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Unravelling the impact of harvesting pressure on canopy-forming macroalgae

Doriane Stagnol [a,b*], Renaud Michel [a,b], Dominique Davoult [a,b]

[a] Sorbonne Universités, UPMC Univ Paris 6, Station Biologique, Place Georges Teissier, F-29682 Roscoff, France

[b] CNRS, UMR 7144 AD2M, Place Georges Teissier, F-29682, Roscoff, France

[*] Corresponding author: doriane.stagnol@gmail.com

Abstract

Canopy-forming macroalgae create a specific surrounding habitat (the matrix) with their own ecological properties. Previous studies have shown a wide range of responses to canopy removal. Magnitude and strength of the effects of harvesting are thought to be context-dependent, with the macroalgal matrix that can either soften or exacerbate the impact of harvesting. We experimentally examined *in situ* the effect of harvesting on targeted commercial species, and how these potential impacts might vary in relation to its associated matrix. We found that patterns of recovery following the harvesting disturbance were variable and matrix specific, suggesting that local factors and surrounding habitats characteristics mediated the influence of harvesting. The greatest and longest effects of harvesting were observed for the targeted species that created a dominant and monospecific canopy on their site prior to the disturbance. Another relevant finding was the important natural spatiotemporal variability of macrobenthic assemblages associated with canopy-forming species, which raises concern about the ability to discriminate the natural variability from the disturbance impact. Finally, our results support the need to implement ecosystem-based management, assessing both the habitats conditions and ecological roles of targeted commercial species, in order to insure the sustainability of the resource.

Introduction

Intertidal macroalgae are commonly recognized as foundation species that have an important effect on community structure by creating habitats and modifying environmental conditions, species interactions, and resource availability (Bruno and Bertness 2001). Loss of habitat-forming species, for example through harvesting, is a key threat to ecosystems. Previous studies have shown a wide range of responses to canopy removal, including reduction or loss of diversity, decrease in invertebrate abundance and richness (Benedetti-Cecchi *et al.* 2001), shifts in community composition (Schiel and Lilley 2007), replacement by grazers or turfs (Perkol-Finkel and Airoldi 2010), or reduction in algal biomass and primary productivity (Golléty *et al.* 2008; Tait and Schiel 2011). Recovery of algal and invertebrate communities may take up to 4, 6 or even 12 years (Foster *et al.* 2003; Jenkins *et al.* 2004; Araujo *et al.* 2012).

Although the short and long-term consequences of losing habitat-forming species on community structure and composition are progressively understood (Benedetti-Cecchi *et al.* 2001), very little research has been conducted *in situ* to examine the effect of macroalgal manual harvesting depending on the identity of the targeted species, which have different life cycles and population structures. Each canopy-forming macroalgal species creates a specific surrounding habitat (the matrix) with its own ecological properties. The magnitude and the strength of the effects of harvesting are thought to be context-dependent, with the macroalgal matrix that can either soften or exacerbate the impact of harvesting (Mayer-Pinto *et al.*, 2015). The existence of a current global decline in rocky shore habitat-forming macroalgae from a wide range of stressors has been broadly documented (e.g. Airoldi *et al.* 2008; Halpern *et al.* 2007). Intertidal macroalgae are harvested worldwide for human consumption, alginate production, cosmetic and pharmaceutical industries, agricultural supply, or potentially biofuel. As the demand has intensified in recent decades and will most certainly continue to expand, assessing the harvesting impact is of major importance to define the potential consequences of disturbances to critical ecosystem functions (e.g. primary productivity).

In this context, we ask (1) whether harvesting has significant impacts on the targeted species, and (2) how these potential impacts might vary in relation to the targeted species and its associated macroalgal matrix. Further we discuss the suitability of management procedure in place (in Brittany) from an ecosystem-based management (EBM) perspective. EBM is widely accepted as the new paradigm to manage marine ecosystems (McLeod and Leslie, 2009), but

65 is still relatively new in marine habitats and in particular for rocky shores. Besides the
66 scientific interest, this study is also of political and commercial importance since it addresses
67 a practical management issue - the effect of resource harvesting - using the approach of
68 fundamental and applied research. Given the global trend of declining biodiversity (Sala and
69 Knowlton 2006; Butchart *et al*. 2010), the present challenge is to understand the interactive
70 effects of this stressor along with our fundamental knowledge of seaweed ecosystem structure
71 and function, and use the information to facilitate EBM of these important and productive
72 coastal marine systems.

73

Materials and methods

Study area and studied species

76 This study was performed in 2011 in Brittany, the French region in which commercial
77 seaweed harvesting is the most important. Seven study locations, where macroalgae are
78 commonly harvested were selected on the coast between Bloscon (48°N43'30.59",
79 3°W58'05.75") and Landunvez (48°N31'51.10", 4°W45'56.92"). These locations are
80 dominated by hard substratum, they differ, however, in terms of geomorphology, habitat
81 structure (heterogeneity), and exposition to wave action. They were mainly chosen for large
82 seaweed standing crop and accessibility.

83 In each location, the targeted species were making up the canopy on the study site and were
84 considerably larger than the other members of the algal assemblage, forming an extensive
85 layer above them: *Chondrus crispus* at location 1, *Fucus serratus* at location 2, *Palmaria*
86 *palmata* at location 3 (epiphytic on a *F. serratus* canopy), *Porphyra linearis* at location 4,
87 *Porphyra umbilicalis* at location 5, *P. palmata* at location 6 (epilithic), and *Himanthalia*
88 *elongata* at location 7. It is important to note that at location 1, the dominant canopy was a
89 mixture of small canopy species *C. crispus* and *Mastocarpus stellatus* that could not be
90 harvested separately.

Matrices

92 Here we defined 3 types of matrices (derived from T0 sampling) with their representatives
93 locations: matrix A, associated with a monospecific canopy accounting for a high percentage
94 of the seaweed cover in the community and with an intermediate to high associated fauna

95   diversity (locations 2 and 7; with *F. serratus* (A1) and *H. elongata* (A2) as respective

96   dominant canopy-forming species); matrix B, associated with a mixed canopy accounting for

97   an intermediate percentage of the seaweed cover in the community and with an intermediate

98   associated fauna diversity (locations 3, 6, and 1; with *P. palmata*, either epiphytic (B1) or

99   epilithic (B2), and *C. crispus* (B3) as respective dominant canopy-forming species); and

100   matrix C, associated with a monospecific canopy accounting for an intermediate to high

101   percentage of the seaweed cover in the community and with a low associated fauna diversity

102   (locations 4 and 5, with *P. linearis* (C1) and *P. umbilicalis* (C2) as respective dominant

103   canopy-forming species). These seaweed species were chosen because they have been

104   significantly exploited for many decades and because they are mostly found in the midlittoral

105   zone.

106   **Experimental design**

107   Traditional before–after control–impact (BACI) designs consider one impact and one control

108   location without replicating sites (Underwood 1994). Using only one control site, however,

109   prevents from disentangling the effect of the impact from that of different natural variability

110   between the impact and control sites.. Here, the impact of a harvest disturbance event on the

111   ecosystem was investigated experimentally using a multiple before–after control–impact

112   (MBACI) design to address concerns of BACI related to the confounding effects of spatial

113   and temporal variation (Underwood 1994; Stewart-Oaten and Bence 2001). Sampling

114   multiple control sites and multiple impact sites increases the probability that observed

115   differences are due to the impact. Each studied matrix has replicated locations: locations 2 and

116   7 for matrix A, locations 1, 3 and 6 for matrix B; and locations 4 and 5 for matrix C. On each

117   location, one site was experimentally impacted and one site served as control. Harvest was

118   simulated by removing the species biomass. The harvest was carried out according to the legal

119   French recommendations into force in2011: all individuals of *F. serratus and C. crispus* were

120   removed, while only *H. elongata* individuals longer than 80 cm and *P. palmata* and *Porphyra*

121   sp. individuals longer than 25 cm were removed.To really assess the impact of traditional

122   harvesting in Brittany, however, we choose to reproduce the harvest practices as they are

123   really applied by the harvesters. Therefore, the harvesting of *P. palmata*, *P. linearis*, and *P.*

124   *umbilicalis* was made by tearing off the individuals (and not by cutting above the holdfast as

125   stated by the legal French recommendations), which appears to be the most suitable way to

126   harvest, if not the only technically feasible for these species.

127   **Community structure**

128   On each site, five 0.1 m^2 (32 cm x 32 cm) random quadrats were sampled. Sampling was

129   undertaken prior to manipulation and at intervals thereafter for 12 months. For each sample,

130   the cover index of the target species was estimated from the percentage cover of the sampling

131   surface, using the Braun-Blanquet cover scale: 0 (absent), 1]0-25%], 2]25-50%], 3]50-75%]

132   and 4]75-100%]. The taxonomic richness was recorded *in situ* by identifying every taxon

133   (fauna and flora) visible to the eye to the lowest possible taxonomic level. Diversity is thus

134   referred as «taxonomic diversity» hereafter. Animal abundance (as number of individuals)

135   was also recorded *in situ* for each animal taxa, excluding colonial organisms and two

136   polychaetes *Pomatoceros triqueter* and Spirorbidae, whose densities are very difficult to

137   estimate. We also calculated evenness for each quadrat. The removal of the canopy may have

138   different impacts on associated species, depending whether canopy provides them with

139   support, shelter or food. It is therefore interesting to study the effect of harvesting on

140   macrofauna by distinguishing species according to their motility: mobile or sessile, and

141   according to their trophic regime: suspension feeders, grazers or carnivores in the broadest

142   sense, i.e. predators, omnivores, scavengers, etc.

143   **Statistical Analyses**

144   For each matrix type analyses were made to test the effect of the experimental harvest

145   disturbance using a permutational multivariate analysis of variance (PERMANOVA) design

146   that included four factors: (1) before vs. after the disturbance event (BA: 2 levels, fixed and

147   crossed), (2) controls vs. impacted (CsI: 2 levels, fixed and crossed), (3) time (T: 4 levels,

148   fixed and nested within BA), and (4) locations (L: 2 or 3 levels, random and nested in CsI). In

149   the MBACI design, the impact of harvesting is identified by a significant Before-vs-After x

150   Controls-vs-Impacted (BA x CsI) interaction indicating an overall difference between the

151   impacted sites compared to the controls from before to after the harvest disturbance. A

152   significant CsI x T(BA) could also indicate a delayed impact of the harvesting disturbance.

153   We examined biological responses to the harvesting disturbance for four compound measures

154   of community structure (i.e., canopy cover index, algal taxonomic diversity, animal

155   taxonomic diversity, and total animal abundance). We also examined multivariate differences

156   in assemblage structure of the animal community associated with the matrices, using the same

157   design as above. Analyses were made with the PERMANOVA+ add-on package for PRIMER

158   v6 (Anderson *et al*., 2008). To test for any animal taxonomic composition differences

between the assemblages of control and impact sites, separate analysis of similarity (ANOSIM) tests were done for each matrix at each sampling period on animal presence/absence data. If overall significant differences in animal assemblages between the two sites were obtained, we used an analysis of similarity percentages (SIMPER) in PRIMER to determine the species mainly responsible for the dissimilarity between treatments. A Principal Component Analysis (PCA) was made, using Statbox software ©, for the ordination of quadrats based on standardized data of community structure (i.e., canopy cover index, algal taxonomic diversity, taxonomic diversity of both sessile and mobile taxa, total animal abundance, and evenness).

Results

Effects of loss of canopy on harvested species

Harvesting of canopy significantly affected the cover index of the targeted species associated with the matrix A (PERMANOVA, BA x CsI, $p < 0.05$, Table 1). Differences in the cover index of the targeted species between the control and the impact sites were maintained up to 9 months after the disturbance event (Fig. 1a). The cover index of the targeted species associated with the matrix B varied substantially at the spatial scale (PERMANOVA, L(CsI), $p < 0.001$, Table 1), but no significant interaction was observed. Finally, the cover index of the targeted species associated with the matrix C varied significantly before and after the disturbance but with different effects between the two locations (PERMANOVA, BA x L(CsI), $p < 0.001$, Table 1). Note that one month after the initial harvest of *P. linearis*, sand started to silt the study site, reaching a thickness of 1.5 m seven months after the start of the study. After the sand was removed, the initial patchy distribution of *P. linearis* was replaced by a *P. linearis* bloom with a cover of 100% (see Stagnol *et al.* 2013).

Effects of loss of canopy on community structure

Harvesting of canopy affected algal communities associated with the dominant-canopy forming species of matrix A, but only at one location (PERMANOVA, BA x L(CsI), $p < 0.01$, Table 1). Indeed, we observed a significant increase in algal diversity associated with *F. serratus* on the impact site three months after the disturbance event. In contrast, no differences were observed between the control and the impacts sites of *H. elongata* over the whole study. PERMANOVA revealed a significant CsI x T(BA) interaction (Table 1) for the animal taxonomic diversity associated with the targeted species of matrix A, indicating that

6

effects of harvesting were significant but variable over time (Fig. 1, Table 1). Regarding the animal abundance, we observed significant effects of disturbance, variable over the two locations (PERMANOVA, BA x L(CsI), $p < 0.05$, Table 1).

The algal and animal diversities and the fauna abundance of communities within matrix B displayed a significant spatial variability (PERMANOVA, L(CsI), $p < 0.05$, Table 1, Fig. 1). This spatial variability between and within locations made it difficult to determine whether the harvesting of the canopy was having an impact that was separate and distinct from natural spatial and temporal variation.

PERMANOVA revealed a significant T(BA) x L(CsI) interaction for the algal and animal taxonomic diversity associated with the targeted species within matrix C (Table 1, $p > 0.001$). This indicates that these parameters varied substantially over spatial and temporal scales. It is interesting to note that similarly to matrix A, we observed a significant increase in algal diversity associated with *P. umbilicalis* on the impact sites three months after the disturbance event. No significant effects or differences were observed for the animal abundance associated with the dominant-canopy forming species of the matrix C.

Harvesting of canopy has significantly affected the benthic macrofauna assemblages associated with the species of matrix A three months after the disturbance event (Table 2). For maxtrix A, these differences were mostly the results of a lesser occurrence of sessile invertebrates on the impact sites, most of them being suspension-feeders, such as the polychaete *Pomatoceros triqueter*, the tunicates *Botryllus schlosseri* and Polyclinidae, the bryozoans *Alcyonidium* sp. and *Schizoporella unicornis*. In addition, we observed a great decrease in the abundance of the dominant species, the gastropod *Gibbula pennanti*, on the impact sites increasing the evenness (and then the diversity) of the associated benthic macrofauna assemblages (SIMPER routine, Primer). We also observed a significant difference between the control and impact sites in the benthic macrofauna assemblages associated with the species of matrix C three months after the disturbance event (Table 2). These differences were mostly the results of a lesser occurrence of the gastropods *Nucella lapillus* and *G. pennanti* on the impact sites (SIMPER routine, Primer).

Variation in relation to the targeted species and its associated matrix

The means of canopy cover index ranged from 0.8 to 4, number of sessile taxa from 0 to 5.2 species, number of mobile taxa from 0 to 7.4 species, animal abundance from 0 to 676

individuals, evenness from 0 to 1. PCA revealed the dynamics of impacted and control communities of the six species through the 1-year study (Fig. 2). The first two axes explained 62% of the variance in the benthic macrofauna assemblages, with 40% explained by the first axis and 22% by the second one. Pearson correlations of input variables suggested a significant correlation of both the number of sessile and mobile taxa with the algal diversity ($p < 0.05$), while the canopy cover index is significantly correlated with the animal abundance ($p < 0.05$).

The first principal component axis (PC1) differentiated plots along a gradient from high number of mobile taxa ($r = 0.93$) and high animal abundance ($r = 0.84$) at positive PC1 scores, to low number of mobile taxa and low animal abundance at negative PC1 scores. To a lesser extent, the number of sessile taxa ($r = 0.62$) and algal diversity ($r = 0.58$) also contributed to the first axis. The second principal component axis (PC2) differentiated plots along a gradient from high evenness ($r = 0.7$) and low canopy cover index at positive PC2 scores, to low evenness and high canopy cover index ($r = - 0.48$) at negative PC2 scores.

The impact of harvesting was not clearly witnessed for the communities associated with *P. palmata* (B1), i.e. epiphytic *P. palmata*, *P. linearis* (C1), and *P. umbilicalis* (C2). The eight samples of *P. palmata* (B1), i.e. epiphytic *P. palmata*, were noticeably adjacent regardless of the sampling time, and visibly separated from the other communities by the second axis. The benthic community associated with *P. palmata* had generally a great evenness, which is the major determinant factor for this community. Benthic communities associated with *P. linearis* (C1) and *P. umbilicalis* (C2) were structurally similar, occupying a similar PCA space. The close association of the *P. linearis* and *P. umbilicalis* samples in the PCA (Fig. 2) reflects the relative similarity of the benthic communities associated with these two species. They are characterized by low number of mobile taxa, low animal abundance, high cover index and low evenness (except 4 plots noticeably separated from the others by the second axis). Besides, the natural variability that occurred on the *P. umbilicalis* site at T9, in the form of a significant sand burial of the site, affected both control and impact plots (C2C9 and C2I9).

On the other hand, communities associated with *F. serratus* (A1), *H. elongata* (A2), *P. palmata* (B2), i.e. epilithic *P. palmata*, and *C. crispus* (B3) displayed an initial impact of harvesting along with a progressive recovery. The benthic community associated with *F. serratus* (A1) changed little over time in the control plots, showing a high number of mobile taxa and a great animal abundance (described by the first axis) as well as a high cover index

and a low evenness (described by the second axis). The impacted plots followed a trajectory away from the control plots, with 2 impacted plots (A1I3 and A1I9) noticeably separated from the others. The impact plot at T3 was separated from the others by both axes, displaying a low number of mobile taxa, a low animal abundance, a low cover index and a relatively high evenness (E = 0.70). On the other hand, the impact plot at T9 was separated from the others by the second axis only, also displaying a low cover index and a relatively high evenness (E = 0.70) but a quite high number of mobile taxa and high animal abundance. A similar pattern was observed for the community associated with *H. elongata* (A2), although the eight plots were more dispatched on the PCA space. Still, two impact plots (A2I3 and A2I9) were remarkably detached from the others by the first axis. Indeed, they both showed a low animal abundance and a low algal diversity, coupled with a low cover index (although this last variable is not discriminated by the first axis).

Although communities associated with *P. palmata* (B2), were not visibly separated from the other communities, the trajectories were different between the control and impact sites in spite of the very little temporal variation. Finally, the benthic community associated with *C. crispus* (B3) also showed different time trajectories between the control plots and the impact plots, in spite all the plots being rather adjacent in the PCA space.

Discussion

1. Different patterns of recovery in relation to the matrix identity (surrounding habitat)

There has been some evidence over the study that ecosystem recovery (after harvest disturbance) has occurred. Twelve months after the initial harvesting, the effects of harvesting on the ecosystem were not detectable at any location: all community structures and assemblages on the impact sites were similar to the ones observed on the control sites. The associated ecosystems impacted by the canopy removal have all returned to a state comparable to the ones seen on an undisturbed zone. Patterns of recovery, however, were quite variable and matrix specific, suggesting that local factors and surrounding habitat characteristics mediated the influence of harvesting on the ecosystem (Foster *et al.* 2003).

The three matrices in our study demonstrated strikingly different patterns of recovery following experimental harvesting. The greatest and longest effects of seaweed harvesting were observed for the targeted species associated with the matrix A, *F. serratus* and *H. elongata*. These brown algae clearly created a dominant (in terms of cover and biomass)

and monospecific canopy on their site prior to the disturbance. While the canopy cover index was strongly affected up to 9 months after the disturbance event for both species, the cascading effects triggered by the canopy loss strongly diverged between the two species. Indeed, our study showed a significant decrease of the animal diversity and abundance associated with *F. serratus* up to 9 months after the harvesting, followed by a significant increase in algal diversity. On the other hand, the only cascading effect observed after the harvesting of *H. elongata* was a decrease in the animal diversity 3 months after the initial disturbance. The main explanation is that *F. serratus* forms a perennial canopy while *H. elongata* is a seasonal canopy-forming species. Therefore, while the removal of *F. serratus* canopy left a barren area, the *H. elongata* canopy loss on the impact sites was mediated by the natural and seasonal reduction in *H. elongata* canopy on the control sites. Recent monospecific studies on perennial brown algae have shown that harvesting affects the size structure of the population (Vega *et al*. 2014) and the abundance of invertebrates (Phillippi *et al*. 2014). Besides, Migné *et al*. (2015) concluded that *F. serratus* canopy was acting on the community not by reducing the abiotic stress, but by providing food, habitat, or both. We also observed significant short-term effects of the harvesting on the communities associated with species of the matrix C but the natural variability of this matrix was over and above the disturbance effects. The removal of targeted species within matrix B (*P. palmata* either epiphytic or epilithic, and *C. crispus*) did not clear the impact sites of its algal biomass, leaving patches of non-targeted species (e.g., *F. serratus*). It explains partly why we did not observe significant effects on either the community structure or the assemblage following the canopy removal. Moreover, recovery is assumed to be higher in the presence of herbivores (Aquilino and Stachowicz 2012), whose densities were maintained in impact plots with non-targeted canopy species present. Herbivores promoted succession by grazing on early successional fast-growing ephemeral species that would otherwise prevent establishment of perennial algae (Aquilino and Stachowicz 2012).

2. <u>Important natural spatiotemporal variability in benthic assemblages</u>

Another relevant finding of this study was the important natural spatiotemporal variability of communities associated with the canopy-forming species within the matrices B and C. For example, *Porphyra* spp. live on upper rocky shore where abiotic conditions are highly variable, creating a stressful environment (high light, long exposure to ultraviolet light, desiccation, extremes of temperature and salinity, and nutrient unavailability). Eulittoral species are expected to be better adapted to tolerate such environmental challenges than

317 sublittoral species (Lüning *et al.* 1990). Moreover, we observed that both *Porphyra* spp. were
318 restricted to spatially patchy populations, which is thought to be the results of grazing patterns
319 (Branch *et al.* 1990; Griffin *et al.* 1998). Grazers may act to clear young sporelings from areas
320 shortly after their recruitment (Griffin *et al.* 1998). This hypothesis is supported by our
321 observation that, after the sand burial on the *P. linearis* site had killed most grazers present,
322 the initial patchy distribution of *P. linearis* was replaced by a *P. linearis* bloom with a cover
323 of 100%. Branch *et al.* (1990) observed the same pattern, after freshwater floods had killed
324 most grazers present on their study site. Therefore, at a broad scale, abiotic factors define
325 distribution patterns on the upper rocky shore, and within these patterns, other processes may
326 occur at smaller scale and modify the species distribution and abundance (Gimenez *et al.*
327 2005; Smale *et al.* 2010). As a result, any potential impact of *Porphyra* sp. harvesting is
328 unclear.

329 Such complex heterogeneity may have obstructed the detection of canopy harvesting effects.
330 Marine benthic assemblages have been found to be highly variable across different scales of
331 time and space (Fraschetti *et al.* 2005), which raises concern about the ability to discriminate
332 this natural variability. The scale and relative magnitude of variability has important
333 implications for the design of the experiment because it can give rise to ambiguity about the
334 effects of putative impacts or stressors (Underwood, 1994; Heino *et al.*, 2004). Although our
335 data clearly cannot provide mechanistic explanations for the patterns observed, it is quite
336 conceivable that most of the variation among assemblages could be explained at the scale of
337 quadrats. Unfortunately, as small-scale variability in macrobenthic assemblage properties is
338 often remarkable (Fraschetti *et al.* 2005), a few small-scale samples may not be enough to
339 detect the overall effect of canopy harvesting. Such small-scale spatial and temporal variance
340 should not be considered simply as a statistical nuisance (Coleman 2002). Indeed, quantifying
341 the range of the natural heterogeneity of marine benthic assemblages may help to identify the
342 physical and biological factors that are the most relevant to be explored first under an
343 experimental approach. There is thus a need for monitoring methods that allow clear
344 discrimination between natural spatiotemporal variability and human pressures.

345   3. Conclusions and implications for the management of seaweeds harvest

346 Canopy-forming macroalgae provide a wide range of ecosystem services, notably trough their
347 contribution to the primary production and carbon cycling (Kaldy and Dunton 2000; Golléty
348 *et al.* 2008) and the formation of biogenic habitat that create the foundation for entire

communities, enhancing the species diversity and the abundance of many species (Wikstrom and Kautsy 2006; Smale 2010). Intuitively, these foundational species should be the focus of conservation efforts but our study also highlights that seaweed management plans need to move away from a single species focus and account for the whole ecological role of targeted commercial species.

In the light of our results, the recovery of the canopies and of their associated communities seems realistic within the current frame of management plans in France. The current methods used coupled to the French laws regulating seaweeds exploitation result generally in continuous vegetative growth of remaining individuals and greater recruitment of new individuals. Seaweed harvest conservation plans, however, are currently based on single-species management in order to maximize seaweed population biomass while the underlying effects of harvesting on the whole ecosystem are mostly ignored. In Chile, the management of *Lessonia nigrescens*, a brown alga, protects its associated biodiversity by focusing on the harvest methodology, which is based on ecological and biological recommendations, rather than on the harvest quantities (Vasquez *et al*. 2012). On the Atlantic coast of Canada, the management program of the perennial brown alga *Ascophyllum nodosum* focused on a precautionary approach to habitat use and natural bed sustainability, for almost two decades (Ugarte and Sharp 2011). There is also a need to complement the management plans with monitoring and research programs centered on the biology, habitat, and associated fauna of the harvested seaweeds.

There are environmental dynamics that occur and also need to be approached. These are storm frequency and severity, sand flooding events and continued warming of waters. This appears to be crucial given the large body of literature that suggests that the cumulative effects of local anthropogenic and other stressors (e.g. rising sea surface temperatures and increasing wave exposure) have negative effects on the growth and survival of canopy-forming algae (Halpern *et al.* 2007). Therefore, these environmental factors should be monitored on a regular basis and if necessary, the legislation should be amended accordingly.

EBM is an integrated approach to manage marine resources that considers the entire ecosystem, not simply individual components of the ecosystem (McLeod and Leslie 2009), seeking to sustain resources and promote the conservation of the biodiversity as a keystone to maintain overall ecosystem health, diversity, and resilience (Curtin and Prellezo 2010).The application of EBM, however, is still largely based on single-species assessments and

disregards the broader ecosystem context and impact. Here, our results strongly support the need to implement ecosystem-based management, assessing both the habitat conditions and ecological roles of targeted commercial species, in order to insure the sustainability of the resource. Understanding the mechanisms driving the patterns of spatio-temporal variability should also be an important step to devise sensible and efficient policies for conservation and management.

Acknowledgement

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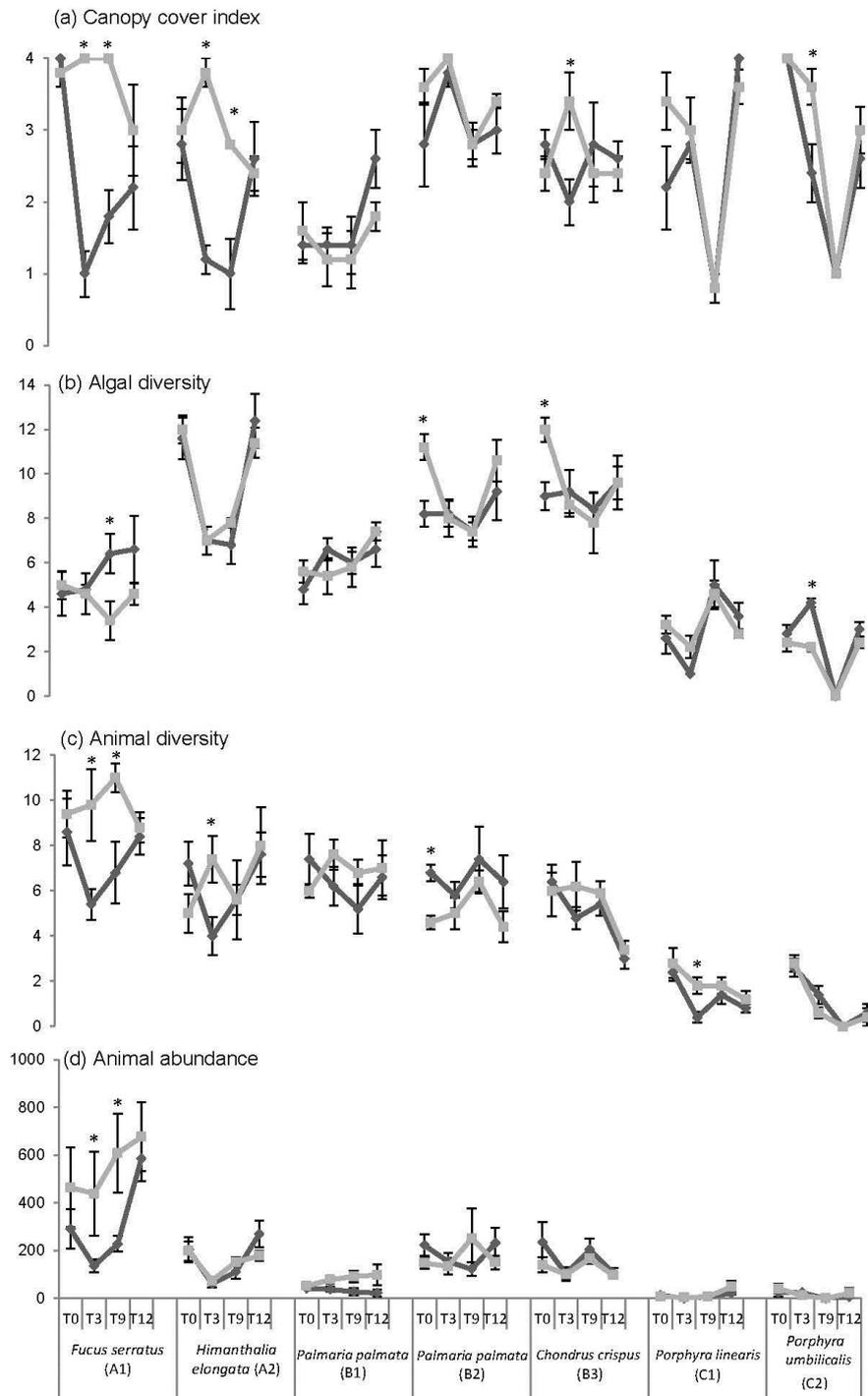
Fig. 1 Temporal variation in the mean (± SE) canopy cover index (a), taxonomic algal diversity (b), taxonomic animal diversity (c), and animal abundance (d) in both control and impact plots (grey and black lines respectively) for each studied species and site. Signifiance codes: * P < 0.05.

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Table 1. Summary of Permutational Multivariate Analysis of Variance of the MBACI model for canopy cover index, algal taxonomic diversity, animal taxonomic diversity and total animal abundance.

Matrix A

Source	df	Canopy cover Index		Algal taxonomic diversity		Animal taxonomic diversity		Total animal abundance	
		MS	F	MS	F	MS	F	MS	F
BA	1	4680.30	20.547	721.94	0.727	45.27	0.099	1134.30	1.449
CsI	1	4231.50	3.727	63.66	0.008	506.88	0.293	586.63	0.109
T(BA)	2	469.50	0.752	1450.00	2.359	829.94	**9.791****	7219.20	**5.501***
L(CsI)	2	1135.40	**2.700***	8099.70	**40.166*****	1731.40	**5.363****	5387.80	**7.470*****
BAxCsI	1	3693.50	**16.215***	535.81	0.539	2048.10	4.473	93.68	0.120
BAxL(CsI)	2	227.78	0.542	993.20	**4.925****	457.85	1.418	782.99	1.086
CsIxT(BA)	2	2661.40	4.261	216.47	0.352	1056.30	**12.462****	1122.10	0.856
T(BA)xL(CsI)	4	624.66	1.486	614.65	**3.048****	84.76	0.26	1310.30	**1.817***
Res	64	420.45		201.66		322.84		721.26	

Matrix B

Source	df	Canopy cover Index		Algal taxonomic diversity		Animal taxonomic diversity		Total animal abundance	
		MS	F	MS	F	MS	F	MS	F
BA	1	199.66	0.674	432.17	2.990	622.68	2.800	295.79	0.294
CsI	1	163.18	0.037	817.75	1.144	649.48	1.036	1483.20	0.163
T(BA)	2	968.97	1.515	280.50	1.818	1083.30	2.519	1189.80	1.274
L(CsI)	4	4411.10	**10.306*****	714.94	**6.915*****	626.79	**2.614***	9119.50	**10.822*****
BAxCsI	1	546.01	1.842	716.23	4.955	696.06	3.130	837.60	0.833
BAxL(CsI)	4	296.40	0.692	144.54	1.398	222.36	0.927	1005.40	1.193
CsIxT(BA)	2	677.49	1.059	163.10	1.057	381.88	0.888	482.05	0.516
T(BA)xL(CsI)	8	639.51	1.494	154.27	1.49	430.04	1.79	933.63	1.11
Res	96	428.02		103.39		239.82		842.70	

Matrix C

Source	df	Canopy cover Index		Algal taxonomic diversity		Animal taxonomic diversity		Total animal abundance	
		MS	F	MS	F	MS	F	MS	F
BA	1	4362.60	2.070	99.53	0.721	18812.00	6.076	19274.00	4.648
CsI	1	1004.40	1.997	58.72	0.054	574.95	0.192	1192.60	0.339
T(BA)	2	14686.00	**26.613****	1469.80	0.425	3145.90	0.537	4520.10	0.881
L(CsI)	2	502.85	1.261	1082.00	**3.8761***	2991.60	1.301	3518.80	1.299
BAxCsI	1	284.36	0.135	250.41	1.814	617.99	0.200	791.83	0.191
BAxL(CsI)	2	2107.90	**5.284*****	138.01	0.494	3096.10	1.346	4146.80	1.531
CsIxT(BA)	2	348.06	0.631	369.80	0.107	2863.40	0.489	3687.90	0.719
T(BA)xL(CsI)	4	551.83	1.383	3455.80	**12.380*****	5859.00	**2.547*****	5132.50	1.894
Res	64	398.93		279.14		2300.10		2709.30	

Significance codes: $^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

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Table 2 ANOSIM results: global R and significance level of differences between the assemblages of the control and the impact sites for each matrix at 3 months, 9 months and 12 months after the simulated harvest, based on presence/absence data matrices. Bold labels indicate a significant difference.

	Before harvest		3 months		9 months		12 months	
	R-value	Signif. Level	R-value	Signif. Level	R-value	Signif. Level	R-value	Signif. Level
Matrix A	-0.042	0.771	0.163	**0.025**	0.081	0.123	-0.041	0.644
Matrix B	0.005	0.393	-0.027	0.717	-0.014	0.570	-0.030	0.749
Matrix C	-0.041	0.651	0.112	**0.039**	-0.044	0.838	-0.040	0.822
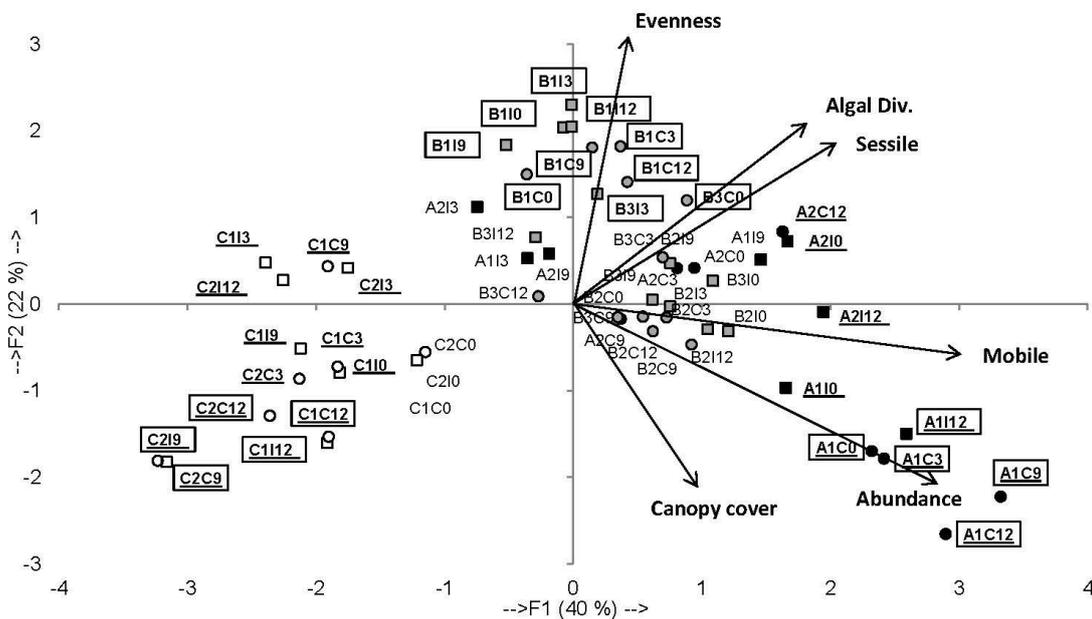
Fig. 2 Plot of Principal components 1 and 2, showing variables vectors. Species coded as A1 for *F. serratus*, A2 for *H. elongata*, B1 for *P. palmata* (epiphytic), B2 for *P. palmata* (epilithic), B3 for *C. crispus*, C1 for *P. linearis*, and C2 for *P. umbilicalis*, for each zone (circle = control; square = impact) and each matrix (black filled = matrix A; grey filled = matrix B; white filled = matrix C). Labels code for species, treatment zone (C or I) and the number of months after the harvest. Bold labels have a significant contribution to the first or second axis (or both): underlined labels significantly contribute to the first axis while framed labels significantly contribute to the second axis.

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