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Algal life-history strategies and resistance to digestion

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ABSTRACT: The capacity to resist digestion is emerging as a widespread adaptation of benthic algae, especially among some opportunistic forms. This study examines differences in digestion resistance among macroalgae having different degrees of tissue differentiation and different life strategies. Opportunistic Chlorophyta and Bangiophycidae are able either to release protoplasts or to regenerate new tissues from undigested algal remains, suggesting 100 % grazing mortality to be a rare event among these species. In species with differentiated reproductive structures, swarmer and protoplast release does not occur in algal fragments: survival depends on the capacity of meristematic cells to pass through the digestive tract undamaged. Survival after digestion is higher among densely branched, filamentous forms with apical cell or diffuse growth, and lower in late successionists where meristematic tissues are restricted to particular regions of the thallus. Reproductive cells in all species with differentiated reproductive organs show greater sensitivity to digestion than vegetative, meristematic cells. Since resistance to digestion is closely related to morphological organization, life-history phases in heteromorphic species (e.g. leafy and filamentous phases of *Porphyra*) may have completely different sensitivity to digestion. Overall, these results suggest that algae presently recognized as opportunistic forms include species with very different morphological and reproductive responses to grazing. Likewise algal mortality induced by grazing varies significantly among species of grazers. Some grazers induce high algal mortality while others stimulate swarmer and protoplast release, allowing survival of apical and intercalary meristems. Some of these grazers may have important ecological roles in dispersing, redistributing and even increasing the number of macroalgal propagules being dispersed.

INTRODUCTION

The ability to survive digestion by grazers seems to be a general adaptation of benthic algal propagules. The phenomenon is frequent for the algal species found in the guts of common intertidal and shallow subtidal sea urchins (Santelices et al. 1983), and intertidal grazing molluscs (Santelices & Correa 1985). Ongoing research indicates it is also evident among species grazed by amphipods and spores ingested by filter feeders.

A common, yet unexplained, observation in these studies is a greater ability of opportunistic algal species to survive passage through the digestive tract of grazers, as compared to late successional forms. Several as yet untested hypotheses have been advanced. Since opportunistic species usually have little division of labour and reproductive organs develop over much of the thallus, grazers consuming these species would, on average, have a much higher chance of eating propagules than those consuming late successional forms (Santelices et al. 1983). Germination and growth of propagules from opportunistic forms may perhaps be stimulated by nutrient released in the feces more than propagules from late successional forms. Alternatively, since the examination of algal cultures has often revealed growth from undigested algal remains, perhaps opportunistic species intrinsically have increased regeneration capacities compared to late successional forms (Santelices & Correa 1985).

A second general pattern emerging from these studies is conspicuous differences in digestion resistance among opportunistic algal species. This was especially clear in the Rhodophyta where Bangiophycidae are frequent survivors in fecal cultures while Ceramiales rarely survive. Differential sensitivity to digestive enzymes due to differences in cell wall structure was suggested as an explanation (Santelices & Correa 1985).

In this study we look for the causes of these patterns

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and test the above hypotheses through feeding experiments using intertidal grazing molluscs and selected algal species with varying morphologies and degrees of tissue differentiation, and different life strategies.

MATERIALS AND METHODS

A total of 10 algal species (Table 1) and 4 herbivorous molluscs were employed. Taxonomic authorities for the invertebrate and algal species identified in this study are to be found in Marinkovich (1973) and Santelices et al. (1981). *Littorina peruviana* (Littorinidae), *Collisella zebrina* (Acmaeidae), *Siphonaria lessoni* (Siphonariidae) and *Fissurella crassa* (Fissurellidae) are common intertidal grazers which modify in different degrees the survival capacities of common intertidal macroalgae in exposed habitats of Central Chile (Santelices & Correa 1985). The algal species used are common food items of these 4 grazers and they represent different morpho-functional groups (*sensu* Littler & Littler 1980). *Enteromorpha compressa, Ulva rigida* and *Porphyra columbina* are considered foliose opportunists; *Ectocarpus* sp., the filamentous *(Conchocelis)* phase of *Porphyra columbina, Chaetomorpha firma* and *Centroceras clavulatum* constitute filamentous opportunists; while the corticated, structurally more complex *Gelidium lingulatum* and *Iridaea laminarioides* and the calcareous crust *Leptophytum* sp. were all used as representatives of late successional forms. Leathery macrophytes (*sensu* Steneck & Watling 1982) and articulated corallines are infrequent food items among these grazers and therefore were excluded from the study.

Table 1. Collection data and reproductive stages for algal species used in this study

Species	Collection date	Reproductive state
Enteromorpha compressa	12 Jan 1985	Vegetative
Ulva rigida	13 Feb 1985	Vegetative
Porphyra columbina	15 Mar 1985	Reproductive
Ectocarpus sp.	2 Apr 1985	Polysporangial
Conchocelis phase of *Porphyra columbina*	28 Apr 1985	Vegetative
Chaetomorpha firma	15 May 1985	Vegetative
Centroceras clavulatum	3 Jun 1985	Vegetative
Gelidium lingulatum	5 Jul 1985	Tetrasporangial
Iridaea laminarioides	7 Aug 1985	Cystocarpic
Leptophytum sp.	21 May 1986	Tetrasporangial

Algae and invertebrates were collected at various dates from intertidal rocky habitats at Pelancura, near San Antonio Bay (33°35' S, 71°38' W) in Central Chile. For each experiment 30 haphazardly collected individuals of each invertebrate species were carefully rinsed up to 7 times in sterile seawater to remove algal remains from the invertebrate surface. Then they were transported to the laboratory in a temperature-controlled container and maintained with no macroscopic food in a circulating seawater aquarium for 10 d. Then, and for the next 3 d, a given algal species attached to the walls and bottom of plastic trays and maintained with circulating seawater was offered as food to each of the 4 species of grazer. The invertebrates were then removed, rinsed in sterile seawater and maintained in plastic containers with sterile seawater and bubbling air.

Fecal pellets from these grazers were collected with sterile forceps each morning for the next 3 d and examined under a microscope. A total of 60 fragments of algal thalli of each species were removed from the fecal pellets and transferred to 3 replicate sterile Petri dishes filled with 25 ml of SWM-3 culture medium (McLachlan 1973) and incubated 20 to 25 d under constant temperature (14 °C), photon flux-density (50 $\mu E\ m^{-2}\ s^{-1}$) and photoperiod (12:12). Uningested thalli of each algal species tested (non-exposed to grazers) were sectioned with razor blades and 60 thallus fragments of approximately similar size to those recovered from fecal remains were used as controls.

Resistance to digestion was defined as the ability either to grow and regenerate new cells or to produce propagules by the cells surviving in each of 60 thallus fragments recovered from the invertebrate fecal pellets. It was quantified as the number of living fragments out of the total number of thallus fragments (60) recovered from the pellets of each species of grazer. Comparisons of digestion resistance between vegetative and reproductive cells was made by simultaneously offering both types of tissues to grazers. Reproductive cells (tetraspores or carpospores) were always offered as part of a reproductive branch or tissue normally protected by the cortical cells.

Spontaneous swarmer release often occurred in some of our experiments both in the cultures started from fecal remains and in those started from non-ingested, control fragments. These swarmers eventually developed into sporelings. Frequently the resulting densities of sporelings in both types of treatments were different, but the sporeling density in the control culture was always ½ to ⅓ that in other experimental treatments. After 8 d of incubation, a total of 50 sporelings per treatment were transferred to a larger container (1000 ml) to compare elongation rates between sporelings arising from ingested and non-ingested thallus fragments. One-way ANOVA followed by *a priori* comparisons (Sokal & Rohlf 1969, p. 226) were used to evaluate the significance of differences in

growth between these treatments. Similar methods were used to test for growth differences between ingested and non-ingested algal fragments of filamentous opportunists, as well as meristematic and reproductive cells of late successionists. In these experiments, however, the number of replicates used in each treatment often was less than 50 due to scarcity of surviving tissues.

RESULTS

Foliose opportunists

The ability of blade tissues of the 3 foliose opportunists to resist digestion varied according to grazer type (Fig. 1). Almost 90 % of the thallus fragments from *Enteromorpha compressa* and *Ulva rigida* recovered from fecal pellets of *Siphonaria lessoni* and *Fissurella crassa* remained healthy. Survival of tissue from both algal species was much lower with *Collisella zebrina* and *Littorina peruviana*. *Porphyra columbina* resisted digestion only when consumed by *S. lessoni*. Survival of control fragments ranged from 80 to 85 % in *E. compressa* and *U. rigida* and 70 % in *P. columbina*.

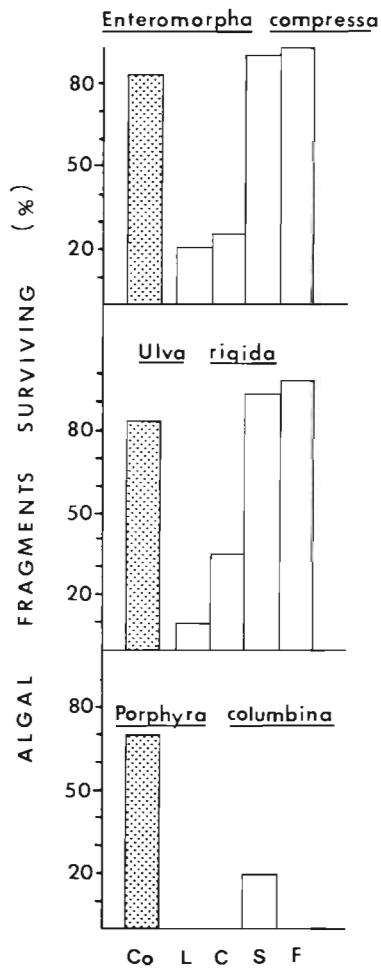

Fig. 1. *Enteromorpha compressa*, *Ulva rigida* and *Porphyra columbina*. Percent survival of 3 foliose opportunists consumed by 4 species of grazing molluscs (L: *Littorina peruviana*, C: *Collisella zebrina*, S: *Siphonaria lessoni*, F: *Fissurella crassa*); Co: control, non-ingested thalli

Two types of responses were common in the 3 foliose species over the 8 d period following their recovery from the fecal pellets. In some algal fragments the cytoplasm of the surviving cells was condensed toward one side of the cell, then the wall disintegrated, the tissue lost integrity and protoplasts were set free in the culture medium. In *Enteromorpha compressa* and *Ulva rigida* the protoplasts developed flagella, behaved like swarmers and settled down on the bottom of the culture vessels to form new thalli. In *Porphyra columbina*, protoplasts arising from vegetative cells developed into thin and short filaments which then formed a callus on the bottom of the culture dishes; protoplasts arising from reproductive cells normally originated *Conchocelis* filaments, although in one culture dish they developed directly into a thin *Porphyra* blade.

A second type of response, tissue regeneration from cells surviving in the algal fragments, was shown by *Ulva rigida* and *Enteromorpha compressa*.

The grazer strongly influenced the type of response shown by the algae (Fig. 2). Probably stimulated by the sectioning of the algal tissue, swarmer release occurred even in the non-ingested algal fragments used as control (12 to 25 %). However, the number of fragments of both Chlorophyta species releasing swarmers was much higher than the control when consumed by *Siphonaria lessoni* or *Fissurella crassa* or when *Enteromorpha compressa* was recovered from fecal pellets of *Collisella zebrina*. The number of algal fragments of the 2 Chlorophyta able to release swarmers after passing through *Littorina peruviana* and of *Ulva rigida* passing through *C. zebrina* was approximately similar to that shown by the control thalli.

Regeneration of new tissues was a response normally shown by the non-ingested, control fragments and, in smaller quantity, by some of the experimental fragments, especially of *Enteromorpha compressa* when passing through *Collisella zebrina* or *Fissurella crassa*. With the exception of a few fragments surviving through *C. zebrina*, ingested *Ulva rigida* was unable to regenerate.

In *Porphyra columbina*, protoplast release was the only response shown by ingested tissues and this was restricted to fragments recovered from *Siphonaria lessoni*. Non-ingested fragments of this species used as control either regenerated new tissues (72 %) or bleached and died. Not a single control fragment showed protoplast release.

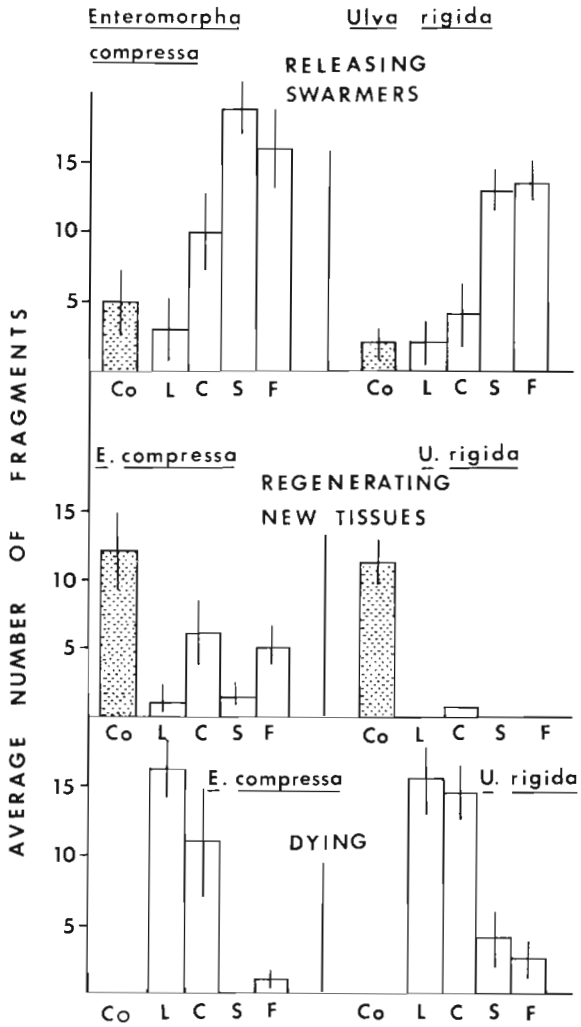

Fig. 2. *Enteromorpha compressa* and *Ulva rigida*. Average number of fragments (sample size = 20, n = 3) releasing swarmers, regenerating new tissues or dying after passing through the digestive tract of 4 species of grazing molluscs (L, C, S, F and Co as in Fig. 1). Bars correspond to range

Sporelings of both Chlorophyta species arising from swarmers released by ingested tissues grew significantly faster (Fig. 3; Table 2) than sporelings originating from non-ingested, control thalli. The effect was most pronounced in sporelings arising from swarmers passing through *Fissurella crassa*. As previously explained (see 'Materials and Methods'), during the 8 d following recovery of algal fragments from fecal pellets, sporeling density was much reduced in the control thalli than in the 2 other treatments, therefore growth stimulation cannot be explained as a density-related phenomenon. Probably growth stimulation was produced by unknown factors in the fecal remains of both grazers.

The reduced number of ingested algal fragments of the 2 Chlorophyta showing regeneration capacity did not allow a comparison of growth rates with regenerating, non-ingested, control fragments.

Filamentous opportunists

Survival of filamentous opportunists also varied with the algal and the grazer species tested (Fig. 4). *Chaetomorpha firma*, the filamentous phase of *Porphyra columbina*, and *Ectocarpus* sp. survived best when consumed by *Siphonaria lessoni* or *Fissurella crassa* and least well when ingested by *Littorina peruviana*. Only a few fragments of *Centroceras clavulatum* survived and only when consumed by *S. lessoni*.

Microscopic examination revealed that these filamentous species could either produce new swarmers or regenerate new tissues. Swarmer formation (8 to 12 per cell) occurred in the remains of *Chaetomorpha firma* recovered from the fecal pellets of all 4 grazers. In contrast, control filaments regenerated by growth of the apical cell without swarmer formation. Ingested as well as non-ingested fragments of *Ectocarpus* sp., the filamentous *(Conchocelis)* phase of *Porphyra columbina*, and *Centroceras clavulatum* regenerated from terminal branch cells. No evidence of protoplasts formation and release was ever found in these species. Upon recovery from the fecal pellets, the apical and intercalary cells of these 3 species, the cortical cells of *C. clavulatum* and the plurangia of *Ectocarpus* sp. revealed structural damage and pigment destruction. Recovery and growth occurred later from undamaged apical cells. The increased abundance of lateral branches, each with terminal branch cell in *Ectocarpus* sp. and in the *Conchocelis* filaments corresponded with increased survival capacity of these species relative to the lower values shown by the sparingly branched *C. clavulatum*.

Sporelings of *Chaetomorpha firma* which arose from swarmers passing through *Siphonaria lessoni* and the *Conchocelis* filaments which survived consumption by *S. lessoni* and *Fissurella crassa* grew significantly faster than the non-ingested control thalli under laboratory conditions (Fig. 5).

Late successionists

Survival capacity in culture of *Gelidium lingulatum* and *Iridaea laminarioides* fragments recovered from fecal pellets varied according to the cell type (vegetative or reproductive) and to the type of grazer tested (Fig. 6; Table 2).

Vegetative tissues of *Gelidium lingulatum* generally resisted digestion (80 to 82 ‰) when consumed by

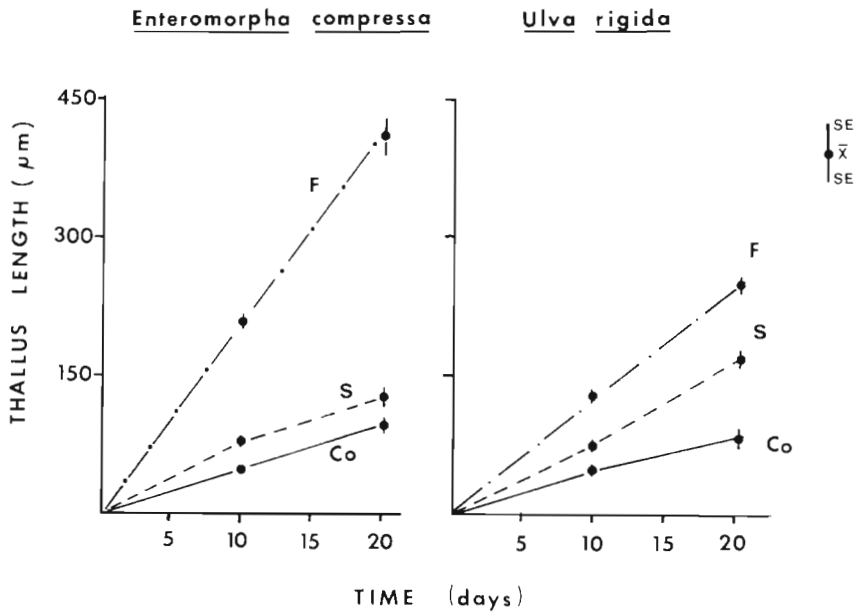

Fig. 3. *Enteromorpha compressa* and *Ulva rigida*. Growth (measured as thallus length increments) of 50 sporelings recovered from fecal pellets of *Siphonaria lessoni* and *Fissurella crassa* (indicated S and F respectively)

Table 2. ANOVA tables with treatment sum of squares decomposed into planned comparisons for the results of growth of opportunistic and late successional forms surviving digestion through *Siphonaria lessoni* and *Fissurella crassa*. Comparison have been performed with growth achieved at the end of each experimental period (20 d). • Significant differences at $p \leq 0.05$; •• significant differences at $p \leq 0.01$

Opportunistic forms	Sporelings of *Enteromorpha compressa*			Sporelings of *Ulva rigida*			Filaments of *Chaetomorpha firma*			Filaments of *Porphyra columbina*		
Source of variation	df	MS	F_s	df	MS	F_s	df	MS	F_s	df	MS	F_s
Treatments	2	104 149.0	224,0••	2	87 945.0	143,0••	2	270 105.0	149,1••	2	12 224.0	17,5••
Ingested *vs* uningested	1	123 384.0	265,3••	1	134 786.0	219,1••	1	1 820.0	1,0	1	24 338.0	34,9••
Siphonaria vs Fissurella	1	84 914.0	183,0••	1	41 103.0	66,8••	1	538 390.0	293,0••	1	110.0	0,2
Within	147	464.9		147	615.0		132	1 812.0		38	697.4	
Total	149			149			134			40		

Late successionists	Meristematic cells of *Gelidium lingulatum*			Meristematic cells of *Iridaea laminarioides*			Tetraspores of *Gelidium lingulatum*			Carpospores of *Iridaea laminarioides*		
Source of variation	df	MS	F_s	df	MS	F_s	df	MS	F_s	df	MS	F_s
Treatments	2	7 563.0	14,3••	1	4 454.0	103,8••	2	6 716.0	98,5••	2	18 088.0	53,5••
Ingested *vs* uningested	1	13 408.0	25,4••				1	10 773.0	158,0••	1	34 612.0	102,4••
Siphonaria vs Fissurella	1	1 718.0	3,3				1	2 658.0	39,0••	1	1 563.0	4,6•
Within	147	529.0		39	42.9		58	68.2		57	338.0	
Total	149			40			60			59		

Siphonaria lessoni and *Fissurella crassa* but not when consumed by *Collisella zebrina* or *Littorina peruviana*. Apical initials and cortical cells of *G. lingulatum* exhibited pigment destruction and structural damage after recovery from the feces. However, a number of apical initials remained alive in most fragments recovered from *S. lessoni* and *F. crassa* and were able to grow in culture. In a few fragments where all apical cells showed pigment destruction, regeneration occurred by differentiation of cortical cells into apical initials. This did not occur in fragments recovered from *L. peruviana* or *C. zebrina*.

Few tetraspores of *Gelidium lingulatum* resisted digestion by any grazer (Fig. 6). Often the cortical cells around the tetraspores showed pigment destruction and may have protected the few surviving spores from digestion. Although the survival rates of reproductive cells were slightly higher when consumed by

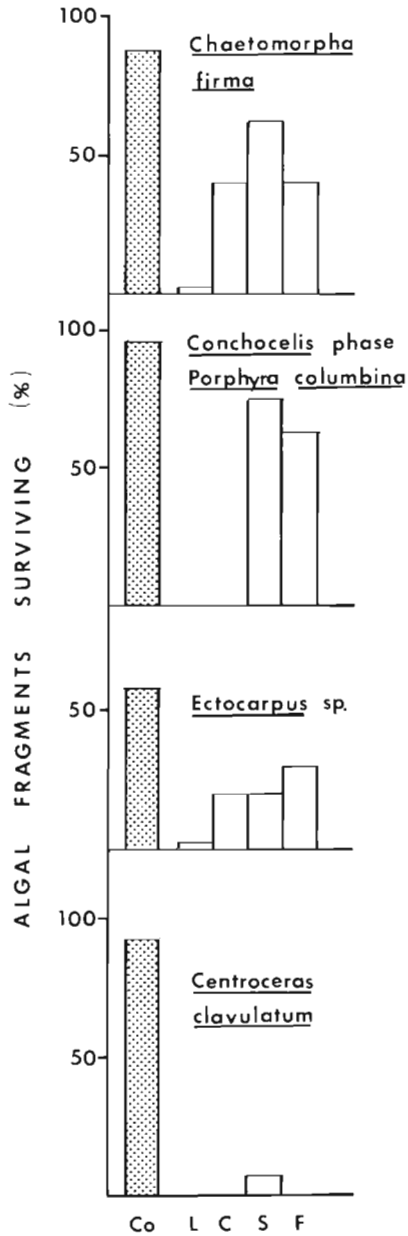

Fig. 4. *Chaetomorpha firma*, *Conchocelis* phase of *Porphyra columbina*, *Ectocarpus* sp. and *Centroceras clavulatum*. Percentage survival of 4 filamentous opportunists consumed by 4 species of grazing molluscs (L, C, S, F and Co as in Fig. 1)

Fissurella crassa and *Siphonaria lessoni*, they were much lower than vegetative cells, indicating higher sensitivity of reproductive cells to digestive enzymes.

Holdfast fragments were the only tissue of the *Iridaea laminarioides* thallus with regeneration capacity. Other frond fragments were unable to regenerate under ingested or non-ingested conditions. Holdfast fragments of *I. laminarioides* had very low digestion resistance and survived only when consumed by *Siphonaria lessoni* or *Colisella zebrina* (Fig. 6). Carpospores of *I. laminarioides* survived only when eaten by *Siphonaria lessoni* or *Fissurella crassa* and in higher percentage than vegetative fragments (Fig. 6).

Thallus fragments of *Gelidium lingulatum* and *Iridaea laminarioides* surviving in the fecal pellets of *Siphonaria lessoni* or *Fissurella crassa* grew significantly faster in cultures than non-ingested thallus fragments used as control (Fig. 7; Table 2). However, these algal fragments did not attach themselves to the culture dishes during the experiments. In contrast, the reproductive cells of *G. lingulatum* and *I. laminarioides* resisting digestion could attach themselves but their growth rates were significantly smaller than the non-ingested control spores.

Vegetative tissues of *Leptophytum* sp. failed to grow under any experimental condition. Growth of calcareous crusts normally requires longer experimental periods to detect significant differences. Tetraspores ingested by any of the 4 grazers did not have any growth capacity after recovery from the fecal pellets. Control spores showed 60 % germination capacity and kept growing in our cultures up to the end of the experiments (20 d).

DISCUSSION

Swarmer and protoplast release shown by opportunistic Chlorophyta and Bangiophycidae that survive digestion is perhaps the most significant result of this research. These protoplasts and swarmers in generating new individuals act as accessory means of reproduction. This result is not completely unexpected since swarmer release is a common response among Chlorophyta when exposed to stressful situations (Vidaver 1972) and protoplast release after application of abalone gut enzymes to *Porphyra perforata* has been reported (Polne-Fuller & Gibor 1984). Our findings, however, add an evolutionary perspective to this response suggesting it could be analogous to some dispersal mechanisms observed in land plants, where seed germination is sometimes stimulated by digestion tract passage. In these algae, swarmer and protoplast production is often stimulated by the passage through the digestive tract of these grazers.

The combination of results allows us to establish digestion resistance patterns among algae with different life strategies, and to evaluate some of the hypotheses previously proposed to explain survival differences. Opportunistic Chlorophyta and Bangiophycidae are able either to release protoplasts or to regenerate new tissues from undigested algal remains, suggesting that 100 % grazing mortality might be a rare event among these species when consumed by these grazers. High grazing mortality is expected only

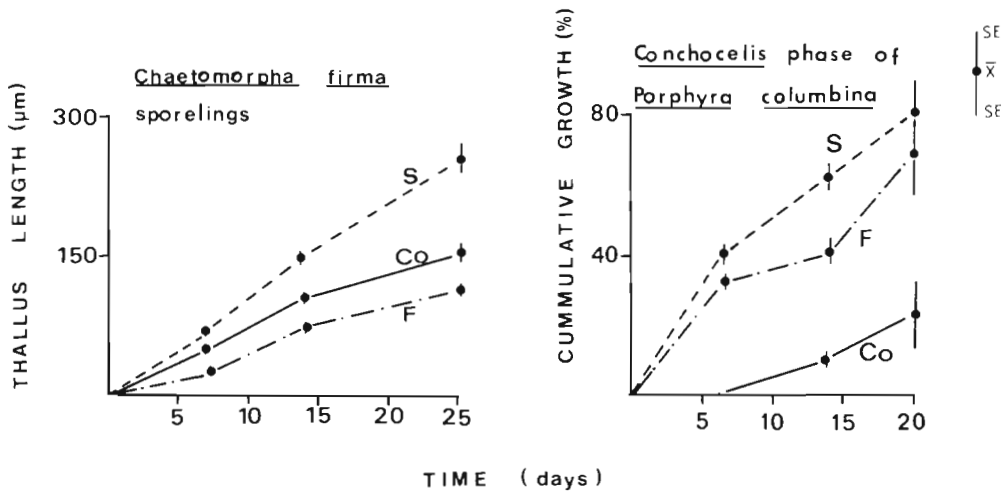

Fig. 5. *Chaetomorpha firma* sporelings and filaments of *Conchocelis* phase of *Porphyra columbina*. Growth (measured as thallus length increments) after recovery from the fecal pellets of *Siphonaria lessoni* and *Fissurella crassa* (indicated as S and F respectively)

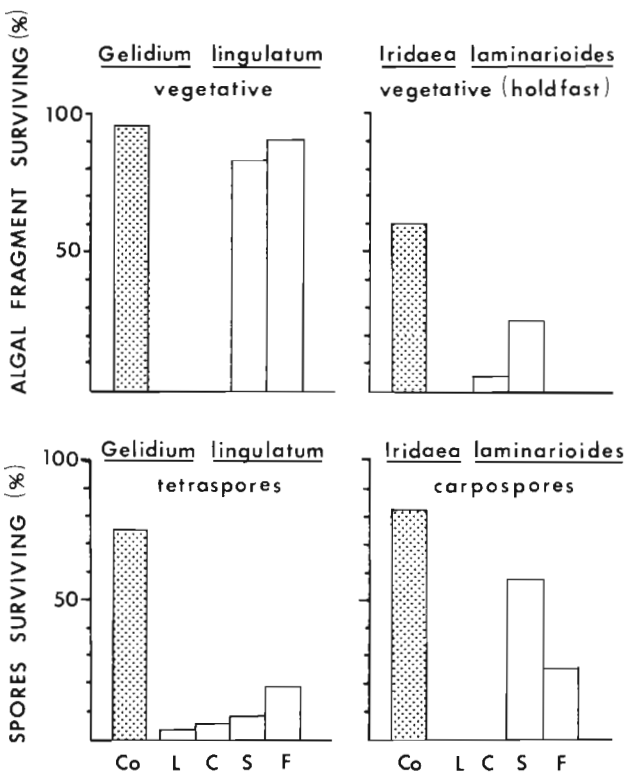

Fig. 6. *Gelidium lingulatum* and *Iridaea laminarioides*. Percentage survival of reproductive and vegetative cells of 2 middle successionists consumed by 4 species of grazing molluscs (L, C, S, F and Co as in Fig. 1)

for *Porphyra columbina* when consumed by grazers other than *Siphonaria lessoni*. This also explains the increased ability to survive digestion shown by these opportunists as compared to other algal forms in previous experiments (Santelices et al. 1983, Santelices & Correa 1985). Furthermore, the differences in survival capacity among opportunistic Rhodophyta (Bangiales *vs* Ceramiales) could also be explained by the above results rather than by differences in cell wall constituents as previously thought (Santelices & Correa 1985).

Swarmer and protoplast release from undigested algal remains does not occur in species with differentiated reproductive structures. Survival in these cases is wholly dependent upon the capacity of meristematic cells to pass alive through the digestive tract of grazers. In many filamentous opportunists, the probability of survival is higher in densely branched morphologies (e.g. *Ectocarpus* sp. *vs Centroceras clavulatum*). These results also suggest that filamentous opportunists with intercalary meristems may perhaps be of greater advantage than apical meristems for survival.

Meristematic cells of late algal successional forms can also resist digestion. However, since the meristematic tissues in these species are localized in the thallus, the probability of their consumption by grazers is reduced as compared to the meristems of opportunistic filamentous taxa.

Reproductive cells in all species with differentiated reproductive organs showed greater sensitivity to digestion than meristematic cells. Since surviving spores were able to attach themselves to the culture containers, in nature they are expected to be able to generate new individuals upon settlement. In contrast, vegetative cells and tissues were unable to produce new attachment structures in culture, even though growth was often stimulated by unknown substances in the fecal remains. Therefore they could be considered dead from the point of view of generating new individuals although they are probably important from

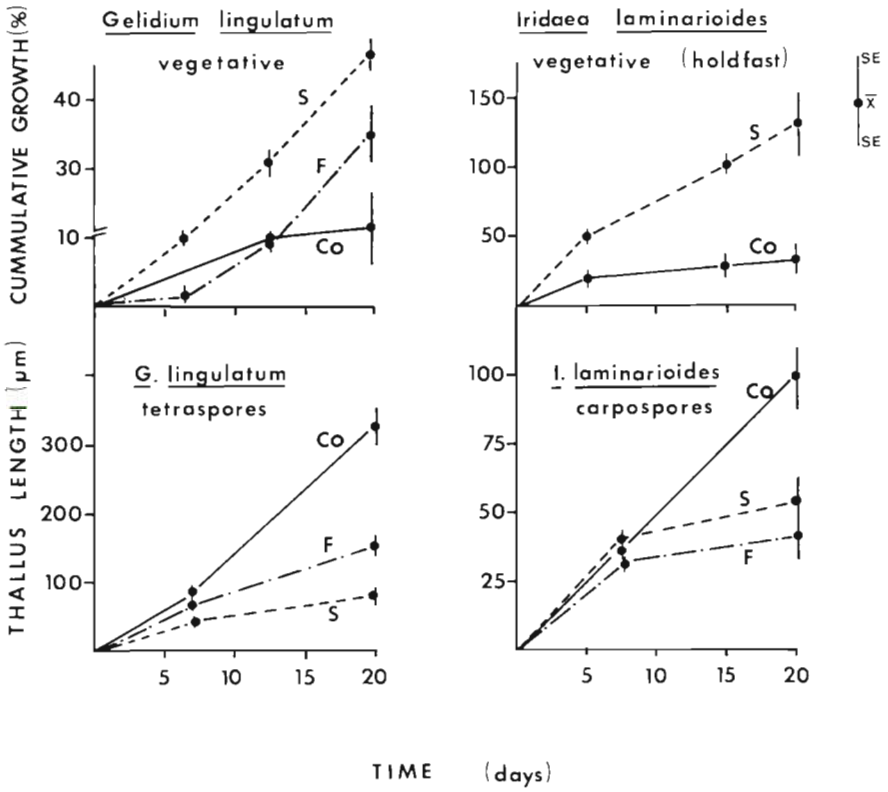

Fig. 7. *Gelidium lingulatum* and *Iridaea laminarioides*. Growth (measured as length or surface area increments) of sporelings and regenerated tissues recovered from fecal pellets of *Siphonaria lessoni* and *Fissurella crassa* (indicated as S and F respectively)

the viewpoint of trophic relations arising from these partially digested though living materials.

Our results also indicate that the variety of algae currently recognized as opportunistic forms include species with qualitatively different responses to grazing digestion. From this viewpoint the opportunistic algae are a highly heterogeneous group. The capacity to release swarmers and protoplasts by tissues that resist digestion clearly segregates the opportunistic Chlorophyta and Bangiophycidae from all other opportunists. Further, the capacity to regrow or regenerate new individuals from branch tips in single, highly branched filaments as in the Ectocarpaceae contrasts with the reduced capacity shown by morphologically different filaments as in the Ceramiaceae. These results are consistent with recent reports indicating that some Ceramiaceae had a more restricted space-time spore production than other filamentous opportunists (Hoffmann & Ugarte 1985). Future comparative studies will probably show additional life strategy differences among the variety of algal species now pooled together as filamentous opportunists.

The different response shown by the leafy (haploid) and the filamentous (diploid, *Conchocelis*) phase of *Porphyra columbina* is noteworthy. While the leafy form released protoplasts and only when consumed by *Siphonaria lessoni,* the filamentous phase had only diffuse growth and survived grazing by 2 of the 4 grazers. These differences are consistent with the well-known differences in morphological organization and physiological and ecological responses of these 2 phases and suggest that the type of response shown by digestion-resistant tissues is closely related to morphological organization and degree of differentiation.

Differences in algal mortality induced by different grazers in our experiments are in good agreement with previous results (Santelices & Correa 1985) where we reported conspicuous differences in ability to survive in relation to the grazer. Differences were explained on the basis of damage produced to the algal thallus by the feeding apparatus of the corresponding grazer. Present results, however, suggest that the phenomenon might be more complex, perhaps involving selective digestive enzymes as algal survival capacity is not restricted to tissue regeneration but also to swarmer production. For example, digestion by *Siphonaria lessoni* stimulated swarmer or protoplast release in several species and resulted in high survival rates of vegetative and reproductive tissues of several filamentous opportunists and late successionists. It is possible that this and similar grazers have important ecological roles dispersing and redistributing propagules and, in some cases, even increasing the number of macroalgal propagules being dispersed.

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LITERATURE CITED

Hoffmann, A. J., Ugarte, R. (1985). The arrival of propagules of marine macroalgae in the intertidal zone. J. exp. mar. Biol. Ecol. 92: 83–95

Littler, M. M., Littler, D. S. (1980). The evolution of thallus form and survival strategies in benthic marine macroalgae; field and laboratory test of a functional form model. Am. Nat. 116: 25–44

McLachlan, J. (1973). Growth media-marine. In: Stein, J. R. (ed.) Handbook of phycological methods: culture methods and growth measurements. Cambridge University Press, Cambridge, p. 25–51

Marinkovic, L. (1973). Intertidal molluscs of Iquique, Chile. Nat. Hist. Mus. Los Angeles Cty. Sci. Bull. 16: 1–49

Polne-Fuller, M., Gibor, A. (1984). Developmental studies in *Porphyra*. Blade differentiation in *Porphyra perforata* as expressed by morphology, enzymatic digestion, and protoplast regeneration. J. Phycol. 20: 609–616

Santelices, B., Correa, J. (1985). Differential survival of macroalgae to digestion by intertidal herbivore molluscs. J. exp. mar. Biol. Ecol. 88: 183–191

Santelices, B., Montalva, S., Oliger, P. (1981). Competitive algal community organization in exposed intertidal habitats from Central Chile. Mar. Ecol. Prog. Ser. 6: 267–276

Santelices, B., Correa, J., Avila, M. (1983). Benthic algal spores surviving digestion by sea urchins. J. exp. mar. Biol. Ecol. 70: 263–269

Steneck, R. S., Watling, L. (1982). Feeding capabilities and limitations of herbivorous molluscs: a functional group approach. Mar. Biol. 68: 299–319

Sokal, R. S., Rohlf, F. J. (1969). Biometry. W. H. Freeman & Co., San Francisco

Vidaver, W. (1972). Pressure: Plants. In: Kinne, O. (ed.) Marine ecology, Vol. 1, Environmental factors, Part 3. Wiley, London, p. 1389–1405

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