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Banks of microscopic forms and survival to darkness of propagules and microscopic stages of macroalgae

Bancos de formas microscópicas y supervivencia a la oscuridad de propágulos y formas microscópicas de macroalgas

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ABSTRACT

Previous studies have found that the number of species conforming a bank of microscopic forms in tide pools in central Chile accounted only for half the number of species present in the macroscopic vegetation around the pools. An elemental condition for survival in these banks is the ability of microscopic forms to tolerate darkness or very low irradiances for extended periods. To test this ability, spores of 17 green, brown and red algal species, present and absent from the bank, were incubated at different combinations of irradiances and day lengths. Propagules of 47 % of the species tested (eight species) germinated in total darkness while the propagules of the other nine species germinated under conditions of very low irradiance (2-10 μmol $m^{-2} s^{-1}$). In most species, microforms showed a higher tolerance to darkness than the propagules. Some survived for over a year and one species (*Gelidium lingulatum*) could live under complete darkness for 500 days. The ability to survive in total darkness did not relate to presence or absence of a species in the banks of microscopic forms previously studied, to phylogenetic relatedness, life history style, propagule size, morphology of microscopic forms or to successional status (fugitive versus late successional). Thus, tolerance to darkness appears to be common to propagules and microscopic stages of most benthic algae. The growth patterns exhibited by the microforms of *Lessonia nigrescens*, *Chaetomorpha firma* and *Glossophora kunthii* suggest high irradiances on these recruits might determine the shallower limits of distribution of these species.

Key words: benthic algae, dark tolerance, germination, growth, microscopic forms.

RESUMEN

Estudios previos han encontrado que el número de especies formando un banco de formas microscópicas en pozas de mareas de Chile central incluyó sólo la mitad del número de especies presentes en la vegetación macroscópica en las cercanías de las pozas intermareales. Una primera condición para sobrevivir en estos bancos radica en la capacidad de las formas microscópicas para tolerar oscuridad total o baja iluminación por períodos prolongados. Para evaluar dicha capacidad, los propágulos de 17 especies de algas verdes, pardas y rojas, presentes y ausentes del banco de formas microscópicas fueron incubadas a distintas combinaciones de intensidad luminosa y fotoperíodo. Propágulos del 47 % de las especies evaluadas (ocho especies) germinaron en oscuridad mientras que los propágulos de las otras nueve especies requirieron valores muy bajos de intensidad luminosa (2-10 μmol $m^{-2} s^{-1}$) para germinar. En una mayoría de las especies, las formas microscópicas mostraron una mayor tolerancia a la oscuridad que los propágulos. Algunos sobrevivieron en la oscuridad por sobre un año y una especie (*Gelidium lingulatum*) pudo sobrevivir en oscuridad absoluta por 500 días. La habilidad para sobrevivir en oscuridad total no se relaciona con presencia de la especie en los bancos de formas microscópicas, con grupos filogenéticos o con historias de vida específicas, con tamaño de propágulo, morfología de la forma microscópica o estatus sucesional (especies fugitivas versus sucesionales tardías). Por lo tanto, tolerancia a la oscuridad aparece como un patrón común a propágulos y formas microscópicas de una mayoría de algas bentónicas. Los patrones de crecimiento exhibidos por las formas microscópicas de *Lessonia nigrescens*, *Chaetomorpha firma* y *Glossophora kunthii* sugiere que el efecto de altas intensidades luminosas sobre estos reclutas podría determinar los límites superiores de distribución vertical de estas especies.

Palabras clave: algas bentónicas, crecimiento, germinación, formas microscópicas, tolerancia a la oscuridad.

INTRODUCTION

Rocky intertidal and shallow subtidal habitats often contain collections of microscopic algal forms that under adequate environmental conditions would eventually develop into macroalgal vegetation. These “banks of microscopic forms” (sensu Chapman 1986) are expected to be most

common in disturbed habitats (Santelices 1990), including environments with high rates of substratum turn-over or high grazing pressure.

Recent experimental studies on the bank of microscopic forms suggest that in various habitats these microforms may determine the presence of the macroscopic vegetation (e.g., *Macrocystis, Desmarestia,* Graham 1996, Ladah et al. 1999, Edwards 2000), enhance seasonal recruitment (Edwards 2000), determine interspecific differences in population dynamics (Lotze et al. 1999, 2000, Lotze & Schramm 2000, Worm et al. 2000) and, together with grazers, even determine the capacity of some of these systems to use anthropogenic nutrient loading (Worm et al. 2000).

While characterizing an assemblage of microscopic forms in tide pools from central Chile, Santelices et al. (1995) found that the 25 species conforming the bank amounted only to half the number of species present in the macroscopic vegetation around the bank. The unrepresented species could be missing from the bank because they have not arrived to the bank or because they lack the physiological capacity to survive in these banks. A first condition necessary for survival in the banks relates to the ability of these microscopic forms to tolerate darkness or dim light for extended periods. Propagules and microscopic forms of Laminariales and a few red and green algae have been found to be able to survive in darkness or in very dim light (Burrows 1958, Kain 1964, Neushul & Dahl 1964, Chapman & Burrows 1970, Lünning 1980, Schonbeck & Norton 1980, Hay & Norris 1984, Reed et al. 1992, tom Dieck 1993, Leukart & Lünning 1994, Schories 1995). However, it is unknown whether this capacity is general to all types of microscopic forms of macroalgae. Therefore, in this study we first evaluate the ability of seaweed propagules to germinate and of microforms to survive in darkness, comparing such a response in species represented with that of species unrepresented in the banks of microscopic forms described for tide pools in central Chile.

In some species (e.g., *Macrocystis pyrifera* Graham 1996) the sensitivity of microforms to high levels of irradiance may determine the upper vertical limits of the macroforms distribution on the shore. Therefore, in this study we also evaluate the sensitivity of the microscopic forms to various light levels by measuring growth patterns of algal microforms under controlled laboratory conditions of light intensity and photoperiod.

Little is known about the dynamics of microforms or the types of seaweeds for which a bank of microscopic forms might provide greater survivorship of the species (see review by Hoffmann & Santelices 1991). Among land plants, early successional pioneering species usually contribute to seed banks more than late successional species (Harper 1977, Grime 1979, Leck et al. 1989). Therefore, we also investigated: if differences in the duration of survival are related to the successional position of the species, if responses are related to the life history of the species, if microforms of similar morphologies have similar responses, and if different responses of microforms are related to the species phylogenetic position (e.g., Phaeophyta, Chlorophyta, Rhodophyta).

MATERIAL AND METHODS

Habitat characteristics

All algal samples were collected at Los Molles (32°46' S, 71°33' W) in central Chile between April and December 1997. In that locality, daylength fluctuates from 10.5 h in June (austral winter) to 16 h in December (austral summer). Average surface water temperature ranges from 12.5 °C in August to 15 °C in January (Prado & Sievers 1987, Santelices 1991). Irradiance values measured at rocky surfaces vary from 1500 $\pm$ 300 μmol $m^{-2} s^{-1}$ in January to 600 $\pm$ 200 μmol $m^{-2} s^{-1}$ in July. The corresponding values for micro-habitats such as 5-10 cm deep rocky crevices or underneath the *Lessonia* canopy was 0.5 to 3.0 $\pm$ 0.5 μmol $m^{-2} s^{-1}$ (measured with a LAMBDA Quantum/Radiometer/Photometer LI-COR 185A).

General culture conditions

After collection, samples were placed in individual plastic bags and carried to the laboratory in refrigerated containers. Spores were obtained using the dehydration method. Spores were then placed in Petri dishes (50 x 10 mm) containing SWM-3 culture solution (McLachlan 1973) and incubated in growth chambers under controlled conditions of irradiance (0, 2, 10, 25, 50, 75 and 100 μmol $m^{-2} s^{-1}$), daylength (8, 12 and 16 h of daily light) and temperature (15 °C). The culture medium was changed every six days. Change of culture medium under 0 μmol $m^{-2} s^{-1}$ was aided with a 5 μmol $m^{-2} s^{-1}$ red light lamp. Each individual culture was exposed between 20 and 40 s to this irradiance source during the change of culture medium.

Specific experimental conditions: ability to germinate in total darkness and minimum light requirement for germination

The ability of seaweed propagules to germinate in darkness and the minimum light requirement for germination were determined for a total of 17 species. Seven of these *(Enteromorpha compressa, E. intestinalis, Ulva rigida, Ectocarpus confervoides, Hincksia mitchelliae, Gelidium lingulatum* and *Mazzaella laminarioides)* have been previously found in the banks of microscopic forms (Santelices et al. 1995), while the other 10 species *(Chaetomorpha firma, C. linum, Adenocystis utricularis, Endarachne binghamiae, Scytosiphon lomentaria, Glossophora kunthii, Lessonia nigrescens, Montemaria horridula, Centroceras clavulatum* and *Chondrus canaliculatus)* had not been found in the bank.

Six replicate dishes each containing spores of one of the above species were incubated under each combination of irradiance and photoperiod for all 17 species listed above. Total darkness was obtained by placing the culture dishes into light-tight boxes. Absence of light was confirmed using a light sensor (LI-COR 185A). After 4 days of incubation, the presence of germinating spores was determined by examining 10 microscopic fields in three of the culture dishes from each treatment. Germination was judged positive when at least 25 % of the alive spores found in the microscopic field exhibited germination. Since ungerminated spores normally became paler and suffered cell lysis, exact counts of germination frequency (or germination rate) could not be obtained. A second evaluation of germination under each combination of irradiance and photoperiod in darkness was completed after six days of incubation, using the remaining three replicate Petri dishes per treatment. In the case of *Ectocarpus confervoides*, evaluation of germination in darkness was repeated with a larger number (24) of replicates. After 6 days, evaluations were repeated weekly, for up to 8 weeks.

The relationship between the ability to survive in darkness and the presence or absence of the species in the bank of microscopic forms was analyzed using chi-square test (Sokal & Rohlf 1981).

Specific experimental conditions: ability of the microscopic forms to survive in darkness and their growth rate under different irradiances

To evaluate the ability of the microscopic forms to survive in darkness, a subsample of 15 species was used (all the above except *Chaetomorpha linum* and *Centroceras clavulatum)*. This combination of species included microscopic forms with different morphologies (germling-like, filaments and discs), differential tolerance to germination in darkness and differential presence in the banks of microscopic forms. A total of 60 to 80 Petri dishes per species, with germinated spores and 6 day-old microscopic forms were placed in light-tight boxes. Three dishes were removed from darkness at monthly intervals, from which the microscopic forms were examined for pigmentation and then incubated for 15 days under optimal light conditions to evaluate their recovery capacity. In the cases of *Chondrus canaliculatus* and *Mazzaella laminarioides*, evaluation was done weekly. In the case of *Enteromorpha compressa* and *Gelidium lingulatum*, the total number of replicate dishes used were 150 and 200, respectively.

The growth rates of the various microforms under various irradiances and photoperiods were measured using three replicate culture dishes incubated under each combination of irradiance and daylength described above. Growth of microscopic forms was determined weekly for up to 21 days. The area of crustose germlings was measured from outline drawings made with a drawing mirror on a Wild microscope; the length of filamentous forms was measured with a micrometer. Mean values were calculated from measurements of 30 microscopic forms (10 in each replicate dish) and compared using a two-way ANOVA followed by a posteriori Tukey's tests (Sokal & Rohlf 1981). Spore abundance not always was enough for the 21 treatments used. In those cases a few intermediate treatments were omitted (e.g., normal day regimes in *Enteromorpha compressa* or *Scytosiphon lomentaria*).

RESULTS

Ability to germinate in total darkness

Propagules of eight of the 17 species tested (47 %) germinated under total darkness, while propagules of the remaining nine species did not germinate in darkness (Table 1). Among these, the zooids of *Ectocarpus confervoides* could survive without germination under total darkness for up to 45 days, after which they became colorless and died. Propagules of the other eight species under 0 μmol $m^{-2} s^{-1}$ became colorless and died within 48-96 h.

The ability to germinate in darkness is unrelated to the presence or absence of these species

TABLE 1

Ability of propagules to germinate in total darkness and relationships to presence in the bank of microscopic forms and to specific characters: (Z) zoospores; (T) tetraspores; (C) carpospores; (E) ephemeral; (P) perennial

Capacidad de los propágulos para germinar en oscuridad y relación con su presencia en el banco de formas microscópicas y con caracteres específicos; (Z) zoosporas; (T) tetrasporas; (C) carposporas; (E) efímeras; (P) perennes

Species	Presence in the bank of microscopic forms	Minimum light requirement for germination (μmol $m^{-2}s^{-1}$)	Propagule type	Propagule diameter (μm)	Life history type	Successional status
Chlorophyta						
Chaetomorpha firma Levring	No	0	Z	10.7	Isomorphic	P
Chaetomorpha linum (Müller) Kützing	No	0	Z	10.0	Isomorphic	E
Enteromorpha compressa (Linnaeus) Greville	Yes	0	Z	4.0	Isomorphic	E
Enteromorpha intestinalis (Linnaeus) Link	Yes	0	Z	5.2	Isomorphic	E
Ulva rigida C. Agardh	Yes	5	Z	9.9	Isomorphic	E
Phaeophyta						
Ectocarpus confervoides (Roth) Le Jolis	Yes	2-5	Z	4.2	Isomorphic	E
Adenocystis utricularis (Bory) Skottsberg	No	2-5	Z	7.5	Heteromorphic	E
Endarachne binghamiae J. Agardh	No	10	Z	5.6	Isomorphic	E
Hincksia mitchelliae (Harvey) Silva	Yes	2-5	Z	3.7	Isomorphic	E
Scytosiphon lomentaria (Lyngbye) J. Agardh	No	2-5	Z	18.0	Heteromorphic	E
Glossophora kunthii (C. Agardh) J. Agardh	No	0	Z	28.0	Isomorphic	P
Lessonia nigrescens Bory	No	0	Z	5.7	Heteromorphic	P
Rhodophyta						
Montemaria horridula (Montagne) Joly & Alveal	No	0	T	22	Isomorphic	P
Centroceras clavulatum (C. Agardh) Montagne	No	0	T	26	Isomorphic	E
Chondrus canaliculatus (C. Agardh) Greville	No	2-5	T	25	Isomorphic	P
Gelidium lingulatum Kützing	Yes	2-5	C	29	Isomorphic	P
Mazzaella laminarioides (Bory) Fredericq	Yes	2-5	C	25	Isomorphic	P

in the banks of microscopic forms ($\chi^2 = 1.63$, P = 0.2014). Only two of the seven species found in the bank were able to germinate in total darkness, while the other five required a minimum irradiance of 2-5 μmol m^{-2} s^{-1} to germinate. On the other hand, six other species absent from the bank of microscopic forms were able to germinate in darkness (e.g., *C. firma, C. linum, G. kunthii, L. nigrescens, M. horridula, C. clavulatum*).

The relative representation of species with ability to germinate under total darkness within each major algal Division seems to be unequal. Germination under darkness appears most abundant among Chlorophyta and least abundant among Phaeophyta. However, the number of species tested is small and the tendency could change with larger sample sizes.

No relationship was found between the ability to germinate in darkness and some propagule characteristics such as propagule diameter (Table 1), presence or absence of flagella, life history of the species (isomorphic/heteromorphic) or successional status. Propagules of four species regarded as fugitive *(Chaetomorpha linum, Enteromorpha compressa, E. intestinalis* and *Centroceras clavulatum)* as well as those of four late successional *(Chaetomorpha firma, Glossophora kunthii, Lessonia nigrescens, Montemaria horridula)* exhibit the ability to germinate in total darkness.

Minimum light requirement for germination

With the exception of *Endarachne binghamiae*, all species that could not germinate under total darkness could do so under irradiances as low as 2-5 μmol m^{-2} s^{-1} (Table 1). Germination of *E. binghamiae* needed irradiance values equal or above 10 μmol m^{-2} s^{-1}.

Ability of the microscopic forms to survive in darkness

The microscopic forms of 13 of the 15 species tested (86.7 %) were able to survive in total darkness (Table 2). Maximum survival time for the dark-tolerant species was 500 days (germlings of *Gelidium lingulatum)* and the minimum was 60 days (crustose microforms of *Scytosiphon lomentaria).* These microscopic forms did not grow while in darkness, but did so when transferred to light.

The ability of microforms to survive in darkness is widespread among species previously found as well as among those not found in the banks of microscopic forms in boulder fields (Table 2) and also among the three major Divisions of benthic algae, among different types of morphologies (germlings, cell filaments or discs), life history types and successional status. Only the juvenile discs of two red algal species *(Chondrus canaliculatus* and *Mazzaella laminarioides)* did not tolerate darkness for more than a few (5-7) days.

Growth rates of microforms under different irradiances

The growth rates exhibited by the microforms under the various combinations of irradiance and daylength tested (Fig. 1, Table 3) indicated a diversity of responses. Species such as *Ulva rigida, E. confervoides, A. utricularis, G. lingulatum* and *M. laminarioides* exhibit little growth under either low irradiances, short photoperiods or both. In these species, increasing growth rates are exhibited with increasing irradiances or longer photoperiods. On the other hand, the microforms of species such as *Scytosiphon lomentaria* and, to a lesser extent, *Enteromorpha compressa* grew equally well under most of the laboratory conditions tested (Fig. 1, Table 3), while the microscopic stages of *Chaetomorpha firma, Glossophora kunthii* and *Lessonia nigrescens* did not grow at the higher irradiances tested (100 µmol m^{-2} s^{-1}). The germlings of *C. firma* were the most light sensitive (Fig. 1) as they grew best under irradiances between 2 and 25 µmol m^{-2} s^{-1}. They were unable to tolerate 75

TABLE 2

Number of days microscopic forms of macroscopic algae could survive in total darkness and relationships of survival in darkness to other characteristics of the species; (E) ephemeral; (P) perennial

Número de días que las formas microscópicas de algas macroscópicas pueden sobrevivir en completa oscuridad y las relaciones entre capacidad para sobrevivir en la oscuridad y otras características de la especie; (E) efímeras; (P) perennes

Species	Presence in the bank of microscopic forms	Survival time in total darkness (days)	Morphology of the microform	Successional status
Chlorophyta				
Chaetomorpha firma	No	270	Germling	P
Enteromorpha intestinalis	Yes	130	Germling	E
Ulva rigida	Yes	120	Germling	E
Enteromorpha compresa	Yes	397	Germling	E
Phaeophyta				
Ectocarpus confervoides	Yes	190	Filament	E
Hincksia mitchelliae	Yes	225	Filament	E
Adenocystis utricularis	No	266	Disc	E
Endarachne binghamiae	No	70	Disc	E
Scytosiphon lomentaria	No	60	Disc	E
Glossophora kunthii	No	225	Germling	P
Lessonia nigrescens	No	90	Filament	P
Rhodophyta				
Montemaria horridula	No	90	Germling	P
Gelidium lingulatum	Yes	500	Germiling	P
Chondrus canaliculatus	No	5	Disc	P
Mazzaella laminarioides	Yes	5	Disc	P

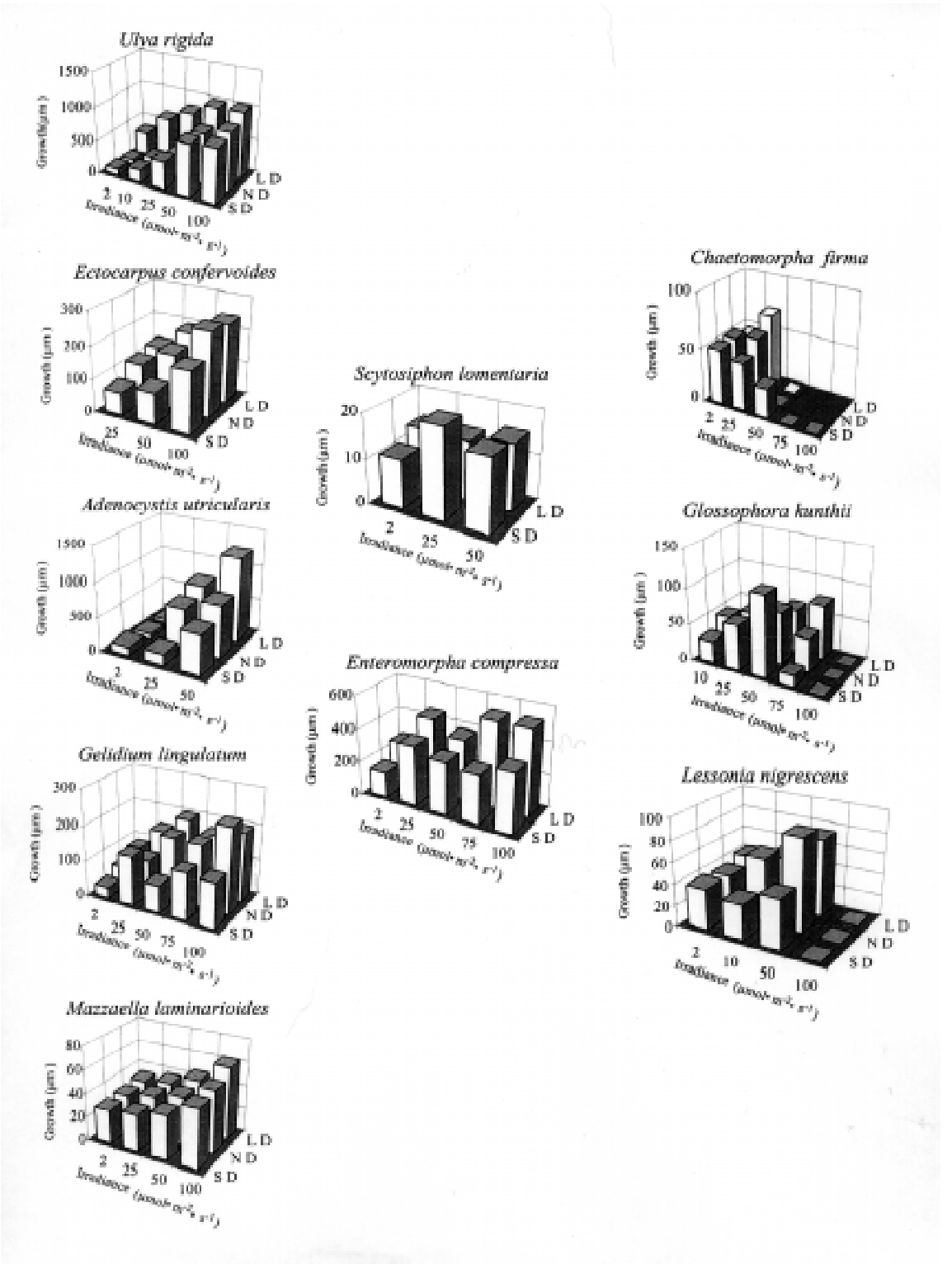

Fig. 1: Interactiv effects of irradiance (µmol m^{-2} s^{-1}) and daylength on the growth of microscopic forms of macroscopic algae. Key to abbreviations of daylength: (SD) short day; (ND) normal day; (LD) long day.

Efectos interactivos de irradiación y longitud del día en el desarrollo de formas microscópicas de algas bentónicas. Clave de las abreviaciones de longitud del día: (SD) día corto; (ND) día normal; (LD) día largo.

TABLE 3

The effects of photon fluence rate and photoperiod on the growth rate of microscopic forms. For each condition, values sharing same letter are not significantly different (P < 0.05, Tukey test); (SD) = short day; (ND) normal day; (LD) long day; (P x PF) photoperiod x photon flux interaction

Los efectos de flujo fotónico y fotoperíodo sobre el crecimiento de las formas microscópicas. Para cada condición, los valores compartiendo una misma letra no son significativamente diferentes (P < 0,05; prueba de Tukey); (SD) día corto; (ND) día normal; (LD) día largo; (P x PF) interacción fotoperíodo x flujo fotónico

Species	Photoperiod	Photon flux (μmol m^{-2} s^{-1})	Photoperiod x photon flux
Ulva rigida	SD^a=ND^a<LD^b	2^a<10^b<25^c<50^d = 100^d	Non significant
E. confervoides	SD^a<ND^b<LD^c	25^a<50^b<100^c	Significant
A. utricularis	SD^a<ND^b<LD^c	25^a<50^b<100^c	Significant
G. lingulatum	SD^a<ND^{ab}<LD^b	2^a<25^b= 50^b= 75^b= 100^b	Non significant
M. laminarioides	SD^a= ND^a = LD^a	2^a= 25^a<50^b<100^c	Non significant
S. lomentaria	SD^a= LD^a	2^a< 25^b= 50^b	Significant
E. compressa	SD^a< LD^b	2^a= 25^a= 50^a= 75^a= 100^a	Non significant
C. firma	LD^a<ND^b=SD^b	100^a= 75^a<50^b<25^c=2^c	Significant
G. kunthii	LD^a<ND^b<SD^c	100^a<75^b<10^c=25^c<50^d	Significant
L. nigrescens	LD^a= SD^a<ND^b	100^a<2^b= 10^b<50^c	Non significant

to 100 μmol $m^{-2}s^{-1}$ and could tolerate up to 50 μmol m^{-2} s^{-1} only when incubated under short day regimes.

DISCUSSION

Our results confirm the hypothesis that survival in darkness or under dim light is a widespread response among microscopic stages of macroalgae. Propagules of almost half the number of species tested germinated in total darkness, while the remaining species required very low irradiances for germination (2-10 μmol m^{-2} s^{-1}). Similarly, the microforms of 13 of the 15 species tested were able to survive in darkness, some of them with survival time extending 400 *(Enteromorpha compressa)* and 500 days *(Gelidium lingulatum).*

The above results agree well with previous literature reports. Under laboratory conditions, spores of several algal species (reviewed in Hoffmann & Santelices 1991) have been found to be able to germinate under complete darkness, giving rise to microscopic forms. On the other hand, spore survival in darkness without germination, as found in our experiments with *Ectocarpus confervoides* has also been found in *Scytosiphon lomentaria* and *Ulva pertusa* (Whoodhead & Moss 1975). Similarly, spores of *Enteromorpha* spp. have been reported to survive more than 10 months in darkness (Schories 1995); those of *Laminaria hyperborea* survived for 50 days (Kain 1964), while the propagules of *Chaetomorpha melagonium* and *Halarachnion ligulatum* survived for up to one year in darkness without germination (Leukart & Lünning 1994). Regarding the microscopic forms, the gametophytes or the embryos of a total of 16 species have been reported to survive between 2 and 8 months under darkness or very low irradiance conditions (e.g., 1 μmol m^{-2} s^{-1}; see Hoffmann & Santelices 1991 for data).

The physiological basis for germination not dependent on light are unknown. It has been suggested (Clayton 1992, Reed et al. 1992) that the process is perhaps based on the utilization of polysaccharides and lipid reserves of the propagules. In fact, Brzezinski et al. (1993) observed lipid droplet consumption during spore germination in *Macrocystis pyrifera.* The availability of light appeared to delay, but did not reduce lipid use. Such carbon and nitrogen reserves could be especially significant in spores and zygotes that settle in dark habitats.

In the case of the microscopic forms, the ability to survive in darkness or dim light could depend on the capacity of the microform to incorporate some of the organic compounds present in the boundary layer, living heterotrophically (Amsler & Neushul 1991, Amsler et al. 1992, Reed et al. 1992, Fries 1993). Alternatively, the microscopic form could be metabolically active even under very low irradiances. In the case of *Desmarestia lingulata,* Edwards (2000) found that the over-

wintering gametophytes were metabolically active and sensitive to changes in environmental quality, being able to photosynthetize even under very low irradiances (8 μmol m^{-2} s^{-1}).

The ability of the spores to germinate in darkness or the survival capacity of the microforms under dark conditions appears unrelated to taxonomic membership, life history style, propagule size or successional status. Microforms of both fugitive and perennial species survived in darkness, suggesting that microforms of species with either strategy have the capacity to function as survival stages in a bank of microscopic forms. Similarly, no relationship was evident between the ability to germinate and survive in darkness and the previous presence of these species in the bank of microscopic forms (Santelices et al. 1995). Absence from the bank may thus be due to other factors, such as short dispersal shadow or low colonization capacity.

The growth patterns of the microforms under various irradiance regimes suggested that three species *(C. firma, G. kunthii* and *Lessonia nigrescens)* are sensitive to high irradiances. It is as yet unknown if this sensitivity of the microscopic stage determines any aspect of the spatial distribution of any of these species. However, a similar situation was described by Graham (1996) for *Macrocystis pyrifera* in California, U.S.A. Using a combination of field and laboratory experiment, Graham (1996) concluded that high irradiance on the recruits regulates the upper vertical limit of *M. pyrifera* prior to the temperature and desiccation stresses inherent to intertidal regions. Perhaps a similar process is occurring with these three above species, which are most abundant in the lowest intertidal-shallow subtidal habitats of central Chile.

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