

# Responses of algae with different life histories to temporal and spatial variability of disturbance in subtidal reefs

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**ABSTRACT:** Colonisation of patches disturbed at different times of the year and at different locations was investigated from November 1995 to August 1997 in subtidal, rocky-shore, algal assemblages (Mediterranean Sea, Italy). A field experiment tested specifically: (1) whether and how the success of turf-forming, encrusting and erect algae are influenced by the timing of disturbance and (2) whether recovery of these species is consistent across space (from about 1 m to 100s of metres). Clearings were made at 8 different times within 1 year, in order to identify possible temporal trends in responses of algae to disturbance. Reproductive traits of the most abundant algae were also investigated. Encrusting, turf-forming and erect algae responded differently to spatial and temporal variation in disturbance, depending on their varying abilities to colonise available space and on spatial and temporal differences in rates of recruitment and growth. Turf-forming algae colonised space by vegetative propagation and quickly regained spatial dominance in patches cleared at all times of the year and at all locations. Conversely, encrusting and erect species occupied space mostly by colonisation of propagules; their recruitment was influenced by the timing and location of disturbance, probably depending on the concomitant availability of bare rock, viable propagules and favourable environmental conditions. A regime of disturbance adverse to recruitment of erect algae was identified as the probable cause of their low abundance in the study area. Overall, results suggested that while recruitment by sexual propagules can be highly variable through space and time, recovery by vegetative propagation can be constant and highly predictable over a range of environmental conditions, and that vegetative reproduction is likely to be fundamental to spatial dominance in a variety of habitats.

**KEY WORDS:** Disturbance · Patch dynamics · Spatial and temporal scale · Recruitment · Vegetative propagation · *Polysiphonia setacea* · *Acetabularia acetabulum* · Encrusting coralline algae

## INTRODUCTION

Disturbances in natural environments occur over a wide range of spatial and temporal scales (Sousa 1984a, Pickett & White 1985), and their frequency and intensity have been shown to exert an important effect on the distribution and dynamics of species (Dayton 1971, Paine & Levin 1981, Kennelly 1987, Dayton et al. 1992). Many assemblages are commonly affected by disturbance events that are small relative to the area of

the habitat (Palumbi & Jackson 1982, Hawkins & Hartnoll 1983, Dye 1993, Benedetti-Cecchi & Cinelli 1994). These disturbances cause the partial or total removal of some organisms within the assemblage, thus generating localised, discrete, gaps of open space (referred to as 'non-isolated' or Type 1 patches, Pickett & White 1985) that are often colonised soon after they are formed.

Colonisation of disturbed patches is largely controlled by local environmental characteristics, by the time of the year when the assemblage is disturbed and by the life-histories of the individual species (Connell & Slatyer 1977, Sousa 1980, Hawkins 1981, Keough 1984, Breitbart 1985, Reed 1990, Menge et al. 1993).

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Of particular importance appears to be the different abilities of species to colonise available space by recruitment of sexual propagules or by vegetative propagation. In some marine and terrestrial habitats, for example, it has been suggested that recovery of small patches proceeds mostly by lateral encroachment of neighbouring individuals, while larger patches are mainly colonised by immigration of propagules (Sousa 1979, 1984b, Paine & Levin 1981, Pickett & White 1985, Farrell 1989, but see Airoidi 1998). Experimental work has also shown that time of patch formation may have greater effects on colonisation of species that persist by sexual reproduction than on species that colonise space by vegetative propagation (Kim & DeWreede 1996). Variable responses to disturbance by species with different abilities to colonise space may, therefore, be fundamental in influencing the structure and dynamics of assemblages (Foster 1975, Sousa et al. 1981, McCook 1994, Shumway & Bertness 1994, Airoidi 1998). Yet, while recruitment of species that secure space by dispersal of propagules has received great attention (for reviews and discussions see Gaines & Roughgarden 1985, Underwood & Fairweather 1989, Santelices 1990, Booth & Brosnan 1995), comparably fewer studies have investigated the role of space occupancy by species via vegetative growth (Abrahamson 1980, Sousa 1980, McCook & Chapman 1992, 1997).

Subtidal habitats on exposed rocky shores south of Livorno (Ligurian Sea, Italy) are colonised by a dense assemblage consisting mostly of filamentous turf-forming algae, encrusting calcareous algae and a few species of erect algae (Airoidi et al. 1995). Previous observations and experiments have indicated that these algae have different abilities to procure and hold available space (Airoidi 1998, 2000). Turf-forming algae were able to retain space by vegetative propagation, while encrusting and erect algae needed bare rock for settlement of sexual propagules. Moreover, erect algae were outcompeted by turf-forming algae, while encrusting algae were able to grow and dominate primary substrata despite a cover of turf-forming algae. Overall, success of different species was suggested to be potentially related to temporal variability in rates of colonisation following disturbance (Airoidi & Cinelli 1997, Airoidi 1998). Limited temporal replication of previous experiments, however, did not allow quantitative predictions of colonisation of patches disturbed at different times of the year. The degree of variation was also potentially influenced by the scale of observation (Airoidi & Virgilio 1998), as the relative abundance of species varied in proximate locations of the shore (Airoidi 1998). Predicting colonisation success of different species needed, therefore, extensive investigations across a range of spatial and temporal scales.

In this study, I investigated variations in spatial and temporal recovery of turf-forming, encrusting and erect algae in discrete patches of bare rock produced at different times of the year and at different locations. A multifactorial field experiment was conducted to test specifically: (1) whether and how the overall success of turf-forming, encrusting and erect macroalgae were influenced by the timing of disturbance events and (2) whether patterns of recovery of these species were consistent across a range of spatial scales (from about 1 m to 100s of metres). Experimental clearings were produced at 8 different times over 1 year, in order to identify possible predictable temporal trends in algal responses to disturbance. Reproductive traits and natural fluctuations in cover of the most abundant algae were also investigated to assess whether and how patterns of recovery were related to the life-histories of the different species and to spatial and/or temporally variable availability of propagules. This paper will focus on responses of individual most abundant algae to variable disturbance, while responses at an assemblage level will be presented in a subsequent paper (L.A. unpubl.).

## STUDY AREA

The research was conducted using SCUBA at 3 stations on a wave-exposed rocky reef south of Livorno (Fig. 1A), at depths of 10 to 13 m. Stations were chosen at random and were located 100s of metres apart (Fig. 1B). At the depths where the study was done, macro-herbivores were virtually absent during most of the year, and disturbance was mainly related to wave action and sediment scour. Previous studies showed that the intensity of these factors varied greatly through time (Airoidi et al. 1996), with maximal disturbance generally occurring in the autumn (mid-September to mid-December), and winter (mid-December to mid-March). Disturbance by sediments and waves generally did not affect the overall cover of turf-forming and encrusting algae (Airoidi & Virgilio 1998, Airoidi 2000), but violent, episodic, perturbations sometimes produced small, discrete patches of bare rock ranging from 5 cm<sup>2</sup> up to about 500 cm<sup>2</sup>.

At all stations, the bottom consisted of gently sloping sandstone platforms that had eroded to form fields of dense rocky outcrops. On their upper surfaces, the outcrops supported an assemblage dominated by encrusting and turf-forming algae (Airoidi et al. 1995). Encrusting algae mostly consisted of non-geniculate corallines. Also present were some species of *Peyssonnelia*, usually *Peyssonnelia harveyana* P. L. et H. M. Crouan ex J. Agardh and *Peyssonnelia squamaria* (Gmelin) Decaisne. Encrusting algae were covered by

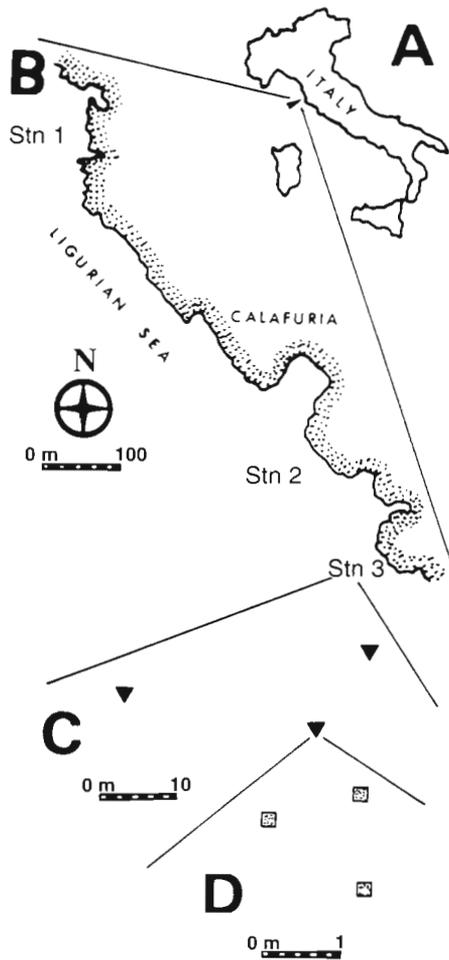


Fig. 1. (A) Location of the study area; (B) location of the 3 stations (Stns 1, 2 and 3); (C) example of location of 3 randomly chosen sites within a station; (D) example of location of 3 randomly chosen plots within a site. Symbols for stations, sites and plots are not to scale

a dense filamentous turf up to 1 cm high, mostly consisting of the species *Polysiphonia setacea* Hollenberg, which alone generally represented more than 95% of the total biomass of turf algae (Airoldi et al. 1995; further information about the ecology of *P. setacea* is given in Airoldi 1998). A few erect algae were also present, but they were generally small in size (rarely more than 5 cm high) and they did not form a canopy. Most of these algae, including *Dictyota dichotoma* (Hudson) Lamouroux, *Padina pavonica* (Linnaeus) Lamouroux and *Acetabularia acetabulum* (Linnaeus) P. C. Silva, were apparent seasonal annuals, which were present as visible macroscopic fronds for a few months during the spring and summer. Conversely, *Halimeda tuna* (Ellis et Solander) Lamouroux and *Flabellia petiolata* (Turra) Nizamuddin were persistent as visible macroscopic fronds throughout the year.

## METHODS

Spatial and temporal variability in colonisation of algae following discrete disturbances were investigated by means of a  $3 \times 3$  factorial experiment in which patches of bare rock were produced at different times and locations. In the study area, natural patches were generally smaller than  $500 \text{ cm}^2$  (pers. obs.), and previous experiments with patches ranging from  $144$  to  $400 \text{ cm}^2$  showed that patch size was relatively unimportant in influencing recovery of this assemblage compared to timing of disturbance (Airoldi 1998). An intermediate patch size of  $225 \text{ cm}^2$  ( $15 \times 15 \text{ cm}$ ) was used in this experiment. Patches were cleared of all resident organisms, including encrusting algae, by using a hammer and chisel. The heterogeneity of the substratum, rich in crevices, made scraping sometimes difficult; prostrate axes of algae in the deepest crevices were probably not completely removed, which is similar to the natural situation observed in the area after disturbance (pers. obs.), but the amount of such remnants was always less than 1% cover. Patches were cleared at 8 randomly chosen times from October 1995 to September 1996 (Table 1). At each time, 3 patches were cleared at each of 3 sites (about  $9 \text{ m}^2$ ) randomly placed 10s of metres apart within each of the 3 stations (Fig. 1C,D). Patches were randomly established on the horizontal, top surface of outcrops 1 to 2 m apart, and permanently marked at their edges with epoxy putty (Subcoat S., Veneziani). Three additional sites, each with 3 unmanipulated  $15 \times 15 \text{ cm}$  plots, were established at each station to monitor spatial and temporal variations in abundance of natural algae during the experiment.

Percentage cover of algae in experimental patches was scored at 1 to 3 mo intervals over 1 yr since clearing. A central surface of  $10 \times 10 \text{ cm}$  was photographed by using a Nikonos III underwater camera equipped with an electronic flash and a 1:3 extension tube. In the laboratory, slides were projected onto a grid of 100

Table 1. Experimental design used to investigate spatial and temporal variability in colonisation of algae in a subtidal rocky reef

Timing of clearing	Stations	Sites	Patches
Oct 95	1, 2 and 3	1, 2 and 3	1, 2 and 3
Dec 95	1, 2 and 3	1, 2 and 3	1, 2 and 3
Jan 96	1, 2 and 3	1, 2 and 3	1, 2 and 3
Feb 96	1, 2 and 3	1, 2 and 3	1, 2 and 3
Mar 96	1, 2 and 3	1, 2 and 3	1, 2 and 3
May 96	1, 2 and 3	1, 2 and 3	1, 2 and 3
Jul 96	1, 2 and 3	1, 2 and 3	1, 2 and 3
Sep 96	1, 2 and 3	1, 2 and 3	1, 2 and 3

equally spaced dots, and the percentage cover of each species was expressed as the number of hits, after correction for points which laid over unidentifiable substratum (see Littler & Littler 1985). Algae present but not scored under grid intercepts (percentage cover <1%) were given an arbitrary cover value of 0.1%. Young specimens of *Halimeda tuna* and *Flabellia petiolata* were sometimes difficult to distinguish from photographs. Due to the relative scarcity of *F. petiolata* and to similarity in their life histories (van den Hoek et al. 1995), these 2 species were grouped as 'pluriannuals'. *Polysiphonia setacea* was by far the dominant turf-forming alga, but, as other species were mixed with it (Airoidi et al. 1995), the non-specific category 'turf' was used to designate the thick mat of filamentous species. Similarly, encrusting algae were difficult to identify from photographs and were grouped as 'crusts'.

The effects of timing and location of disturbance on colonisation success of different algae were analysed using 3-way, analyses of variance (ANOVAs), with Timing (8 times), Station (3 stations) and Site (3 sites) as random factors. Timing and Station were orthogonal to each other, while Site was nested in each combination of Timing and Station. Patterns of recruitment of some algae were highly seasonal, showing peaks of abundance during summer months (see 'Results'). Date-by-date comparisons of patches cleared at different times of the year would have confounded differences due to timing of disturbance with either seasonal trends or different ages of patches. Statistical analyses were, therefore, generally run by using as the dependent variable the percentage covers of each species in each plot averaged over sampling dates. This procedure allowed the estimation of the overall effects of location and timing of disturbance on the recruitment success of species, independent of their temporal periodicities. In the case of crusts, analyses were done on percentage covers after 2 to 3 mo from the beginning of each colonisation, as, after that time, recruits of crusts were covered by turf (see 'Results'); thus it was no longer possible to quantify their abundance. In the case of turf, visual inspection of graphs showed that it reached a plateau in all the experimental patches, with values above 70% cover (see 'Results'). Although restoration of a dense, adult turf takes longer (Airoidi & Virgilio 1998), recovery to values above 70% is an important stage in the maintenance of spatial dominance by turf (Airoidi 1998). The effects of timing and location of disturbance on the overall success of turf were, therefore, quantified in terms of differences in colonisation rates rather than in average abundance, and the analysis was run by using the slopes of the regression lines of percentage covers as the dependent variable in individual plots over those months before cover reached values above 70%. Spatial variability of adult, unmanipulated algae was an-

alysed by using 2-way ANOVAs, with Station (3 stations) and Site (3 sites, nested in Station) as random factors, and with the average percentage cover of each species over sampling dates as the dependent variable. Due to non-independent sampling of individual plots over time, temporal trends were analysed by visual inspection of graphs. Before running ANOVAs, the assumption of homogeneity of variances was examined using Cochran's *C*-test, and angular transformations were used to stabilise variances when necessary. When Timing was found to have a significant effect on colonisation of algae, Ryan's tests were used for *a posteriori* multiple comparisons of means among plots cleared at different times (Day & Quinn 1989), in order to identify possible temporal trends in the responses of algae to disturbance.

At each time when patches were cleared, algae removed were collected and sorted in the laboratory, to assess their reproductive status. All erect algae were collected and examined, while for crusts and turf only a random subsample of 5 × 5 cm was analysed. *Acetabularia acetabulum* and crusts were the only conspicuous algae that were found to be fertile (see 'Results'). Reproduction of crusts was detected under a stereomicroscope as presence of conceptacles. Gametangia, carposporangia and sporangia were not separated. Crusts were decalcified using 5% HCl, and fertile and non-fertile portions of the thallus were divided. The wet biomass of each component was weighed. Fertility was measured as ratio of the biomass of fertile portions over the total biomass of crusts (fertile + non fertile), expressed as a percentage. Spatial and temporal variability in fertility of crusts was analysed with a 3-way ANOVA, with Time (8 times), Station (3 stations) and Site (3 sites, nested in each combination of Times and Station) as random factors. The relationship between early recruitment of crusts and fertility of within-site adult crusts at the time when patches were cleared was measured with a linear correlation between the average fertility of crusts at each site and time and the average cover of crusts at each site after 2 to 3 mo from the beginning of each colonisation.

## RESULTS

### Spatial and temporal patterns of unmanipulated algae

Crusts were abundant on primary substrata, but due to overgrowth by turf they could not be quantified by photographic sampling. Turf and pluriannuals were persistent during the study, although their cover fluctuated over time (Fig. 2). Cover of turf was generally greater than 70%, reaching maximal values during

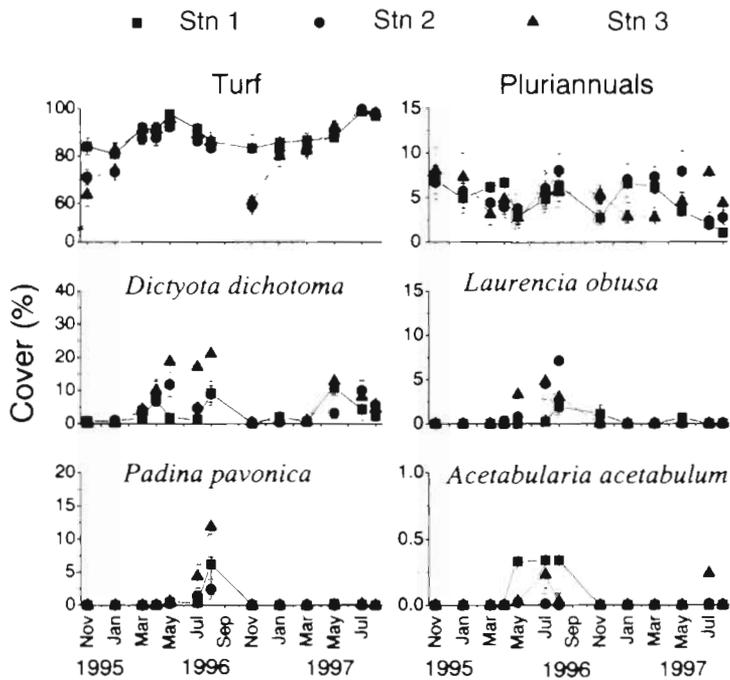


Fig. 2. Temporal variations of most abundant macroalgae in subtidal rocky reefs South of Livorno. Data are mean percentage covers ( $\pm$ SE,  $n = 9$ ) at 3 stations (Stns 1 to 3) from November 1995 to August 1997. Data were pooled across 3 sites within each station

spring and summer months at all stations. Cover of pluriannuals fluctuated between 1 and 8%, but no clear temporal trends were observed (Fig. 2). Abun-

dance of apparent seasonal erect algae was low during most of the year. *Dictyota dichotoma*, *Laurencia obtusa* (Linnaeus) Lamouroux, *Padina pavonica* and *Acetabularia acetabulum* were present in the area as macroscopic detectable stages only for a few months during spring and summer (Fig. 2). Only a few other erect species were observed, including *Wrangelia penicillata* (C. Agardh) C. Agardh and *Tricleocarpa fragilis* (Linnaeus) Huisman et Townsend, but these occurred too sporadically for meaningful analyses.

Cover of turf was similar among sites, while significant differences were detected among stations (Table 2). Differences among stations occurred mostly during November 1996 (Fig. 2). Covers of pluriannuals and *Dictyota dichotoma* varied significantly among sites, while no differences were observed in the overall abundance of these species among stations. Abundance of other species varied greatly among nearby patches within sites, as suggested by large standard errors (Fig. 2), possibly masking patterns at larger spatial scales.

### Reproductive traits

*Acetabularia acetabulum* and crusts were the only common algae that were found to be fertile. *A. acetabulum* first occurred as a macroscopic visible stage in May (Fig. 2), when it appeared as elongated sterile

Table 2. ANOVAs of covers of dominant macroalgae at different stations and sites. Factors: Station (3 stations, random) and Site (3 sites, random, nested in Station). Analyses were run using the covers (%) of each alga in each plot averaged over sampling dates as the dependent variable. ns = non-significant, \* $p < 0.05$ , \*\* $p < 0.01$

	Source of variation	df	MS	F	Cochran's C-test (transformation)
Turf	Station	2	67.29	6.31*	C = 0.46 ns
	Site	6	10.66	1.12 ns	(None)
	Residual	18	9.45		
Pluriannuals	Station	2	1.40	0.11 ns	C = 0.41 ns
	Site	6	12.65	6.06**	(None)
	Residual	18	2.08		
<i>Dictyota dichotoma</i>	Station	2	42.27	0.88 ns	C = 0.44 ns
	Site	6	48.11	5.49**	(None)
	Residual	18	8.76		
<i>Laurencia obtusa</i>	Station	2	1.13	0.43 ns	C = 0.47 ns
	Site	6	2.66	2.63 ns	(None)
	Residual	18	1.01		
<i>Padina pavonica</i>	Station	2	2.46	1.88 ns	C = 0.37 ns
	Site	6	1.31	1.69 ns	(None)
	Residual	18	0.77		
<i>Acetabularia acetabulum</i>	Station	2	0.01	0.98 ns	C = 0.87**
	Site	6	0.01	1.21 ns	(None)
	Residual	18	0.01		

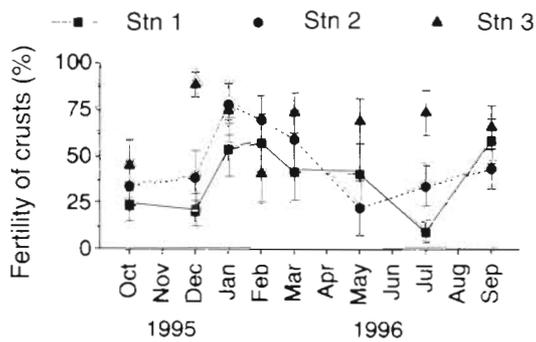


Fig. 3. Fertility of crusts from October 1995 to September 1996 at 3 stations (Stns 1 to 3). Data are means ( $\pm$ SE,  $n = 9$ ) pooled across 3 sites within each station. Fertility was quantified as the ratio of the biomass of fertile portions over the total biomass of crusts (fertile + non fertile), expressed as %

stalks. Within 1 to 2 mo, these developed reproductive cups, consisting of whorls of gametangial rays. Release of gametes by gametangial cysts generally occurs shortly before cups become senescent (Bonotto 1994), which happened towards the end of the summer at all stations.

Crusts were reproductive throughout the year. Fertility fluctuated over time (Fig. 3), but these differences were not significant (Time:  $F_{7,48} = 1.4$ ,  $p > 0.05$ ; Time  $\times$  Station:  $F_{14,48} = 1.38$ ,  $p > 0.05$ ). Fertility was similar across nearby sites (Site [Time  $\times$  Station]:  $F_{48,144} = 1.27$ ,  $p > 0.05$ ), whereas significant differences were observed among stations (Station:  $F_{2,48} = 6.69$ ,  $p < 0.01$ ), with higher values at Stn 3 compared to Stns 1 and 2 (Fig. 3).

No sexual reproductive structures were recorded for the turf-forming alga *Polysiphonia setacea*. So far, vegetative propagation is the only form of reproduction that has been observed both in the field and in culture for specimens of this species from various areas of the Mediterranean (Airoldi 1998 and references therein, Rindi et al. 1999). No reproductive structures were detected for any of the other species, for which sexual reproduction is known to commonly occur throughout the time period that they are present as visible stages. Fertile specimens (gametangia) of *Halimeda tuna* were observed in the field in August and September. Only sterile individuals were, however, present in the samples collected.

### Effects of timing and location of disturbance

#### Crusts

Crusts were always among the first colonisers of bare rock, reaching up to 68% cover in 2 mo (Fig. 4). After that time, recruits of crusts became largely covered by turf, which made it difficult to

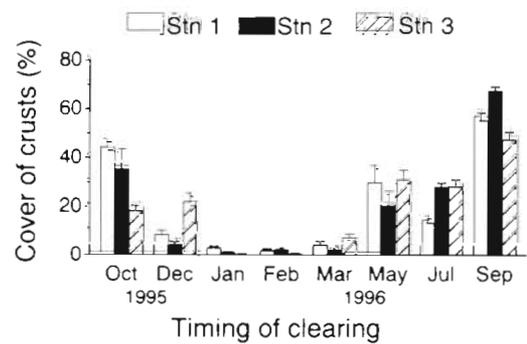


Fig. 4. Recruitment of crusts in patches of bare rock cleared at 3 stations (Stns 1 to 3) and at 8 different times (October 1995 to September 1996). Data are mean percentage covers ( $\pm$ SE,  $n = 9$ ) measured after 2 to 3 mo since patches were cleared. Data are pooled across 3 sites within each station

quantify their growth over a longer time. Crusts colonised space mostly by recruitment of propagules and subsequent vegetative growth, but lateral invasion by surrounding specimens was also occasionally observed. Early recruitment of crusts was highly variable in time and space (Table 3). Recruitment was generally less in patches cleared from December 1995 to March 1996 (Fig. 4), but responses of crusts to timing of disturbance differed across stations, as indicated by the significant Timing  $\times$  Station interaction and by Ryan's tests (Table 3). Recruitment of crusts also differed significantly among sites within stations (Table 3). This spatial and temporal variability was not related to differences in fertility of within-site adult crusts at the times when patches were cleared (linear correlation:  $r^2 = 0.01$ ,  $p > 0.05$ ).

#### Turf

Visual inspection of plots showed that turf colonised bare space mostly by lateral encroachment from the periphery and regrowth of surviving prostrate axes. Recovery of turf was always quick, generally following an S-shaped curve (Fig. 5). After an initial exponential growth phase, turf reached a plateau in a few months with values of about 70 to 100% cover. Rates of recovery of turf significantly differed among patches cleared at different times and locations (Table 3). Recovery was generally quicker in patches cleared in December 1995 and January 1996 (Fig. 5), but this pattern was significant only at Stn 2 (Ryan's test, Table 3). Recovery of turf also differed significantly among sites within stations (Table 3). Initial differences in rates of recovery, however, decreased over time, and after 1 yr the percentage cover of turf was similar at all stations, independent of the original timing of clearing (Fig. 5).

Table 3. ANOVAs of effects of timing and location of disturbance on colonisation success of dominant macroalgae. Factors: Timing (8 times, random), Station (3 stations, random) and Site (3 sites, random, nested in Timing  $\times$  Station). Dependent variables: for Crusts, the covers (%) after 2 to 3 mo from the beginning of colonisation; for Turf, the slopes of the regression lines of covers (%) in each plot over those months before cover reached values above 70%; for all other species, the covers (%) in each plot averaged over sampling dates (for more information see 'Methods'). ns = non-significant, \* $p < 0.05$ , \*\* $p < 0.01$  \*\*\* $p < 0.001$

Source of variation	df	MS	F	Cochran's C-test (transformation)	Ryan's test
<b>Crusts</b>					
Timing = T	7	1.927	19.96***		
Station = S	2	0.001	0.01 ns	C = 0.107 ns	Stn 1: Sep = Oct > May > Jul = Dec = Mar = Jan = Feb
T $\times$ S	14	0.097	3.87***	(Angular)	Stn 2: Sep > Oct = Jul = May > Dec = Mar = Feb = Jan
Site (T $\times$ S)	48	0.025	2.58***		Stn 3: Sep > May = Jul = Dec = Oct > Mar = Feb = Jan
Residual	144	0.009			
<b>Turf</b>					
Timing = T	7	351.9	6.73**		
Station = S	2	257.4	4.92*	C = 0.069 ns	Stn 1: Jan = Dec = Mar = Jul = Oct = May = Sep = Feb
T $\times$ S	14	52.3	2.21*	(None)	Stn 2: Jan = Dec > Oct = Mar = Jul = May = Sep = Feb
Site (T $\times$ S)	48	23.7	2.24***		Stn 3: Jan = Mar = Jul = May = Dec = Oct = Sep = Feb
Residual	144	10.5			
<b>Pluriannuals</b>					
Timing = T	7	5.97	1.93 ns		
Station = S	2	0.67	0.22 ns	C = 0.078 ns	
T $\times$ S	14	3.09	1.66 ns	(None)	
Site (T $\times$ S)	48	1.86	3.14***		
Residual	144	0.59			
<b><i>Dictyota dichotoma</i></b>					
Timing = T	7	141.1	3.17*		
Station = S	2	11.5	0.26 ns	C = 0.113 ns	Stn 1: Mar = May > Sep = Feb = Jan = Jul = Oct = Dec
T $\times$ S	14	44.5	2.88**	(None)	Stn 2: May = Sep = Jul = Mar = Oct = Feb = Dec = Jan
Site (T $\times$ S)	48	15.5	1.59*		Stn 3: May = Feb > Jan = Sep = Mar = Jul = Dec = Oct
Residual	144	9.7			
<b><i>Laurencia obtusa</i></b>					
Timing = T	7	37.1	0.64 ns		
Station = S	2	43.1	0.75 ns	C = 0.093 ns	Stn 1: Sep = Oct = Jul = Mar = Dec = May = Feb = Jan
T $\times$ S	14	57.8	4.73***	(Angular)	Stn 2: Mar = May = Feb = Dec = Jan = Oct = Jul = Sep
Site (T $\times$ S)	48	12.2	2.27***		Stn 3: Oct > May = Mar = Dec = Feb = Jan = Jul = Sep
Residual	144	5.4			
<b><i>Padina pavonica</i></b>					
Timing = T	7	119.5	4.25*		
Station = S	2	149.9	5.33*	C = 0.107 ns	
T $\times$ S	14	28.1	1.41 ns	(Angular)	Jul > Sep = Oct = Mar = Dec = May = Feb = Jan
Site (T $\times$ S)	48	19.9	1.35 ns		
Residual	144	14.7			
<b><i>Acetabularia acetabulum</i></b>					
Timing = T	7	419.0	9.82***		
Station = S	2	85.5	2.01 ns	C = 0.096 ns	Stn 1: Sep > Oct = Jul = Jan = Dec = May = Mar = Feb
T $\times$ S	14	42.6	2.76**	(Angular)	Stn 2: Oct = Sep > Jul = Feb = Jan = Mar = May = Dec
Site (T $\times$ S)	48	15.4	2.21***		Stn 3: Oct = Sep > Dec = Jul = May = Mar = Jan = Feb
Residual	144	7.0			

### Erect algae

All erect algae colonised patches of bare rock by immigration of propagules. Colonisation of pluriannuals showed an increasing trend over time (Fig. 6). This pattern generally reflected an increase in size of firstly settled individuals rather than an increase in number of new recruits. Pluriannuals were not affected by timing or by location of disturbance (Table 3), as colonisation rates were similar among patches cleared at different

times and stations (Fig. 6). Conversely, colonisation of pluriannuals differed among patches in nearby sites (Table 3). Patterns of recruitment of other erect algae were highly variable over time, showing peaks of abundance during summer months. Timing of clearing significantly influenced their recruitment success, although its effects generally varied depending on the species and location of patches, resulting in significant Timing  $\times$  Station effects for all species except *Padina pavonica* (Table 3). Recruitment of apparent seasonal

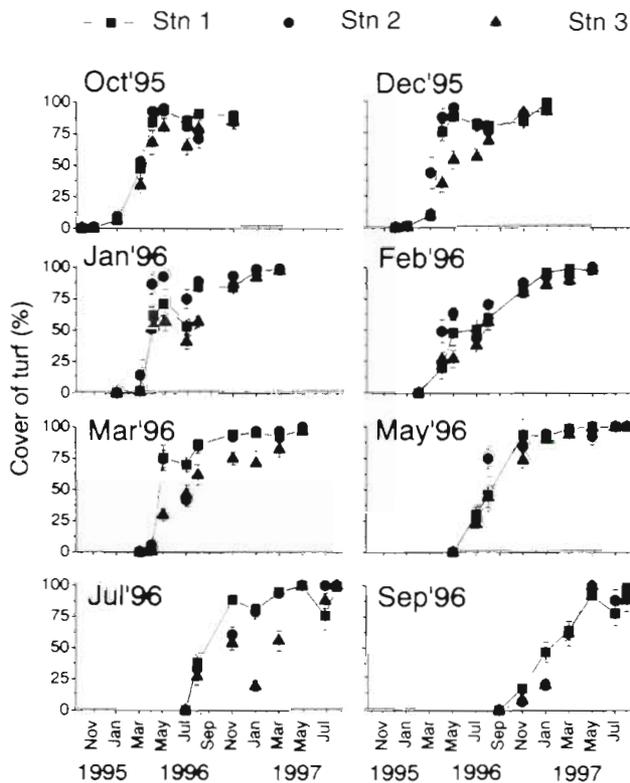


Fig. 5. Cover of algal turf in patches of bare rock cleared at 8 different times (October 1995 to September 1996) and at 3 different stations (Stns 1 to 3). Data are mean percentage covers ( $\pm$ SE,  $n = 9$ ) over 1 yr since patches were cleared. Data are pooled across 3 sites within each station

algae was also generally variable among sites within stations (Table 3). For the sake of brevity, only graphs relative to *Dictyota dichotoma* and *Acetabularia acetabulum* are shown (Figs. 7 & 8). Recruitment of *D. dichotoma* was generally greater in patches cleared during February to May 1996 (Fig. 7), but patterns were significant only at Stns 1 and 3 (Ryan's test, Table 3). *A. acetabulum* (Fig. 8) and *P. pavonica* recruited almost exclusively in patches cleared in September and October 1996 and in July 1996, respectively, and such patterns were generally consistent among stations (Ryan's tests, Table 3). *Laurencia obtusa* recruited in patches cleared at all times of the year. Its overall abundance was generally greater in patches cleared in spring and autumn months, but such differences were generally not statistically significant (Ryan's test, Table 3).

## DISCUSSION

Crusts, turf and erect algae responded differently to spatial and temporal variation in disturbance. Such variable patterns appeared to be related to their differ-

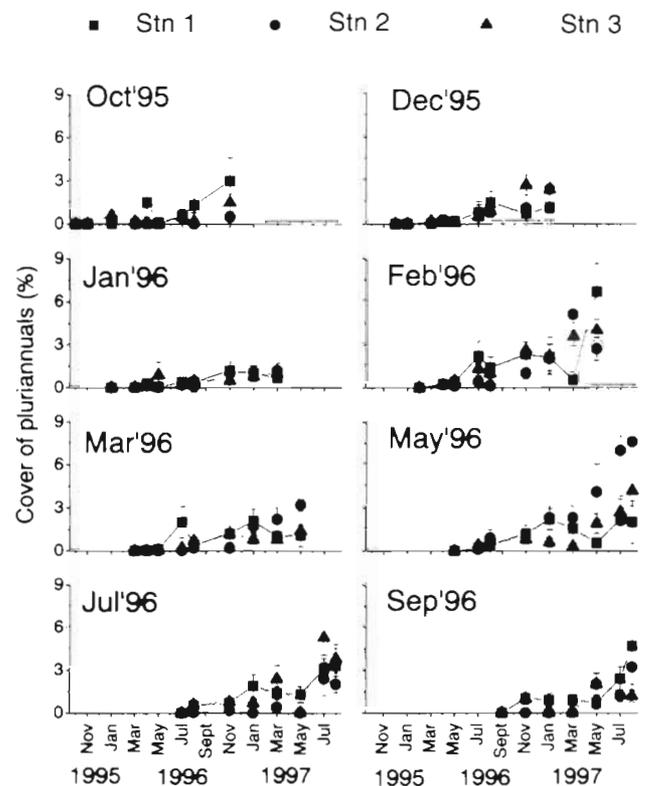


Fig. 6. Cover of plurianual algae in patches of bare rock cleared at 8 different times (October 1995 to September 1996) and at 3 different stations (Stns 1 to 3). Data are mean percentage covers ( $\pm$ SE,  $n = 9$ ) over 1 yr since patches were cleared. Data are pooled across 3 sites within each station

ent abilities to colonise available space and to spatial and temporal differences in rates of recruitment and growth. Algal turf, which occupied space by vegetative propagation, was able to quickly regain spatial dominance in patches cleared at all times of the year and at all locations, despite significant differences in rates of recovery. Conversely, recruitment of crusts and erect species, which occupied space mostly by dispersal of sexual propagules, was influenced by the timing and location of disturbance, probably depending on the concomitant availability of bare rock, propagules and favourable environmental conditions.

In many marine habitats, including the study area, severe disturbances are rare, and often tend to occur at certain times of the year. Examples of periodic, predictable disturbances include storms, sand inundations, desiccation, changes in water chemistry and human-related perturbations (Dayton 1971, Littler et al. 1983, Witman 1987, Breitbart 1992, Williams 1994, Airolidi et al. 1996, Keough & Quinn 1998). The results of this study clearly indicate that temporal variability of disturbance may significantly affect the colonisation and persistence of algae that recruit by propagules. Some erect

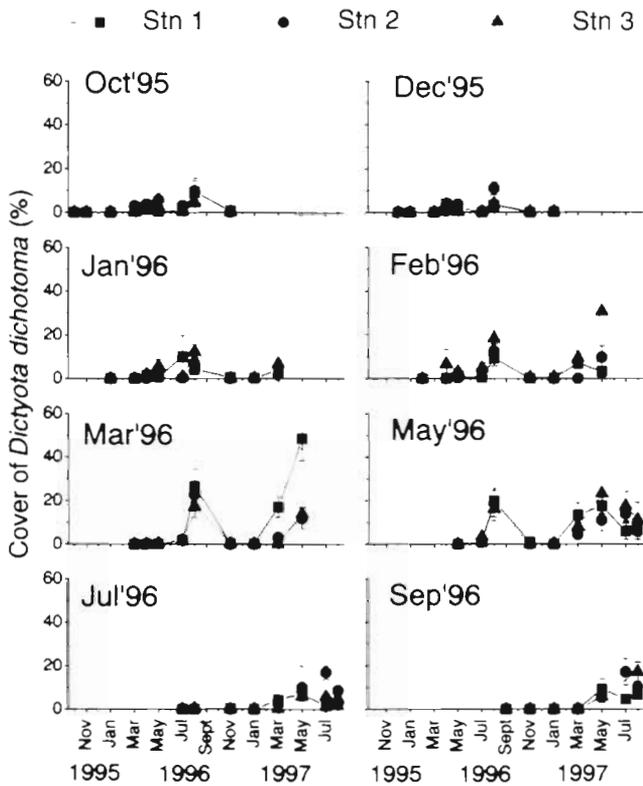


Fig. 7. Cover of *Dictyota dichotoma* in patches of bare rock cleared at 8 different times (October 1995 to September 1996) and at 3 different stations (Stns 1 to 3). Data are mean percentage covers ( $\pm$ SE,  $n = 9$ ) over 1 yr since patches were cleared. Data are pooled across 3 sites within each station

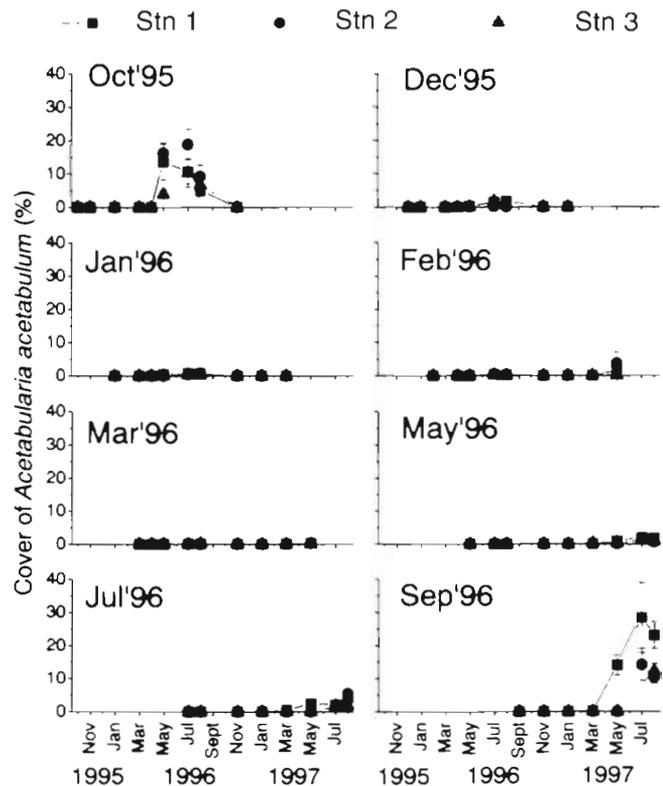


Fig. 8. Cover of *Acetabularia acetabulum* in patches of bare rock cleared at 8 different times (October 1995 to September 1996) and at 3 different stations (Stns 1 to 3). Data are mean percentage covers ( $\pm$ SE,  $n = 9$ ) over 1 yr since patches were cleared. Data are pooled across 3 sites within each station

algae, like *Acetabularia acetabulum* and *Padina pavonica*, had restricted colonisation 'windows' (sensu Reed et al. 1988, Menge et al. 1993), only recruiting in patches cleared during late-summer and early-autumn months. *Dictyota dichotoma* and *Laurencia obtusa*, conversely, colonised bare rock throughout the year, although their abundances were generally greater in patches cleared in spring to early autumn months.

This temporal variability in the responses of algae to disturbance suggests that it might be possible to predict yearly patterns of abundance of some species from annual variations in the timing of disturbance (see also Turner 1983). For *Dictyota dichotoma* this hypothesis was supported by consistency of results of this study with results of previous experiments on the same assemblage (Airoldi & Cinelli 1997, Airoldi 1998). In such experiments, when patches of bare rock were cleared in June and December 1992 and 1994, respectively, recruitment of *D. dichotoma* was always significantly greater in patches cleared in June than in those cleared in December, as also observed in this study. Responses of *Padina pavonica* and *Acetabularia acetabulum* to variable timing of disturbance, how-

ever, were not consistent across experiments done in different years. Moreover, rates of colonisation of species varied in proximate locations on the shore and, in a previous experiment, were affected by the size of the patch and by the amount of sediment deposition (Airoldi 1998). Given this spatial and temporal variability, predicting quantitative differences in the abundance of erect algae among patches disturbed at different times and locations is probably difficult. Nevertheless, results from this and previous experiments and from observations gathered during several years in this area (Airoldi et al. 1995, Airoldi & Cinelli 1997, Airoldi 1998) suggest that patches cleared in late autumn and winter consistently support less erect algae than patches cleared at any other time of the year. At depths where this study was done, herbivores are scarce (Airoldi 2000), and severe disturbance, which opens patches of bare rock, occurs primarily in late autumn and winter from storms and scouring by sediments (Airoldi et al. 1996, Airoldi & Virgilio 1998). This regime of disturbance, unfavorable to recruitment of some erect algae, might be responsible for their low abundance in the study area.

Temporally variable recruitment of algae is often attributed to temporal differences in the availability of propagules in the water column, which is related to the timing of reproduction (Sousa 1984b, Reed et al. 1988, Benedetti-Cecchi & Cinelli 1994, Kendrick & Walker 1994, Kim & DeWreede 1996, but see Ang 1991). Contrary to other species that are not reproductive during the winter, crusts were reproductive throughout the year, as also observed in other studies (Adey & Vassar 1975, Dethier 1981, Davis & Wilce 1987, Kaehler & Williams 1997). Early rates of recruitment of crusts, however, were significantly lower during winter and were spatially very variable. These differences were not related to the fertility of within-site adult conspecifics at the time when patches were cleared, suggesting that spatial and temporal differences in recruitment of crusts were probably influenced by factors other than the potential production of propagules. These factors might include hydrodynamic or other environmental factors affecting the dispersal, settlement, germination rate or survival of propagules. Recruitment of some algae may be negatively affected by sediment deposition and scour (Devinny & Volse 1978, Reed et al. 1988, Kendrick 1991, Umar et al. 1998), which in the study area are intense during autumn and winter and are spatially variable (Airoldi & Virgilio 1998). Previous experiments on this assemblage (Airoldi & Cinelli 1997, Airoldi 1998), involving manipulation of rates of sediment deposition, suggested that early recruitment of crusts was negatively influenced by the presence of sediments (Airoldi unpubl. data). Rapid cover by turf, however, made it difficult to quantify the importance of this process over adequately long times, and further studies are necessary to test the hypothesis that low recruitment of crusts observed during the winter might have been related to high disturbance by sediments.

Regardless of variation in rates of recruitment, crusts were able to colonise patches cleared at all times of the year and at all locations. Crusts were always among the first colonisers of bare rock (see also Adey & Vassar 1975, Dethier 1981, Kendrick 1991, Figueiredo 1997), thus colonising primary space before lateral invasion by turf. Specific long-term experiments on the ecology of crusts have shown that, in contrast to erect algae, crusts were able to grow and colonise additional space even after they became covered by turf (Airoldi 2000). The ability to continuously colonise available space, and the high tolerance for overgrowth by turf over a long time have been identified as the major determinants of the quantitative success of crusts in this assemblage (Airoldi 2000).

Temporal and spatial variability of disturbance had little effect on colonisation by turf, which quickly regained spatial dominance in all clearings by lateral

vegetative encroachment and regrowth of surviving prostrate axes. Recovery was most fast in patches cleared in December 1995 and January 1996 and significantly differed among sites, but differences observed were, quantitatively, small. Similarly, in previous experiments, cover of turf was little affected by variable sizes of disturbance and by different levels of sediment deposition (Airoldi 1998, Airoldi & Virgilio 1998). These results suggest that spatially and temporally variable disturbance has less effect on algae that recover by vegetative propagation than on algae that recruit by sexual propagules (see also Kendrick & Walker 1994, Kim & DeWreede 1996). These different responses to disturbance may depend on the fact that vegetative propagating thalli appear to be less vulnerable to a variety of physical and biological factors (e.g. wave action, sediment stress, bottom instability, herbivory, competition) than are sexual propagules (Hansen 1977, Sousa 1980, Sousa et al. 1981, D'Antonio 1986, Davis & Wilce 1987, McCook & Chapman 1992, Airoldi 1998). Thus vegetative propagation should be an important mechanism of recovery after most common disturbances (Davis & Wilce 1987, Airoldi 1998), especially when damage to algae is patchy (Sousa 1980, McCook & Chapman 1997).

Results show that while recruitment by sexual propagules can be highly variable through space and time, recovery by vegetative propagation can be constant and predictable over a range of environmental conditions. This lack of variability can have important consequences on successional processes and on the dynamics of algal assemblages. Current models of community structure and dynamics emphasise the role of variability in rates and timing of recruitment (Connell 1985, Gaines & Roughgarden 1985, Underwood & Fairweather 1989, Sutherland 1990). The present study, conversely, reinforces the increasing evidence that the ability to rapidly and continuously recover by vegetative reproduction can be a major determinant of persistent spatial dominance in a variety of marine habitats (Karlson 1978, Lubchenco & Menge 1978, Sousa et al. 1981, D'Antonio 1986, Vadas et al. 1990, McCook & Chapman 1992, Airoldi 1998), which is consistent with more extensive observations on terrestrial assemblages (van Groenendael et al. 1997 and references therein). It appears thus important that future research focuses on factors affecting the ability of marine species to propagate vegetatively, and on the potential role of this life-history trait in influencing responses of assemblages to disturbances.

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