

Recovery after trampling disturbance in a canopy-forming seaweed population

Araújo Rita · Sousa-Pinto Isabel · Ester A. Serrão · Åberg Per

Received: 20 July 2011 / Accepted: 21 November 2011
© Springer-Verlag 2011

Abstract The recovery of *Ascophyllum nodosum*, and the associated benthic community, was followed after repeated trampling disturbance at different intensities, from 2005 to 2010, at its southern limit (41°41'27"N; 8°50'57"W). The cover of *A. nodosum* and associated organisms and the demography of *A. nodosum* individuals in the most disturbed areas were followed over a recovery period of 54 months. Recovery of *A. nodosum* assemblages was negatively affected by increasing trampling intensity. After 54 months, the highest intensity plots were still significantly different from control plots. Growth and mortality rates of *A. nodosum* increased shortly after disturbance but progressively recovered to levels close to control plots. The results of this study demonstrate the sensitivity of this habitat-building species to human trampling and also show its plasticity to cope with disturbance events.

Communicated by F. Bulleri.

A. Rita (✉) · S.-P. Isabel
Centre of Marine and Environmental Research,
University of Porto (CIMAR-Porto), Rua dos Bragas,
289, 4050-123 Porto, Portugal
e-mail: ritaraujo@ciimar.up.pt

S.-P. Isabel
Department of Biology, Faculty of Sciences,
University of Porto, Rua do Campo Alegre,
s/n, 4050 Porto, Portugal

E. A. Serrão
Centre of Marine Sciences,
University of Algarve (CIMAR-Algarve),
Campus of Gambelas, 8005-139 Faro, Portugal

Å. Per
Department of Marine Ecology, University of Gothenburg,
Box 461, 40530 Göteborg, Sweden

Introduction

Disturbance is a structuring factor in intertidal habitats. Perturbation events often remove organisms, increasing mortality, and also release resources such as space, nutrients and light that may enhance the appearance of new colonists (Connell et al. 1997). As a result of these contrasting effects, post-disturbance communities are frequently different from initial communities in terms of composition and dominance of species (Paine and Levin 1981; Sousa 1984; Shea et al. 2004).

Intertidal communities are under the influence of a variety of sources of disturbance that shape their structure. These include physical disturbance, resulting among other factors from the effects of waves, sedimentation and ice scouring (Sousa 2001), and anthropogenic disturbance, often related to direct effects of human use of coastal areas for recreational activities and commercial harvesting (Schiel and Taylor 1999; Griffiths et al. 2006; Milazzo et al. 2004).

Foundation species such as canopy algae provide habitat, shelter and food for a number of associated organisms (Keough and Quinn 1998; Schiel and Taylor 1999) and modify the spatial complexity of communities, locally conditioning light, temperature, hydrodynamics, sedimentation and competition for substrate (Reed and Foster 1984; Duggins et al. 1990; McCook and Chapman 1991; Platt and Connell 2003). Disturbance events affecting foundation species may therefore change the structure of the entire community. There is evidence that several intertidal species (including canopy algae) are sensitive to anthropogenic disturbance (Benedetti-Cecchi et al. 2001; Mangialajo et al. 2008) in particular to human trampling-related activities (Milazzo et al. 2002, 2004; Araújo et al. 2009).

Ascophyllum nodosum is a dominant canopy species on sheltered intertidal rocky shores of the North Atlantic, with a marginal isolated population on the northern Portuguese coast. *A. nodosum*-dominated communities are sensitive to disturbance events in general (e.g. Jenkins et al. 1999; Cervin et al. 2004) and in particular to human trampling (Araújo et al. 2009). Previous studies based on manipulative experiments through total clearance of *A. nodosum* plants in experimental plots showed that the composition of communities changed in the short term (Jenkins et al. 1999; Dudgeon and Petraitis 2001; Bertness et al. 2002; Cervin et al. 2004). After few years, canopy cover was restored, but the identity of the dominant canopy species was changed to *Fucus* spp. (Jenkins et al. 2004; Cervin et al. 2005). Studies following the temporal evolution of these communities over longer periods found no recovery to the original pre-disturbance state even after 20 years (Jenkins et al. 2004; Cervin et al. 2005; Ingolfsson and Hawkins 2008).

The short-term negative effects of human trampling in *A. nodosum* communities have been experimentally demonstrated at the species southern limit (Araújo et al. 2009). In this study, at the two highest trampling intensities tested, the structure of the entire community was significantly affected, by lowering the abundance of *A. nodosum*, *Fucus vesiculosus* and understory species and increasing the abundance of ephemeral green algae (Araújo et al. 2009). Recovery from disturbance events is highly related to the amount of damage to the algae, being delayed when the canopy and the holdfast are simultaneously removed (Underwood 1998; Speidel et al. 2001). Thus, depending on the source and intensity of disturbance, different patterns of recovery could be expected. The effects of human trampling on individual algae are not uniform within plots, causing either the removal of the entire canopy (sometimes including also the holdfasts) or the detachment of parts of the plant.

Species life history traits are also important determinants for the recovery of communities following disturbance (Methratta and Petraitis 2008). *A. nodosum* is a dioecious long-lived species (Åberg 1992a, b), with low recruitment rate (Åberg and Pavia 1997; Dudgeon and Petraitis 2005) and extremely slow growth rate of recruits (Åberg and Pavia 1997; Cervin et al. 2005). The temporal development of the *A. nodosum* canopy following trampling should be based on both recruitment rates and on the vegetative growth rate of the remaining algae following trampling. However, in marginal populations at their distributional limits, differentiated life history traits might be expected due to local selective environmental conditions. This differentiation in phenotypic traits was found in border *A. nodosum* population when compared with more central populations in France (Araújo et al. 2011).

Specifically, the edge populations were denser, with smaller individuals and higher recruitment rates than centrally distributed populations. These already differentiated traits might be indicative of adaptive changes that might further reduce the plastic capability to face additional perturbations to the population.

Few studies have attempted to understand the specific life history traits associated with the recovery process following disturbance in populations of seaweeds. The aims of this study were to (i) investigate the long-term (54 months) pattern of recovery in plots of *A. nodosum* subjected to different intensities of trampling and (ii) document the phenotypic traits associated with the recovery of highly disturbed areas.

Materials and methods

Study area

This study was performed in Viana do Castelo (41°41'27"N; 8°50'57"W) on communities dominated by *A. nodosum*, between December 2005 and 2010. In Viana do Castelo, *A. nodosum* occurs at mid-intertidal levels in sheltered areas together with other furoids such as *F. vesiculosus*, *F. spiralis* and *Pelvetia canaliculata* (see Araújo et al. 2009 for a complete description of the shore). The maximum tidal amplitude is about 4.0 m on the northern Portuguese coast, and sea surface temperature varies between 13 and 20°C during a year. Under the *A. nodosum* canopy, temperatures vary approximately between 4 and 25°C with a mean annual value of 16°C (Araújo et al. 2011).

Experimental design and sampling

In December 2005, twelve experimental plots of 2.5 × 2.5 m, dominated by *A. nodosum*, were chosen, and three of these plots were randomly allocated to each of the 4 levels of trampling intensities. The levels of disturbance intensity were categorized as follows: (1) control (no tramples, C); (2) low intensity of disturbance (5 tramples, LD); (3) medium intensity of disturbance (15 tramples, MI); and (4) high intensity of disturbance (30 tramples, HI). The LI and MI were based on field observations of human trampling, and the HI was a scenario of higher trampling intensity. At each of the 10 disturbance events during a period of 5 months, each of the 4 levels of trampling intensities was applied to the corresponding experimental plots (for details about the experimental design during the trampling period, see Araújo et al. 2009). Plots were sampled before the start of the experimental trampling

period, at the end of the trampling period and 3 times during the recovery phase (12, 36 and 54 months after the end of experimental treatments). Experimental plots were divided into 25 quadrats of 50 × 50 cm, and three randomly chosen quadrats were sampled within each plot at each sampling date. Percentage cover of *A. nodosum* and other sessile organisms was assessed by means of non-destructive methods (Dethier et al. 1993) using a plastic frame divided into 25 quadrats of 10 × 10 cm, assigning to each taxon a score ranging from 0 to 4 per quadrat and adding up the 25 estimates. Densities of mobile organisms were expressed as number of individuals per quadrat. Whenever necessary, sampling was stratified in different layers and the estimates of cover were made for each layer separately (Dethier et al. 1993).

To study the dynamics of life history traits of *A. nodosum* during the recovery period in highly disturbed plots (HI) and compare it with undisturbed plots, the demographic variables mortality, fertility and growth rates were estimated and the biomass–frequency distribution of individuals was assessed 3, 9 and 48 months after the trampling disturbance had stopped. Inside each of the 2.5 × 2.5 m HI and control plots, 2 quadrats of 50 × 50 cm were randomly chosen and tagged in the corners with plastic tags and screws. The position of all the *A. nodosum* individuals inside the quadrat was registered, and if the individual was sufficiently large, it was also tagged with a glass bead tag. The dry weight of these individuals was estimated by measuring the maximum length (l) and circumference (c) at each sampling date (Åberg 1990). The predictive equation obtained (Araújo et al. 2011) for the Portuguese populations of *A. nodosum* is $\ln(\text{dry weight}) = 0.7841 * \ln(lc^2) - 3.2066$ ($r = 0.97$; $n = 71$). Monthly estimates of the demographic variables were calculated to allow the comparison between the variables for different time periods.

Monthly mortality was calculated as

$$M = 1 - [(N_{t+x}/N_t)^{(1/x)}]$$

where N_t is number of individuals in a plot at time t and N_{t+x} those who survived to $t + x$ where x is number of months between two sampling events.

Monthly fertility was calculated as

$$F = (N_{juv,t+x}/B_{adult,t})/x$$

where $N_{juv,t+x}$ is the number of new individuals at time $t + x$ and B_t is the total biomass of adult individuals in a plot at time t .

Monthly mortality rates were calculated for recruits and non-recruits separately because the mortality of *A. nodosum* recruits is documented to be very high (Dudgeon and Petraitis 2005).

Monthly growth rate of biomass was calculated as

$$G = (B_{t+x}/B_t)^{1/x}$$

where B is biomass at time t or $t + x$.

Demographic variables were calculated by joining the individuals of the two 50 × 50 cm quadrats of each 2.5 × 2.5 m plot because at the beginning of the recovery period, the total number of individuals in disturbed plots was very low.

The biomass–frequency distribution of *A. nodosum* individuals was represented according to the biomass classes used by Araújo et al. (2011). The biomass classes above 54 g were not included in the analysis since there were no individuals belonging to these groups.

Statistical analysis

The effects of the different intensities of disturbance along the recovery period were tested in individual species using ANOVA and in the structure of the whole assemblage using permutational multivariate analysis of variance [PERMANOVA (Anderson 2001)]. PERMANOVA was done on Bray–Curtis dissimilarity coefficients, calculated on non-transformed data. Analysis included the factors intensity (In), 4 fixed orthogonal levels (0, 5, 15 and 30 tramples) and plot (Pl), 3 fixed levels nested on the factor In, with 9 replicates. Analyses were conducted separately for each sampling date to avoid dependence of data. The effects of the highest source of disturbance in the dynamics of the population over time were tested using ANOVA. To test for significant differences in the demographic parameters growth and fertility, two separate ANOVAs were performed including the factors treatment (2 fixed orthogonal levels corresponding to disturbed and undisturbed plots) and time (2 fixed orthogonal levels corresponding to the sampling times). To test for significant differences in mortality rates, the analysis included the factors treatment (2 fixed orthogonal levels corresponding to disturbed and undisturbed plots), time (2 fixed orthogonal levels corresponding to the sampling times) and life class (2 fixed orthogonal levels corresponding to the recruits and the rest of the individuals of the population). The data from the demographic parameters 3 months after disturbance stopped were only graphically represented and were not included in the statistical analysis since there were no data available for the same time period for undisturbed plots. Before each ANOVA, the assumption of homogeneity of variances was tested using Cochran's test, and when necessary, data were transformed (Underwood 1997). When homogeneity of variances was not fulfilled with any data transformation, significance of the test was considered with $p < 0.01$. Student–Newman–Keuls (SNK) tests were used for post hoc comparisons of significant means.

Effects of experimental treatments on the structure of the whole assemblage were visualized by comparing the temporal trajectories of centroids describing the “average” assemblage. Principal coordinates (Gower 1966) from the Bray–Curtis dissimilarity matrix were calculated, and centroids were then obtained as arithmetic averages of the principal coordinates over the 9 replicates per sampling time (McArdle and Anderson 2001). Multivariate patterns were visualized with the non-metric MDS plot based on Euclidean distance that was generated with PRIMER (Clarke and Gorley 2001).

Results

Overall, the results of this study demonstrated that the trampling intensities tested significantly affected the *A. nodosum* communities over the recovery period.

Specifically, the results of the multivariate analysis showed that the effects of the different trampling intensities tested on the structure of the whole assemblage differed according to the sampling date (Table 1). At the end of the trampling experimental period, control plots differed from the two highest intensity plots (MI and HI), and HI plots differed from LI and MI plots (Table 1; Fig. 1). The highest intensity assemblages (MI and HI) had similar development during the first 3 years of the recovery period (Fig. 1), and at the end of this period, they still differed significantly from LI and C plots (Table 1). At the end of the study (after 54 months), MI plots seem to have totally recovered and were not significantly different from C and LI plots (Table 1). However, HI plots at the end of the study still significantly differed from C plots (Table 1; Fig. 1). In some of the sampling dates, significant differences were recorded between plots (Table 1). The results of temporal development of individual species showed that in LI plots, *A. nodosum* progressively increased its cover during the recovery period, but abundances similar to C plots were only reached after 36 months (Table 2; Fig. 2a).

In the two highest intensity plots (MI and HI), the cover of *A. nodosum* was still below 30% after 36 months, but after this period, it started to increase significantly (Table 2; Fig. 2a). At the end of the recovery period, cover values in MI and HI plots were similar to the ones in C plots. Conversely, *F. vesiculosus* greatly increased its cover in MI and HI plots after the end of the trampling disturbance and was the dominant canopy species until 36 months after disturbance stopped (Fig. 2b). In MI plots, cover of *F. vesiculosus* reached 65.11% (± 9.95 , $N = 9$) after 12 months and 73.11% (± 6.00 , $N = 9$) after 36 months, and in HI plots, 80.77% (± 2.33 , $N = 9$) after 12 months and 77.00% (± 6.00 , $N = 9$) after 36 months (Fig. 2b). However, the cover of *F. vesiculosus* was drastically reduced during the period between 36 and 54 months, and at the end of the recovery period, no significant differences were detected between different trampling intensities and the control (Table 3). Cover of *Ulva* sp. was greatly reduced during the recovery period, and 12 months after the end of disturbance, there were no significant differences recorded between experimental treatments (Fig. 2c, data not shown). Cover of understory macroalgal species fluctuated over the recovery period, but no significant differences were detected between treatments (Fig. 2d, data not shown).

Data obtained for the demographic parameters show that, in general, *A. nodosum* population traits changed in the short term but over time progressively approached the values found in undisturbed patches. During the first 9 months of recovery, population structure in terms of the distribution of individual’s biomass had little variation and remained dominated by the individuals belonging to the two smallest biomass classes (recruits and individuals smaller than 5 g) (Fig. 3). The only noticeable change during this period was the increase in the number of individuals belonging to classes larger than 5 g 3 months after disturbance stopped and the increase in the number of recruits between 3 and 9 months following disturbance (Fig. 3). In the period between 9 and 48 months after

Table 1 PERMANOVA testing the effects of intensity of disturbance on the structure of the whole *A. nodosum* community during the recovery period

Sources of variation	df	Ti 1 (before)		Ti 2 (after)		Ti 3 (12 months)		Ti 4 (36 months)		Ti 5 (54 months)	
		MS	Pseudo- <i>F</i>	MS	Pseudo- <i>F</i>	MS	Pseudo- <i>F</i>	MS	Pseudo- <i>F</i>	MS	Pseudo- <i>F</i>
Intensity (In)	3	914.48	1.32 n.s.	6097.54	8.98***	7322.28	17.03***	5830.01	14.06***	1261.68	3.24**
Plot (Pl)	8	6501.37	1.17 n.s.	1097.38	1.62 n.s.	1466.60	3.41**	56.10	1.24 n.s.	1478.09	3.80***
Residuals	24										
Pair wise <i>a posteriori</i> comparisons (<i>t</i> test)				C \neq MI; C \neq HI; LI \neq HI; MI \neq HI		C = LI \neq MI = HI		C = LI \neq MI = HI		C \neq HI	

n.s. non-significant; ** $p < 0.01$; *** $p < 0.001$

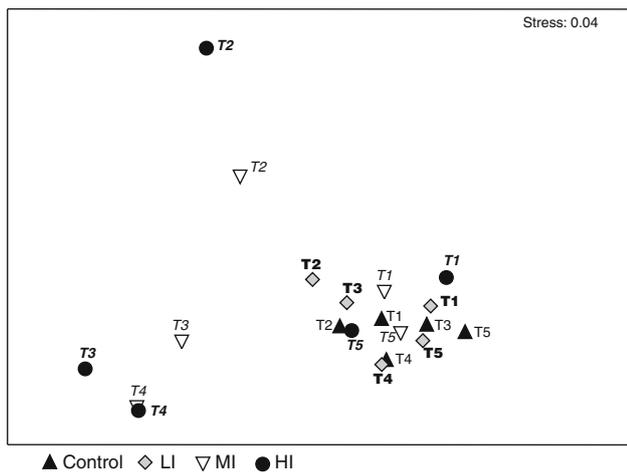


Fig. 1 Temporal trajectories of *A. nodosum* assemblages exposed to different trampling intensities. Symbols represent centroids of the “average” community in each plot and were calculated using principal coordinates (further details in the text). Different times of sampling are numbered from 1 to 5. T1 represents composition of assemblages before trampling disturbance started, T2 corresponds to the assemblages at the end of trampling disturbance, and T3, T4 and T5 correspond to assemblages at 12, 36 and 54 months after disturbance ended, respectively. Control no disturbance; LI low intensity of disturbance (5 tramples), MI medium intensity of disturbance (15 tramples), HI high intensity of disturbance (15 tramples)

disturbance, the number of recruits decreased and the distribution of biomass in the population closely resembled the one of undisturbed patches, except for the number of fronds belonging to the biggest biomass class (>15 g) that was still lower (Fig. 3). At the beginning of the recovery period, mean monthly growth rate of *A. nodosum* biomass in trampled plots was higher than that in control plots. Over the recovery period, the growth rate progressively decreased, but at the end of the study, the rates were still different from the ones of undisturbed patches (Fig. 4; Table 4). The fertility rates followed a pattern similar to the growth rates, progressively decreasing over the study

period, but no significant differences were found between undisturbed and disturbed plots over time (Fig. 5; Table 4). Mortality rates were significantly higher at the beginning of the recovery period, both for the recruits and for the older individuals of the population, but after 48 months, mortality decreased and disturbed plots did not significantly differ from undisturbed ones (Fig. 6; Table 5).

Discussion

The results of this study demonstrate that trampling disturbance caused a long-term change in the structure of *A. nodosum* communities, which had not completely recovered, at the most severe disturbance intensity, after almost 5 years. *F. vesiculosus* was the dominant canopy species in the two highest trampling intensities until 36 months after disturbance but progressively diminished its abundance while being replaced by *A. nodosum*. Previous studies following the recovery of *A. nodosum* communities after disturbance during longer periods than that in our study (7–12 years) reported very slow progressive increase in cover of this species and partial permanent replacement of the canopy by *Fucus* sp. (Jenkins et al. 2004; Cervin et al. 2005). In those studies, the recovery process was exclusively dependent on the recruitment success. Slow growth of recruits, recruitment mortality, grazing by limpets and the presence of turfs were the factors pointed out to explain the limited *A. nodosum* recruitment rates and consequent slow canopy recovery (Bertness et al. 2002; Jenkins et al. 2004; Cervin et al. 2005). In the case of trampling disturbance, the regrowth of the canopy in disturbed areas is expected to be dependent on both newly recruited individuals and vegetative growth of algae that survived the disturbance. This vegetative growth of *A. nodosum* individuals is dependent on the place of frond breakage, the amount of biomass left and the age of the alga (David 1943; Lazo and Chapman 1996). In this study, the increase

Table 2 ANOVA testing the effects of trampling intensities on the percentage cover of *A. nodosum* during the recovery period

Sources of variation	df	T1 (before)		T2 (after)		T3 (12 months)		T4 (36 months)		T5 (54 months)	
		MS	F	MS	F	MS	F	MS	F	MS	F
Intensity (In)	3	262.37	0.43 n.s.	3736.19	16.10***	5876.69	6.28*	4982.26	18.61***	1311.52	1.33 n.s.
Plot (PI)	8	603.56	1.02 n.s.	232.06	1.40 n.s.	935.44	5.11***	267.78	0.80 n.s.	986.89	2.66*
Residuals	35	589.78		165.83		183.19		332.75		370.56	
Cochran’s test		C = 0.22; n.s.		C = 0.28; n.s.		C = 0.28; n.s.		C = 0.26; n.s.		C = 0.27; n.s.	
Transformation		None		None		None		None		None	
				SNK test In (SE = 5.08)		SNK test In (SE = 10.20)		SNK test In (SE = 5.45)			
				In C ≠ LI ≠ MI = HI		In C = LI ≠ MI = HI		In C = LI ≠ MI = HI			

n.s. non-significant; * p < 0.05; *** p < 0.001

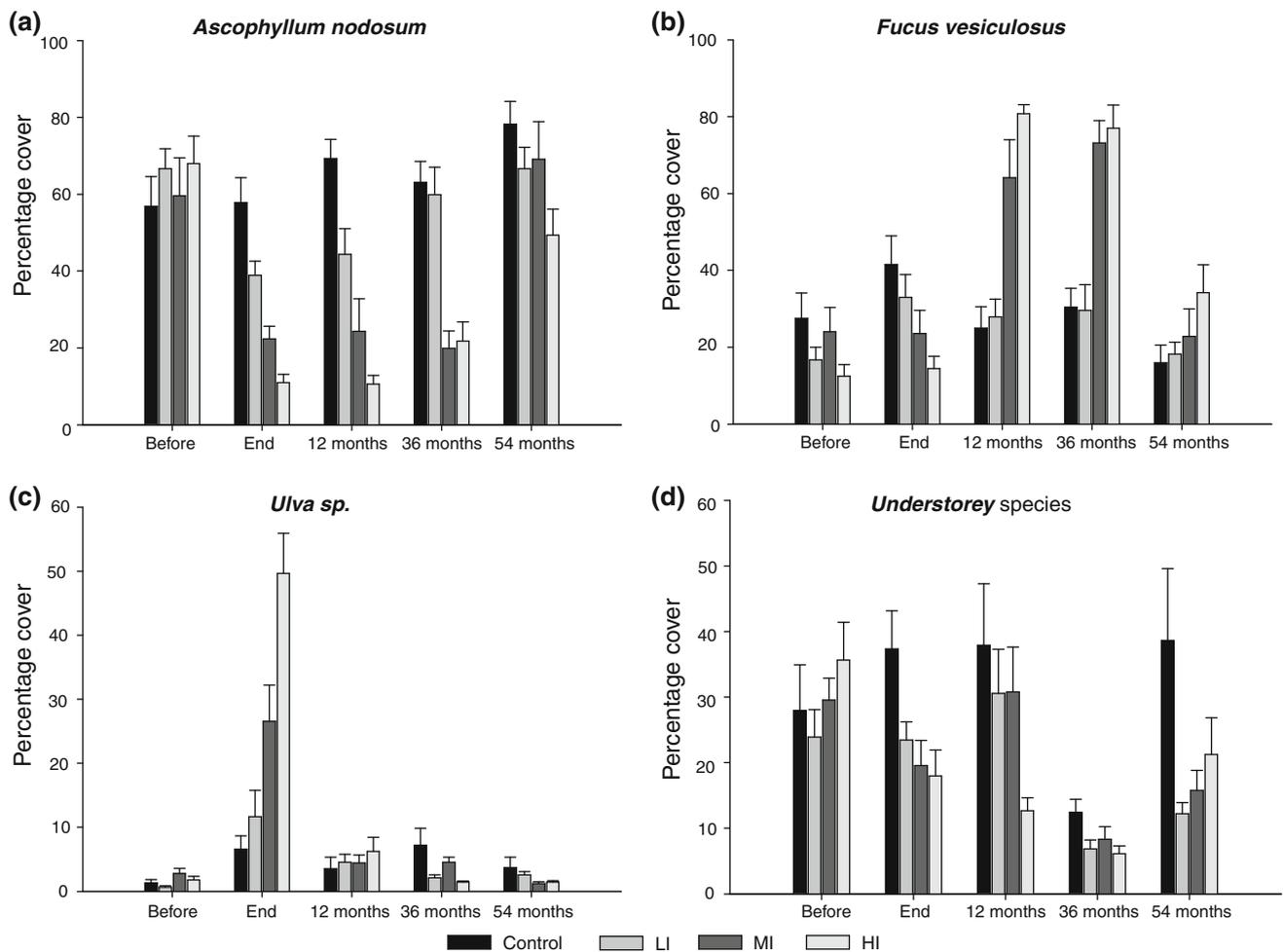


Fig. 2 Percentage cover (mean \pm SE, $n = 9$) of *A. nodosum* (a), *F. vesiculosus* (b), *Ulva* sp. (c) and remaining macroalgae understorey species (d), at different times of sampling and trampling intensities.

Control no disturbance; *LI* low intensity of disturbance (5 tramples), *MI* medium intensity of disturbance (15 tramples), *HI* high intensity of disturbance (15 tramples)

Table 3 ANOVA testing the effects of trampling intensities on the percentage cover of *F. vesiculosus* during the recovery period

Sources of variation	df	T1 (before)		T2 (after)		T3 (12 months)		T4 (36 months)		T5 (54 months)	
		MS	F	MS	F	MS	F	MS	F	MS	F
Intensity (In)	3	423.52	1.83 n.s.	1236.55	1.86 n.s.	6777.19	6.16*	6113.88	12.96**	592.99	0.77 n.s.
Plot (PI)	8	231.22	0.85 n.s.	666.33	2.80*	1100.50	6.84***	471.67	1.51 n.s.	774.92	3.98**
Residuals	35	272.78		237.58		160.97		312.75		194.47	
Cochran's test		C = 0.30; n.s.		C = 0.18; n.s.		C = 0.25; n.s.		C = 0.27; n.s.		C = 0.30; n.s.	
Transformation		None		None		None		None		None	
						SNK test In (SE = 11.06)		SNK test In (SE = 7.24)			
						In C \neq HI; LI \neq HI; LI \neq MI				In C = LI \neq MI = HI	

n.s. non-significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

in *A. nodosum* cover was progressively delayed and slower with the increase in trampling severity, which is in accordance with results obtained for harvested populations of the same species (Keser et al. 1981; Ang et al. 1996). Although

the recovery process in these patches seemed to have been mainly based in the vegetative growth of adult plants, recruitment occurred at all sampling periods in the highest trampled plots, and part of the recruits were able to grow

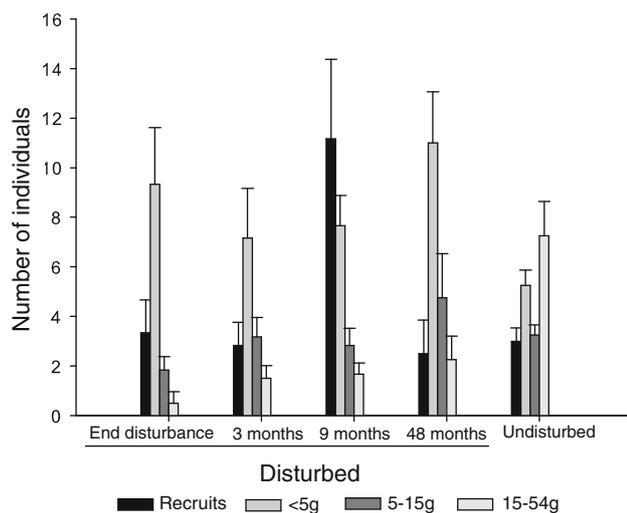


Fig. 3 Biomass–frequency distribution of *A. nodosum* individuals in highest intensity trampled plots at the end of trampling disturbance and 3, 9 and 48 months following disturbance and in undisturbed areas 48 months after disturbance

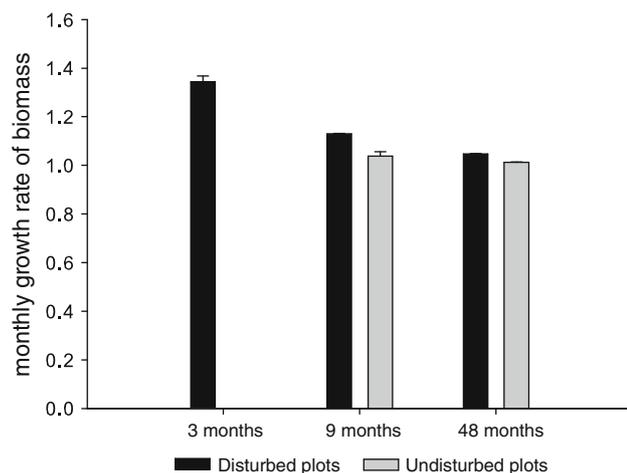


Fig. 4 Temporal variation in the monthly growth rate of *A. nodosum* biomass (mean \pm SE, $n = 3$) over the recovery period in the highest disturbance intensity and undisturbed areas

and switch to higher biomass classes. However, the role of these recruits in restoring the canopy was only visible at the end of the study, with an increase in the number of individuals in higher biomass classes. The incomplete removal of canopy, even in highest intensity treatments, might have been favourable for recruitment by causing an amelioration of living conditions under the canopy. The intermediate reduction in canopy cover (never lower than 10% of cover) presumably caused an increase in light penetration to the substrata (Clark et al. 2004) and diminished the sweeping of the substratum (Dudgeon and Petraitis 2005). On the other hand, this canopy cover might have been enough to reduce the physical stress caused by heat, desiccation and

water movement (Vadas et al. 1990; Brawley and Johnson 1991; Cervin and Åberg 1997) and the pressure of herbivores, which has been shown to be a determinant factor for recruitment of fucoids (Jenkins et al. 1999; Cervin et al. 2005).

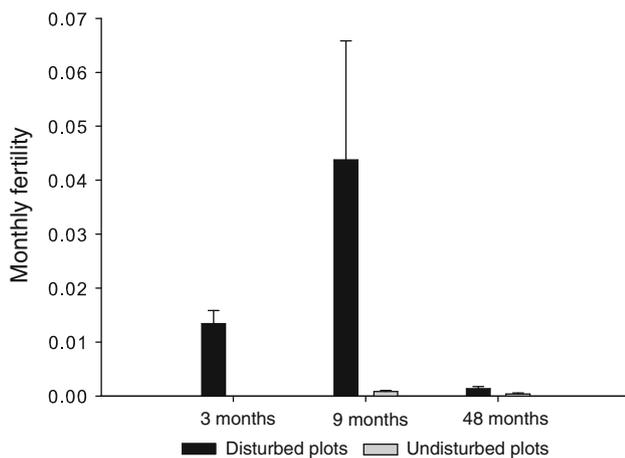
The pattern of temporal development of *F. vesiculosus* was opposite to the one of *A. nodosum*, showing a progressive reduction in cover over time, simultaneously with the increase in *A. nodosum* abundance. A similar result was obtained for the same species in studies of total removal of canopy (Jenkins et al. 2004; Ingolfsson and Hawkins 2008). Strong competition between *A. nodosum* and *F. vesiculosus* at the germling stage has been documented with the latter growing faster and outcompeting the first (Choi and Norton 2005). The rapid colonization of bare areas by *F. vesiculosus* after the removal of *A. nodosum* also show its superior competitive ability at later stages of development, at least in short time periods (Jenkins et al. 1999; Cervin et al. 2004). However, the intrinsic growth rate is only one of the factors influencing the competitive outcome between species. Although *F. vesiculosus* is a faster-growing species than *A. nodosum*, it has a much shorter lifespan, and in the long run, *A. nodosum* can prevail since it survives, even when growing below *F. vesiculosus* (Choi and Norton 2005). During the first succession stages, the presence of the *F. vesiculosus* canopy may positively affect the survival of *A. nodosum* germlings although probably reducing their growth rate (Choi and Norton 2005). Presumably, the disappearance of the first recruited *F. vesiculosus* plants coincided with the start of the recovery of *A. nodosum* canopy in the most severed disturbed plots, and that probably progressively inhibited further extensive *F. vesiculosus* colonization.

Life history traits of organisms might change under stressful conditions (Dethier et al. 2005) and populations' response might involve phenotypic differentiation via phenotypic plasticity (Fowler-Walker et al. 2006) to allow their local persistence (Hairston et al. 2005). The results of this study seem to be consistent with these theories since demographic parameters such as growth and mortality changed short after disturbance in the highest intensity plots with rates differentiated from undisturbed areas. However, at the end of the study, and together with the increase in percentage cover of *A. nodosum*, these rates converged to values close to the ones recorded in undisturbed plots. Evidence of phenotypic differentiation via phenotypic plasticity and local adaptation has been described for marine organisms (McAlister 2008; Holander and Butlin 2010) in particular for seaweeds (Shaughnessy 2004; Monro and Poore 2005; Fowler-Walker et al. 2006; Hays 2007). *A. nodosum* populations at northern and central locations show plasticity in life history traits that may increase their ability to cope with environmental variability

Table 4 ANOVA testing the differences in fertility and growth rate between highest intensity disturbed plots and undisturbed areas and sampling dates during the recovery period

Sources of variation	df	Fertility		Growth rate	
		MS	F	MS	F
Treatment (Tr)	1	0.0014	2.61 n.s.	0.0118	34.86***
Time (Ti)	1	0.0014	2.51 n.s.	0.0089	26.18***
Tr × Ti	1	0.0013	2.41 n.s.	0.0023	6.92*
Residuals	8	0.0005		0.0003	
Cochran's test		C = 1.00; $p < 0.01$		C = 0.97; $p < 0.01$	
Transformation		None		Ln(x + 1)	

n.s. non-significant; * $p < 0.05$; *** $p < 0.001$

**Fig. 5** Temporal variation in the monthly fertility of *A. nodosum* individuals (mean ± SE, $n = 3$) over the recovery period in the highest disturbance intensity and undisturbed areas

(Svensson et al. 2009), and phenotypic acclimation of physiological characteristics was described for *A. nodosum* plants living at different heights on the shore (Stengel and Dring 1997). Moreover, the border population here studied show differentiated phenotypic traits in comparison with more centrally distributed populations, having higher

reproductive output but lower growth rates, and this has been hypothesized to be a response to the stressful conditions faced at southern edges (Araújo et al. 2011). On the contrary, in this study, just after trampling disturbance, the recovery process seems to have been based on the allocation of resources for growth without significant changes occurring in fertility. This progressively changed over time, and after 4 years, the values were closer to the ones found for the rest of the population in undisturbed areas.

Differentiation of traits for persistence under unfavourable conditions is assumed to carry a physiological cost that is expressed in other fitness-related traits such as growth rate, defence capability and reproductive output (Jormalainen and Honkanen 2004; Dethier et al. 2005). In general, an increased reproductive investment at the expense of individual growth might be more valuable for individual fitness under stressful environmental conditions and an increase in reproductive effort for seagrasses (Marba and Duarte 1995; Alexandre et al. 2005) and terrestrial plants (Reekie 1998; Welham and Setter 1998) after perturbation has been documented. However, at the short term and when patches of bare space are available for colonization, a quick occupation of the substratum based on plants' vegetative regrowth might be a better strategy

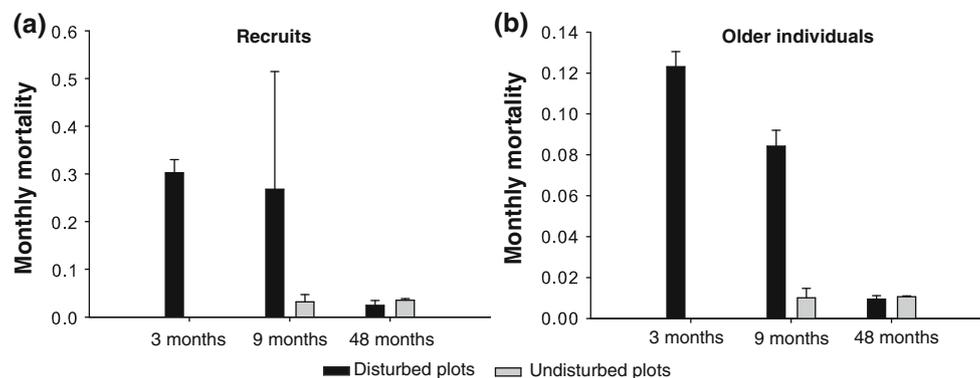
**Fig. 6** Temporal variation in the monthly mortality of *A. nodosum* recruits (a) and older individuals (b) (mean ± SE, $n = 3$) over the recovery period in the highest disturbance intensity and undisturbed areas

Table 5 ANOVA testing the differences in mortality rate between highest intensity trampled plots, sampling dates and life phases (recruits and remaining individuals of the population) during the recovery period

Sources of variation	df	Mortality rate	
		MS	F
Treatment (Tr)	1	0.1084	4.70*
Time (Ti)	1	0.1191	5.17*
Life phase (Lf)	1	0.0878	3.81 n.s.
Tr × Ti	1	0.1184	5.14*
Tr × Lf	1	0.0604	2.62 n.s.
Ti × Lf	1	0.0617	2.68 n.s.
Tr × Ti × Lf	1	0.0662	2.87 n.s.
Residuals	16	0.0230	
Transformation		None	
Cochran's test		0.99; $p < 0.01$	
		SNK test Tr × Ti (SE = 0.06)	
Time 1		Tr Disturbed ≠ Undisturbed	
Time 2		Tr Disturbed = Undisturbed	

n.s. non-significant; * $p < 0.05$

for recovery given the inferior competitive ability of *A. nodosum* embryos (Choi and Norton 2005). In stochastic environments, a higher investment in vegetative growth was recorded for *A. nodosum* plants belonging to the smaller size classes that were more affected by mortality. However, larger individuals with low mortality risk allocated more resources to reproduction (Åberg 1996), and this trend of increased reproductive investment with plant size is also described for other species (Weiner et al. 2009). As referred previously, once the *A. nodosum* canopy is partially restored, *F. vesiculosus* seems to be outcompeted. At that stage, a progressively higher investment for increasing the amount of recruits in the population might become more valuable for the population maintenance under environmental less-favourable conditions, as the ones found at marginal locations. The mortality rate of *A. nodosum* significantly increased in disturbed plots during the first months following disturbance. This might be explained by the fact that plants not removed by trampling were damaged and more susceptible to be affected by other disturbing factors such as wave action or movement of boulders.

The results of this study demonstrate that the negative effects of trampling in *A. nodosum*-dominated communities can persist for long periods at high intensities of disturbance. However, *A. nodosum* is able to increase its percentage cover in areas moderately disturbed by trampling, recovering its structure if the damage to the plants is not too severe. The progressive increase in the percentage cover of *A. nodosum* canopy together with the *F. vesiculosus* reduction in the heaviest trampled areas seems also to indicate that these communities will return to the pre-disturbance state in future. *Ascophyllum nodosum* has shown high plasticity in phenotypic traits during the recovery period, demonstrating its capability to find strategies for

persistence under environmental perturbation. This might be very important for the maintenance of these populations under a scenario of increasing environmental change, but it is yet unknown the extent of environmental change these populations are able to cope with.

These findings have important implications for the management of human frequentation in coastal ecosystems dominated by canopy-forming algae, in particular by *A. nodosum*. The current levels of human frequentation in the study area and the effects of the different trampling intensities tested on *A. nodosum* communities highlight the need of controlling the access to this area to avoid an increase in human frequentation to levels that might compromise the capability of recovery and persistence of these communities. Different management strategies have been proposed to overcome the over-frequentation of intertidal areas such as the construction of elevated boardwalks, fencing of sensitive areas (Carlson and Godfrey 1989), public education (Addison et al. 2008), rotation of frequentation zones (Milazzo et al. 2004) and monitoring programmes (Ferreira and Rosso 2009). Some of these solutions, e.g. the construction of elevated boardwalks, have been shown to have an associated visual and biological impact (Kelaheer et al. 1998). We recommend as management approaches for this area and others with similar conditions to combine the restriction of human frequentation with an increased effort for public education. The strategy to diminish the levels of human frequentation, either by fencing or by rotating frequentation zones, would have to be decided based on future experimental studies to determine the sustainable levels of human frequentation for these communities.

Acknowledgments This study was funded by projects and a fellowship (R.A.) of the Portuguese Foundation for Science and

Technology (FCT), co-funded by POCI 2010, FEDER and FSE, and the EU network of Excellence MARBEF—Marine Biodiversity and Ecosystem Function. We thank Iacopo Bertocci for helping in the data analysis.

References

- Åberg P (1990) Measuring size and choosing category size for a transition matrix study of the seaweed *Ascophyllum nodosum*. *Mar Ecol Prog Ser* 63:281–287
- Åberg P (1992a) A demographic study of 2 populations of the seaweed *Ascophyllum nodosum*. *Ecology* 73:1473–1487
- Åberg P (1992b) Size-based demography of the seaweed *Ascophyllum nodosum* in stochastic environments. *Ecology* 73:1488–1501
- Åberg P (1996) Patterns of reproductive effort in the brown alga *Ascophyllum nodosum*. *Mar Ecol Prog Ser* 138:199–207
- Åberg P, Pavia H (1997) Temporal and multiple scale spatial variation in juvenile and adult abundance of the brown alga *Ascophyllum nodosum*. *Mar Ecol Prog Ser* 158:111–119
- Addison PFE, Koss RS, O'Hara TD (2008) Recreational use of a rocky intertidal reef in Victoria: implications for ecological research and management. *Aust J Environ Manag* 15:169–179
- Alexandre A, Santos R, Serrao E (2005) Effects of clam harvesting on sexual reproduction of the seagrass *Zostera noltii*. *Mar Ecol Prog Ser* 298:115–122
- Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecol* 26:32–46
- Ang PO, Sharp GJ, Semple RE (1996) Comparison of the structure of populations of *Ascophyllum nodosum* (Fucales, Phaeophyta) at sites with different harvesting histories. *Hydrobiologia* 327:179–184
- Araújo R, Vaselli S, Almeida M, Serrão E, Sousa-Pinto I (2009) Effects of disturbance on marginal populations: human trampling on *Ascophyllum nodosum* assemblages at its southern distribution limit. *Mar Ecol Prog Ser* 378:81–92
- Araújo R, Serrão E, Sousa-Pinto I, Åberg P (2011) Phenotypic differentiation at southern limit borders: the case study of two fucoïd macroalgal species with different life-history traits. *J Phycol* 47:461–462
- Benedetti-Cecchi L, Pannacciulli F, Bulleri F, Moschella PS, Airoidi L, Relini G, Cinelli F (2001) Predicting the consequences of anthropogenic disturbance: large-scale effects of loss of canopy algae on rocky shores. *Mar Ecol Prog Ser* 214:137–150
- Bertness MD, Trussell GC, Ewanchuk PJ, Silliman BR (2002) Do alternate stable community states exist in the Gulf of Maine rocky intertidal zone? *Ecology* 83:3434–3448
- Brawley SH, Johnson LE (1991) Survival of fucoïd embryos in the intertidal zone depends upon developmental stage and microhabitat. *J Phycol* 27:179–186
- Carlson LH, Godfrey PJ (1989) Human impact management in coastal recreation and natural areas. *Biol Conserv* 49:141–156
- Cervin G, Åberg P (1997) Do littorinids affect the survival of *Ascophyllum nodosum* germlings? *J Exp Mar Biol Ecol* 218:35–47
- Cervin G, Lindegarh M, Viejo RM, Åberg P (2004) Effects of small-scale disturbances of canopy and grazing on intertidal assemblages on the Swedish west coast. *J Exp Mar Biol Ecol* 302:35–49
- Cervin G, Åberg P, Jenkins SR (2005) Small-scale disturbance in a stable canopy dominated community: implications for macroalgal recruitment and growth. *Mar Ecol Prog Ser* 305:31–40
- Choi HG, Norton TA (2005) Competition and facilitation between germlings of *Ascophyllum nodosum* and *Fucus vesiculosus*. *Mar Biol* 147:525–532
- Clark RP, Edwards MS, Foster MS (2004) Effects of shade from multiple kelp canopies on an understory algal assemblage. *Mar Ecol Prog Ser* 267:107–119
- Clarke KR, Gorley RN (2001) User manual/tutorial. PRIMER Ltd, Plymouth
- Connell JH, Hughes TP, Wallace CC (1997) A 30-year study of coral abundance, recruitment and disturbance at several scales in space and time. *Ecol Monogr* 67:461–488
- David HM (1943) Studies in the autecology of *Ascophyllum nodosum* Le Jol. *J Ecol* 31:178–198
- Dethier MN, Graham ES, Cohen S, Tear LM (1993) Visual versus random-point percent cover estimations: 'objective' is not always better. *Mar Ecol Prog Ser* 96:93–100
- Dethier MN, Williams SL, Freeman A (2005) Seaweeds under stress: manipulated stress and herbivory affect critical life-history functions. *Ecol Monogr* 75:403–418
- Dudgeon S, Petraitis PS (2001) Scale-dependent recruitment and divergence of intertidal communities. *Ecology* 82:991–1006
- Dudgeon S, Petraitis PS (2005) First year demography of the foundation species, *Ascophyllum nodosum*, and its community implications. *Oikos* 109:405–415
- Duggins DO, Eckman JE, Sewell AT (1990) Ecology of understory kelp environments 2. Effects of kelps on recruitment of benthic invertebrates. *J Exp Mar Biol Ecol* 143:27–45
- Ferreira MN, Rosso S (2009) Effects of human trampling on a rocky shore fauna on the São Paulo coast, southeastern Brazil. *Braz J Biol* 69:993–999
- Fowler-Walker MJ, Wernberg T, Connell SD (2006) Differences in kelp morphology between wave sheltered and exposed localities: morphology plastic or fixed traits? *Mar Biol* 148:755–767
- Gower JC (1966) Some distance properties and latent root and vector methods used in multivariate analysis. *Biometrika* 53:325–338
- Griffiths J, Dethier MN, Newsom A, Byers JE, Meyer JJ, Oyarzum F, Lenihan H (2006) Invertebrate community responses to recreational clam digging. *Mar Biol* 149:1489–1497
- Hairston NG Jr, Ellner SP, Geber MA, Yoshida T, Fox JA (2005) Rapid evolution and the convergence of ecological and evolutionary time. *Ecol Lett* 8:1114–1127
- Hays CG (2007) Adaptive phenotypic differentiation across the intertidal gradient in the alga *Silvetia compressa*. *Ecology* 88:149–157
- Holander J, Butlin RK (2010) The adaptive value of phenotypic plasticity in two ecotypes of a marine gastropod. *BMC Evol Biol* 10:333
- Ingolfsson A, Hawkins SJ (2008) Slow recovery from disturbance: a 20 year study of *Ascophyllum* canopy clearances. *J Mar Biol Assoc UK* 88:689–691
- Jenkins SR, Hawkins SJ, Norton TA (1999) Direct and indirect effects of a macroalgal canopy and limpet grazing in structuring a sheltered inter-tidal community. *Mar Ecol Prog Ser* 188:81–92
- Jenkins SR, Norton TA, Hawkins SJ (2004) Long term effects of *Ascophyllum nodosum* canopy removal on mid shore community structure. *J Mar Biol Assoc UK* 84:327–329
- Jormalainen V, Honkanen T (2004) Variation in natural selection for growth and phlorotannins in the brown alga *Fucus vesiculosus*. *J Evol Biol* 17:807–820
- Kelaker BP, Chapman MG, Underwood AJ (1998) Changes in benthic assemblages near boardwalks in temperate urban mangrove forests. *J Exp Mar Biol Ecol* 228:291–307
- Keough MJ, Quinn GP (1998) Effects of periodic disturbances from trampling on rocky intertidal algal beds. *Ecol Appl* 8:141–161
- Keser M, Vadas RL, Larson BR (1981) Regrowth of *Ascophyllum nodosum* and *Fucus vesiculosus* under various harvesting regimes in Maine, USA. *Bot Mar* 24:29–38

- Lazo L, Chapman ARO (1996) Effects of harvesting on *Ascophyllum nodosum* (L) Le Jol. (Fucales, Phaeophyta): a demographic approach. *J Appl Phycol* 8:87–103
- Mangialajo L, Chiantore M, Cattaneo-Vietti R (2008) Loss of fucoid algae along a gradient of urbanisation, and structure of benthic assemblages. *Mar Ecol Prog Ser* 358:63–74
- Marba N, Duarte CM (1995) Coupling of seagrass (*Cymodocea nodosa*) patch dynamics to subaqueous dune migration. *J Ecol* 83:381–389
- McAlister JS (2008) Evolutionary responses to environmental heterogeneity in Central American echinoid larvae: plastic versus constant phenotypes. *Evolution* 62:1358–1372
- McArdle BH, Anderson MJ (2001) Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology* 82:290–297
- McCook LJ, Chapman ARO (1991) Community succession following massive ice-scour on an exposed rocky shore—effects of fucus canopy algae and of mussels during late succession. *J Exp Mar Biol Ecol* 154:137–169
- Methratta ET, Petraitis PS (2008) Propagation of scale-dependent effects from recruits to adults in barnacles and seaweeds. *Ecology* 89:3128–3137
- Milazzo M, Chemello R, Badalamenti F, Riggio S (2002) Short-term effect of human trampling on the upper infralittoral macroalgae of Ustica Island MPA (western Mediterranean, Italy). *J Mar Biol Assoc UK* 82:745–748
- Milazzo M, Badalamenti F, Riggio S, Chemello R (2004) Patterns of algal recovery and small-scale effects of canopy removal as a result of human trampling on a Mediterranean rocky shallow community. *Biol Conserv* 117:191–202
- Monro K, Poore AGB (2005) Light quantity and quality induce shade-avoiding plasticity in a marine macroalga. *J Evol Biol* 18:426–435
- Paine RT, Levin SA (1981) Inter-tidal landscapes—disturbance and the dynamics of pattern. *Ecol Monogr* 51:145–178
- Platt WJ, Connell JH (2003) Natural disturbances and directional replacement of species. *Ecol Monogr* 73:507–522
- Reed DC, Foster MS (1984) The effects of canopy shading on algal recruitment and growth in a giant-kelp forest. *Ecology* 65:937–948
- Reekie EG (1998) An experimental field study of the cost of reproduction in *Plantago major* L. *Ecoscience* 5:200–206
- Schiel DR, Taylor DI (1999) Effects of trampling on a rocky intertidal algal assemblage in southern New Zealand. *J Exp Mar Biol Ecol* 235:213–235
- Shaughnessy FJ (2004) Contrasting patterns of allometry and realized plasticity in the sister species *Mazzaella splendens* and *Mazzaella linearis* (Rhodophyta). *J Phycol* 40:846–856
- Shea K, Roxburgh SH, Rauschert ESJ (2004) Moving from pattern to process: coexistence mechanisms under intermediate disturbance regimes. *Ecol Lett* 7:491–508
- Sousa WP (1984) The role of disturbance in natural communities. *Annu Rev Ecol Syst* 15:353–391
- Sousa WP (2001) Natural disturbance and the dynamics of marine benthic communities. In: Bertness MD, Gaines SD, Hay ME (eds) *Marine community ecology*. Sinauer Associates, Sunderland, pp 85–130
- Speidel M, Harley CDG, Wonham MJ (2001) Recovery of the brown alga *Fucus gardneri* following a range of removal intensities. *Aquat Bot* 71:273–280
- Stengel DB, Dring MJ (1997) Morphology and in situ growth rates of plants of *Ascophyllum nodosum* (Phaeophyta) from different shore levels and responses of plants to vertical transplantation. *Eur J Phycol* 32:193–202
- Svensson CJ, Pavia H, Aberg P (2009) Robustness in life history of the brown seaweed *Ascophyllum nodosum* (Fucales, Phaeophyceae) across large scales: effects of spatially and temporally induced variability on population growth. *Mar Biol* 156:1139–1148
- Underwood AJ (1997) *Experiments in ecology: their logical design and interpretation using analysis of variance*. University Press, Cambridge
- Underwood AJ (1998) Grazing and disturbance: an experimental analysis of patchiness in recovery from a severe storm by the intertidal alga *Hormosira banksii* on rocky shores in New South Wales. *J Exp Mar Biol Ecol* 231:291–306
- Vadas RL, Wright WA, Millar SL (1990) Recruitment of *Ascophyllum nodosum*: wave action as a source of mortality. *Mar Ecol Prog Ser* 61:263–272
- Weiner J, Campbell LG, Pino J, Echarte L (2009) The allometry of reproduction within plant populations. *J Ecol* 97:1220–1233
- Welham CVJ, Setter RA (1998) Comparison of size-dependent reproductive effort in two dandelion (*Taraxacum officinale*) populations. *Can J Bot* 76:166–173