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Abstract

Through experimental harvesting, followed by a 12-month monitoring of demographic attributes, we tested the influence of harvesting on the population dynamics of *Himanthalia elongata*. We further explore the data to test the hypothesis that the canopy would exert a negative effect on the other developmental stages (intraspecific competition) throughout the recovery cycle of the population. This showed that the *H. elongata* canopy plays a marked seasonal role not by precluding the presence of other developmental stages but by delaying or preventing their growth and development. The removal of the canopy facilitates the transition from one developmental stage to another, eventually permitting a fast recovery of size structure in the population. This study allows us to integrate population dynamics and intraspecific relationships in our understanding of macroalgal recovery patterns.

Key-words: intraspecific relationships, intertidal, management, population dynamics, restoration

Introduction

Canopy loss, for example through harvesting, is globally considered a threat to marine ecosystem, seriously impacting biodiversity and functioning worldwide (Bruno and Bertness, 2001). Previous studies have shown a wide range of responses to canopy removal, including reduction or loss of diversity and reduction in primary productivity (Crowe et al., 2013). Fucoids and other intertidal macroalgae are recognized as foundation species (*sensu* Jones et al., 1994) that have an important effect on abiotic conditions, community assembly and ecosystem functioning (Benedetti-Cecchi et al., 2001; Tait and Schiel, 2011). Variations in their distribution may trigger changes in the whole system, such as shifts in community composition (Lilley and Schiel, 2006) or changes in the height and structure of the canopy itself (Golléty et al., 2008).

Among them is *Himanthalia elongata* (L.) S. F. Gray, a brown alga forming dense stands on temperate rocky shores in the Northern hemisphere (Creed, 1995). Unlike other members of the Fucales, it has a biennial life cycle with four identifiable phases: vegetative growth, reproductive growth, reproduction (gametes are released and fuse to form zygotes) and a recruitment phase during which zygotes settle on the substratum (Stengel et al., 1999). Growth usually occurs between September and May, with a growth rate peak during spring when seawater temperatures are approx. 10-12°C (Stengel et al., 1999). The time of reproduction is from June to December, and is strongly site dependent, probably due to water temperature. This alga has a two-stage morphology: first, the 'button-like' stage is initially club-shaped, becoming peltate ('mushroom-shaped') when mature, about 2-3 cm in height and 2-4 cm in diameter, slightly dimpled in the middle, and attached to the substratum by a short stipe and discoid holdfast. Second, the mature peltate stage typically produces two long (up to 3 m) thong-like reproductive receptacles (Stengel et al., 1999), hereafter referred as 'fronds'.

In addition to being ecologically important, *H. elongata* is also of commercial importance. It was traditionally harvested for centuries along the eastern Atlantic in Norway, France, Spain, Scotland, and Ireland for fertilizer, human food, and alginate extracts. *H. elongata* is currently harvested mainly as edible seaweed for human consumption in France, Ireland and Spain. Due to the high food value of *H. elongata* (Plaza et al., 2008), commercial harvesting of this species is likely to expand quickly. In France, *H. elongata* can be harvested all-year round but most of the harvest occurs between March and June, because after June large individuals are thick and grainy, thus less appealing for human consumption. In Brittany, annual harvested quantities of *H. elongata* have increased by 35% between 2009 and 2013 (unpublished data). Despite the sustainably-oriented harvesting practices implemented for seaweeds in Europe these past few years, concern has raised about the broader impacts of harvesting (Isabel et al., 2011; Smale et al., 2013; Stagnol et al., 2016).

Demographic parameters have been used to examine the effect of harvesting in natural populations of brown macroalgae (e.g. Arenas and Fernández, 2000; Rivera and Scrosati, 2006; Santos, 1995). Size

distributions result from differences in individual growth rates, consistent with the asymmetric competition hypothesis of dominance and elimination of smaller individuals by larger ones (Hara, 1988; Weiner and Thomas, 1986). The dynamics of size inequality as a function of plant size and density are important to understand not only the population structure, but also the interactions between individuals (Hara, 1988). Indeed, intraspecific facilitation (positive effects of density) is generally regarded as a major determinant of the dynamics of seaweed populations (Arenas and Fernández, 2000; Courchamp et al., 1999; Stephens and Sutherland, 1999). Creed (1995) confirmed the importance of density as a major regulator in *H. elongata* populations. Despite this, intraspecific relationships in macroalgal populations have usually been ignored (Paine, 1990) and their importance is poorly known. Besides, the development of seaweed population depends largely on the survival and growth of early post-settlement stages (Steen and Scrosati, 2004). In this context, demographic attributes, such as density, biomass, and size structure, could serve as ecological indicators to monitor the population dynamics of commercially important brown macroalgae.

One recent study realized on the same study site and at the same sampling dates as this study, found no or little impact of the harvesting of *H. elongata* on its associated community, while its percentage cover was significantly affected up to nine months after the disturbance (Stagnol et al., 2016). They showed, however, that 12 months after the disturbance, the percentage cover of *H. elongata* on the impacted zone had returned to a state comparable to the one observed on the undisturbed control zone.

Through experimental harvesting, followed by a 12-month monitoring, we tested the influence of the harvesting on the population dynamics of *H. elongata* and the hypothesis that the canopy could exert an effect on the other developmental stages (intraspecific relationships) throughout the recovery cycle of the population. This strategy allowed us to integrate population dynamics and intraspecific relationships in our understanding of macroalgal recovery patterns.

Material and methods

Study site

This study was performed in Brittany, the French region in which commercial seaweed harvesting is the

most important (> 90% of macroalgae harvested in France). Field work was carried out on a site where *H. elongata* is commonly harvested, at Porspoder (48°N31.607', 4°W46.169'). This study site was also chosen for its large *H. elongata* standing crop and accessibility. This site is dominated by rocky substrata and presents a high water movement velocity.

Experimental design and set-up

The experimental design considered two treatments: one control (C) and one manipulated (M) where the canopy was removed, with five replicates each. Regarding *H. elongata*, the French legislation states that only individuals longer than 80 cm can be harvested. Harvest was realized in April 2012, by gathering by hand all individuals longer than 80 cm on a 115 m² surface area. The fronds were cut at least 10 cm from the mushroom-like base. Sampling was done just before frond removal (T0) and then one month later (T1). Sampling frequency was then set to every two months, and then to every three months. Each sample is hereafter referred to as T*n* where *n* is the number of months since harvest. At each sampling date, five 0.1 m² random quadrats were sampled on each treatment zones (C and M)

Density, length, biomass, and developmental stage

Individuals were classified as early club-shaped stage, mature vegetative mushroom-shaped stage and thong-like reproductive receptacles (fronds). Individuals of these developmental stages within the quadrats were counted and the maximal length of each frond was measured. Maximal length was used as size descriptor because length is probably crucial for survival and reproduction of individuals given that light is the primary resource for algae and that longer thalli intercept more light (Carpenter, 1990). As length and biomass were highly correlated in *H. elongata*, the relationship between frond length and dry weight was examined using non-linear regressions. They were applied to fit parameters of the typical allometric power equation:

$$DW = a \times FL^{b}, \qquad \text{equation 1}$$

where DW represents dry weight (g); FL, frond length (cm), and a and b are constants. To fit the parameters, 36 individuals were collected in Roscoff (48°N43.686', 3°W59.282') in front of the Station

Biologique de Roscoff. An attempt was made to obtain samples representative of the full size range of the species. For each individual, the maximal length and dry weight, obtained after drying at 60°C for 48 h, were recorded. An allometric length-weight equation was obtained using a power law equation. Based on density, the maximal length of each individual in the quadrats in each treatment at each sampling date was converted to dry weight using this equation. The average dry weight per m² could then be estimated for each treatment at each sampling date, to investigate the temporal variation of *H. elongata* biomass, as well as stock recovery after harvesting.

Size structure and inequality

The frond size structure was determined for each zone and each sampling date, for which nine size classes (SCs) were previously established on the basis of frond length: 0-25 cm, 26-50 cm, 51-75 cm, 76-100 cm, 101-125 cm, 126-150 cm, 151-175 cm, 176-200 cm and > 200 cm. Frond size (length) inequality was determined for each zone and each sampling date by calculating the Gini coefficient using the length values for all the fronds of the five quadrats of each zone. This size-structure descriptor was selected here because it is the statistic that most accurately reflects the size hierarchy in populations (Weiner and Solbrig, 1984). The Gini coefficient ranges from a minimum of zero, when all individuals are equal in size (perfect equality), and a theoretical maximum of one in an infinite population in which every individual, except one, has a size of zero (perfect inequality). The Gini coefficient is frequently used as a measure of size inequality in seaweed populations (e.g. Arenas and Fernández, 2000; Rivera and Scrosati, 2006; Santos, 1995).

Data analysis

Multivariate analyses were made to test the effect of the experimental harvest disturbance using a permutational multivariate analysis of variance (PERMANOVA) design that included two factors: (i) controls vs. manipulated (CsM: 2 levels, fixed), and (ii) time (T: 6 levels, fixed and crossed). We examined biological responses to the harvesting disturbance for three demographic attributes (i.e. total density, dry standing biomass, Gini coefficient). We also examined multivariate differences in the density

of the different developmental stages of *H. elongata* (i.e. adult fronds, button-like stages, and mushroom-shaped stages), using the same design as above. Analyses were made with the PERMANOVA+ add-on package for PRIMER v6 (Anderson et al., 2008).

Results

Biomass, density and Gini coefficient

The allometric relationship between frond length and dry weight was checked for 36 *H. elongata* fronds ranging from 8 to 281 cm:

$$DW = 0.0041 \times FL^{1.8744},\ R^2 = 0.93,\ p < 0.001 \qquad \text{equation 2}$$

The average dry weight varied over time in both zones (Fig. 1a), with the highest values occurring in September (T5) on the control area. The temporal variation patterns were similar in both treatments, but the biomass was lower on the M treatment than on the C treatment (PERMANOVA, $p < 0.05$, Table 1), during the one-year period, except before harvesting (T0) and at the end of the study (T12) (Pairwise comparison, $p > 0.05$). Highest values of dry standing biomass were observed at T5 on the C treatment and at T12 on the M treatments. Total density varied significantly throughout the year from April 2012 to April 2013 (Fig. 1b) in both treatments (PERMANOVA, $p < 0.05$, Table 1). The density significantly decreased from T1 to T3 on the M treatment, and significantly increased from T8 to T12 on both treatments (Pairwise comparison, $p < 0.05$). Lowest values were observed between T3 and T8 on both treatments. The Gini coefficient varied significantly over time in both zones (Fig 1c, PERMANOVA, $p < 0.05$, Table 1), with the highest values occurring at T3 and T5 for the C treatment and at T1 and T8 for the M treatment.

Developmental stages

The temporal variation patterns of the frond density (Fig. 2a) were significantly different between the two treatments (PERMANOVA, $p = 0.001$, Table 1). Thong-like reproductive receptacles (fronds), which indicate the possible occurrence of sexual reproduction, reached their highest frequency in the population

at T3 in July in the C treatment (14%) and at T8 in December in the M treatment (78%). The peak of fronds observed at T8 in the M treatment was due to a high number of small fronds (n = 56) shorter than 13 cm, except for 2 individuals. At the same time in the C treatment, the fronds (n = 10) consisted of 40% new and young fronds shorter than 6 cm and 60% of old and reproductive fronds longer than 200 cm. Once reproductive tissues were lost in the C treatment, resulting in a loss of biomass, senescent fronds were observed at the end of the study (T12). In the M treatment, the biomass increased from T8 to T12 as the result of the growth of the short fronds observed at T8 (Fig. 1a).

The density of the mushroom-shaped stage (Fig. 2b) did not vary significantly throughout the year in either treatment zones and no significant differences were observed between them (PERMANOVA, $p > 0.05$, Table 1). The density of the club-shaped stage varied significantly over time in both treatments (PERMANOVA, $p < 0.001$, Table 1). Finally, the density of the club-shaped stage (Fig. 2c) followed the same temporal pattern as the total density: it significantly decreased from T1 to T3 on the M treatment, and significantly increased from T8 to T12 on both treatments (Pairwise comparison, $p < 0.001$). Lowest values were observed between T3 and T8 on both treatments.

Size structure and inequalities

Frond size structure varied seasonally during the study period (Fig. 3). The first sample (T0) was taken in April 2012 during the reproductive growth phase of *H. elongata*. After the experimental harvest, two different population dynamics were observed in the different treatments.

In the C treatment, we observed that during the phase of reproductive growth, in spring (T0-T1), the thalli progressively shifted from smaller size classes to larger size classes, resulting in an increase in inequality (Fig. 1c), reaching a peak at the beginning of autumn (T5) (G = 0.89). During this period, longer fronds (> 200 cm) were recorded, representing 100% of the frond population (Fig. 3a). Then, the beginning of winter (T8) coincided with the start of the vegetative growth in the population and the emergence of recruits in smaller size classes. By the end of the study (T12), senescence caused reduction of thalli from the larger size classes to smaller size classes while the number of thalli from smaller size classes (0-25 cm

and 26-50 cm) increased, due to the early growth of recruits. Due to these changes, the control zone reached its minimum inequality (G = 0.36).

In the M treatment, harvest removed the majority of thalli, resulting in only one medium thallus (66 cm) observed at T1. The remaining thalli progressively increased in length while germlings (mushroom-shaped stage) shifted to the thong-like receptacle stage, resulting in an increased number of thalli in the smaller classes. The beginning of winter (T8) also coincided in the population with the emergence of recruits in the smallest size class (0-25 cm), which constituted almost 100% of all plants. By the end of the study (T12), the vegetative growth phase followed by the reproductive growth phase, resulted in the progressive shift of thalli from the smallest size class to larger size classes.

Discussion

The regrowth of the canopy is expected to depend on newly recruited individuals and reproductive growth of algae that survived the disturbance. The recovery process of the M treatment zone appeared to occur in three steps: first, the reproductive fronds of algae that survived the disturbance could reproduce since individuals shorter than 80 cm were not removed (T3). Second, the incomplete removal of the canopy may have been favorable for the growth and development processes, allowing these remaining individuals, as well as the early developmental stages (club-shaped and mushroom-shaped), to grow and occupy higher size classes. Third, the transition of these early developmental stages to the final adult stage was clearly visible in winter (T8) (Fig. 3b), possibly facilitated by the absence of a dense canopy of adults.

Eight months after removal, the number of fronds from the smallest size class [0-25 cm] was highest in the M treatment (112 ± 12.5 ind.m^{-2}) than in the C treatment (20 ± 1.1 ind.m^{-2}), suggesting that transition of these early developmental stages to the final adult stage, was more successful in the M treatment than in the C treatment. This may be explained by a lower competition between the adult stage forming a dense canopy and the early developmental stages living below the canopy. In the M treatment, the lack of a protective structure from the adult canopy during recruitment led to the creation of such micro-habitats, mainly with the rapid colonization of bare areas by red turf algae. It has been shown that the survival and

growth of young buttons were highest in red algal turfs that protect the recruits from wave action and desiccation (Stengel et al., 1999). The role of these recruits in canopy recovery, however, was only visible at the end of the study, with an increase in the number of individuals in higher size classes, similar to the pattern observed in the C treatment. Canopy recovery was also linked with the recovery of the total biomass of *H. elongata* fronds, whose values at T12 were not different between the two treatments and were similar to those prior to the disturbance (T0). The stock renewal of *H. elongata* was, therefore, effective one year after harvesting.

In summary, in the C treatment, cohorts present at the start of the study (T0) grew and ultimately exerted a high intraspecific competition on the other developmental stages, by stopping further growth of juveniles. On the other hand, M treatment seems to have reduced intraspecific competition, allowing juveniles to grow. Then, the juveniles developed continuously, as seen in T8 with the high number of small fronds (Fig. 3b), permitting a fast recovery of size structure in this dynamic population.

Although it is widely reported that the structure and dynamics of most ecological communities are controlled partly by interactions between species (Bertness and Callaway, 1994; Bulleri, 2009; Edwards and Connell, 2012), the role of intraspecific relationships is less often integrated in studies of population dynamics. Recent research has emphasized the central role of positive species interactions as important drivers of community structure and ecosystem functioning (Brooker et al., 2008; Bulleri, 2009). This study showed negative intraspecific relationships (competition) in *H. elongata* in the undisturbed zone (C treatment). Positive effects of high densities on growth have been reported mainly in fucoid algae, where high densities may offer some protection against physical stress related to wave action and desiccation (Choi and Norton, 2005; Steen and Scrosati, 2004; Viejo and Aberg, 2001). In our work, although the impact of adult fronds on juvenile stages (club-shaped and mushroom-shaped button) was not directly measured, it seems likely that the presence of the canopy confers a disadvantage to the juvenile stage by reducing the availability of space, light and/or nutrients and by competing for those limiting resources (Carpenter, 1990). It appears that the *H. elongata* canopy plays a marked seasonal role, when the adult fronds are highly developed (in summer at T3 and T5). At that time, adult fronds do not preclude the

presence of other developmental stages but somehow they delay or prevent their growth and development. Therefore, the removal of the canopy facilitates the transition from one developmental stage to another.

Overall our results suggest that the incomplete removal of the canopy (since individuals smaller than 80 cm remained) may have ensured the continued recruitment and re-growth of *H. elongata*, facilitating the regeneration of the exploited area. Growth and recruitment can be regulated by density-dependent processes operating at small-scale during the early stages of substrate colonization. Furthermore, the health and diversity of the surrounding macroalgal populations play an essential role in recovery, probably through the recruitment process and the magnitude of herbivorous grazing. Moreover, *H. elongata* being a seasonal canopy-forming species, its canopy loss on the impact sites was mediated by the natural and seasonal reduction in the *H. elongata* canopy on the control sites (also see Stagnol et al., 2016). From a conservation point of view, our results support the current legal harvesting techniques in France that enforce minimum harvesting size for specific seaweed including *H. elongata*, to minimize their impact on juvenile plants. Nowadays, *H. elongata* is also gathered by hand on shore in Ireland and Spain. Public authorities from these countries should introduce and enforce minimum harvesting size guidelines for *H. elongata* (if it is not already), and more generally, implement species specific regulations to ensure the sustainability of the algae resources and harvesting activities. In addition, species specific management requires ecological indicators sensitive to harvesting pressures and easy to measure by scientific observers and/or fishermen. In this context, demographic attributes are easily obtainable indicators that can be used as tools for stakeholders and policy makers.

The effects of other factors such as herbivory or extreme environmental conditions may also have operated on the intraspecific relationships of *H. elongata*. Indeed, recovery is assumed to be higher in the presence of herbivores (Aquilino and Stachowicz, 2012), which are thought to promote succession by grazing on early-successional fast-growing ephemeral species that would otherwise prevent establishment of perennial algae (Aquilino and Stachowicz, 2012). Understanding the balance between these factors is

important to understand how settlement patterns affect population dynamics, although understanding the individual influences of each factor can be difficult (Stachowicz and Byrnes, 2006).

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358

359

360

361

362

363

364

365

366

367

368

Figures

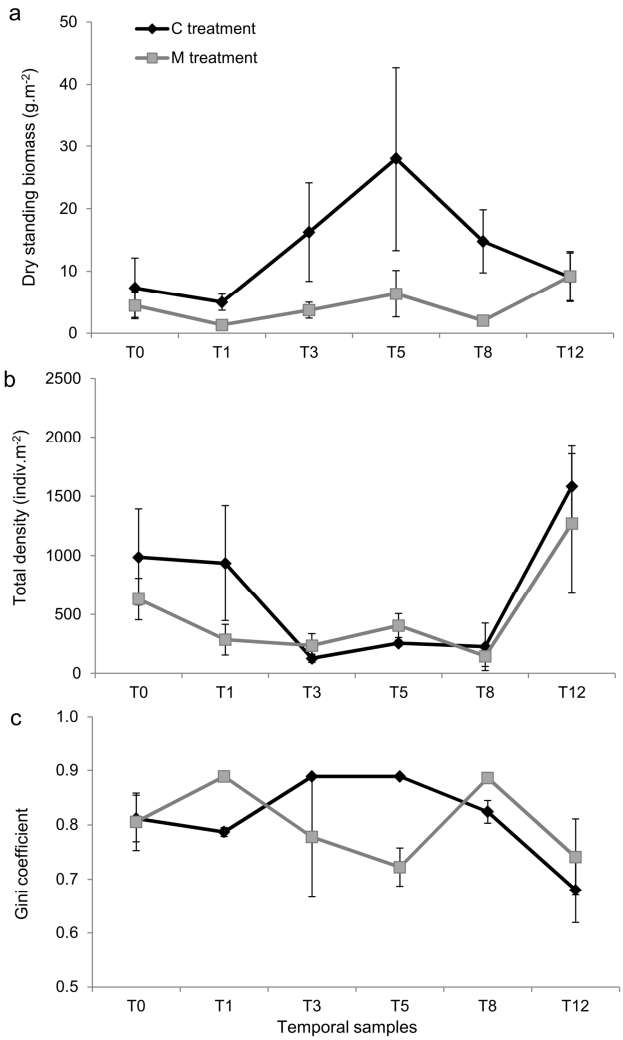

Fig. 1 Temporal variation (mean ± SE) of dry standing biomass

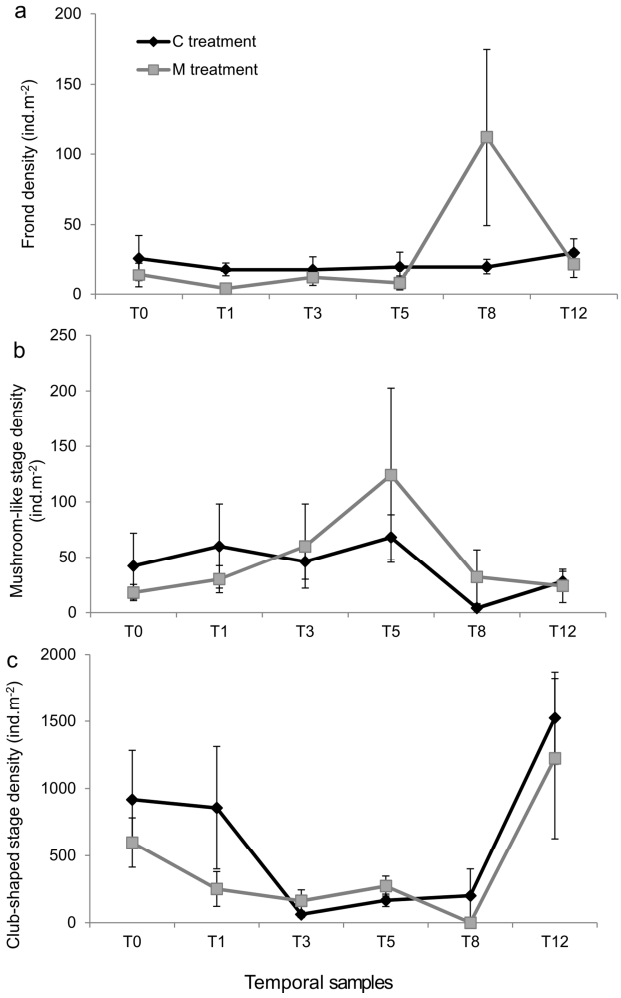

Fig. 2 Temporal variation in densities (individual.m^{-2}; mean

Table 1 Summary of Permutational Analysis of Variance (PERMANOVA) for demographic parameters and developmental stages of *Himanthalia elongata* population. *: p < 0.05; **: p < 0.01; ***: p < 0.001. Factors: controls vs. manipulated (CsM: 2 levels, fixed), and time (T: 6 levels, fixed and crossed).

Demographic parameters

Source of variation	df	Dry standing biomass		Total density		Gini coefficient	
		MS	F	MS	F	MS	F
CsM	1	8311.80	4.70 *	1348.80	0.74	348.79	1.85 ***
T	5	1625.40	0.92	7189.60	3.96 ***	227.24	1.21
CsMxT	5	2078.00	1.18	1238.40	0.68	193.77	1.03
Res	48	1767.70		1813.40		188.14	

Developmental stages

Source of variation	df	Frond density		Club-shaped stage density		Mushroom-like stage density	
		MS	F	MS	F	MS	F
CsM	1	22559.00	13.91 ***	1978.10	0.78	1746.40	0.54
T	5	2126.10	1.31	9880.00	3.88 ***	4130.60	1.27
CsMxT	5	1587.50	0.98	2133.70	0.84	2626.10	0.81
Res	48	1622.10		2548.00		3254.20