



# Population dynamics of the brown alga *Himantalia elongata* under harvesting pressure



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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 *Himantalia 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.

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## 1. 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 *Himantalia 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,

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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.

## 2. Material and methods

### 2.1. 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.

### 2.2. 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 m<sup>2</sup> 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<sub>n</sub> where *n* is the number of months since harvest. At each sampling date, five 0.1 m<sup>2</sup> random quadrats were sampled on each treatment zones (C and M).

### 2.3. 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:

$$DW = a \times FL^b \quad (1)$$

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 m<sup>2</sup> 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.

### 2.4. 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).

### 2.5. Data analysis

Multivariate analyses were made to test the effect of the

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