl. data)
Porphyra columbina	C	June	15		Seguel & Santelices (unpubl. data)
Porphyra columbina	C	September	2		Seguel & Santelices (unpubl. data)
Porphyra columbina	C	March	3.6	1.8	This paper
Porphyra columbina	C	May	46.7	18.6	This paper
Porphyra columbina	C	July	*84.7	9.5	This paper
Porphyra columbina	C	Sept	16.1	–	This paper
Ulva rigida	Z	July	*94.5	9.0	This paper

DISCUSSION

Sinking rates of spores apparently are different in moving water vs. in a still water column. In water constantly stirred, spores tend to stay near the surface and spore sinking is slow, irrespective of size. For instance, spores of *I. laminarioides* and *P. columbina* showed similar sinking rates although those of the former are double the diameter of the latter. In still water, the sinking rate of spores appeared to be related to their diameter. Thus our results confirm earlier findings, that showed (with a different technique) that small spores tend to settle more slowly than larger ones (Okuda & Neushul, 1981). This fact might influence the arrival of spores of both generations at the substratum in species with carpospores and tetraspores of different sizes.

On the other hand, motility and phototaxis may influence significantly the sinking rates of propagules. *E. intestinalis* swarmers showed a very low sinking rate and their

sinking pattern was rather different compared with that of the rest of the species studied. Concentration on the surface increased after 15 min and remained high throughout the experiment. This could be due both to the marked motility of the swarmers in this species (Christie & Evans, 1962) and to positive phototactism. Positive phototactism of swarmers suggests that they could have been gametes. The ability to maintain a high position in the water column could contribute to extend their dispersal range. Swarmers of *E. intestinalis* were found in surface-water samples in North Carolina, 35 km away from the nearest sizable population (Amsler & Searles, 1980), and it was the only species recorded at an off-shore site in the Gulf of Maine (Zechman & Mathieson, 1985). Jones & Babb (1968) found that the positively phototactic swarmers in this species are motile for up to 8 days but in our tests swarmers of *E. intestinalis* presented a marked decrease in germination capacity after 5 days which would be at variance both with their life-history strategy and their allegedly large dispersal capacity.

Although zoospores of *U. rigida* have been reported to be positively phototactic when released, they show a reversal and become negative after a few hours (Smith, 1947). In turn, there is no evidence of phototactism in zoospores of *L. nigrescens*. Within the Laminariales, the only genus having zoospores with an eyespot is *Chorda* (Bold & Wynne, 1985) and random swimming has been reported for zoospores of other phaeophytes, e.g., *Macrocystis* (Lobban et al., 1985). The sedimentation patterns of *L. nigrescens* and *U. rigida* zoospores suggested that they depended more on size than on motility.

Some species showed higher sinking rates of spores so that 50% of the spores had disappeared from the water surface after 2.5 h. Our results suggest some relationship between sinking rates and life history strategies. We found that, whereas the group with small spores and low sinking rates were both opportunistic (e.g., *P. columbina*, *U. rigida*) and late successional species (e.g., *A. durvillaei*, *N. fastigiata*), the group with larger spores ($>15\ \mu m$) and higher sinking rates consisted exclusively of late successional species. It has been proposed that ephemeral opportunistic species are characterized by large dispersal shadows whereas perennial long-lived species would have smaller dispersal shadows (Amsler & Searles, 1980). However, in a study of the composition and abundance of macroalgal propagules arriving at the intertidal zone, Hoffmann & Ugarte (1985) found evidence suggesting that some late successional algae had large dispersal shadows. Our present results support the idea that the spores of not only opportunistic but also of some late successional algal species have slow sinking rates and remain near the water surface for longer periods which would increase their potential for dispersal.

The influence of the mucilage layer on sinking rates has not been analyzed in the present study although it may be significant. As Okuda & Neushul (1981) point out, the sinking rate might change as mucilage is released from the cell. Spore aggregations within mucilage occasionally were observed in *I. laminarioides*, *L. nigrescens*, and *P. columbina*. Aggregated spores probably sink faster than single spores (Coon et al., 1972) but in some species, like *Rhodymenia pertusa*, spores are included in mucilage

"strips" or "skeins" that drift away gradually shedding spores, thus prolonging their pelagic phase (Boney, 1978). Species with both fast- and slow-sinking spores would have larger dispersal shadows.

Marked differences in germination capacity were observed between species, with no relation between germination capacity and life-history strategies. Unfortunately, there are scarce references in the literature about the germination capacity of the study species. In the case of *P. columbina*, our values of spore germination were almost 6-fold higher than those reported by Seguel & Santelices (unpubl. data). This may be attributed to the different methods employed. In *G. furcellatus*, higher germination was found in fall than in winter which is consistent with the finding that in natural populations of species spore production decreases progressively from fall to winter (Santelices & Camus, unpubl. data). Spores of *I. laminarioides* also showed higher germination percentages in fall than in winter (Luxoro, 1987) but no spores germinated through three successive tests performed in our study though they retained their adhesion ability for 10 days.

Species also are markedly different as to the length of time their spores remain viable. Our results suggest that spores of algal species could survive longer than reported in earlier studies (Suto, 1950; Kain, 1964). *U. rigida* spores were viable for >6 days and those of *G. chilense* and *P. columbina* retained their germination capacity for ≈ 10 days. Although *G. chilense* is a late successional species, its behaviour confirms findings of Hoffmann & Ugarte (1985) showing that this species would have a large dispersal shadow. Spores of *A. durvillaei*, *G. furcellatus*, and *N. fastigiata*, all late successional species, retain only scarce viability after 5 days. *L. nigrescens* spores begin to germinate 24 h after adherence to the substratum (Hoffmann & Santelices, 1982) but in our samples spores lost almost 70% of their germination capacity after 5 days in suspension. These spores are small and motile and sink slowly but, because of their limited spore survival, the dispersal shadow of this late successional perennial species is probably small.

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