

Spatial and temporal patterns of recovery of low intertidal Laminaria digitata after experimental spring and autumn removal

Aschwin H. ENGELEN^{1*}, Laurent LÉVÈQUE², Christophe DESTOMBE^{3,4} and Myriam VALERO^{3,4}

(1) Centre of Marine Sciences (CCMAR), CIMAR – Laboratório Associado, Universidade do Algarve,

Campus de Gambelas, 8005-139 Faro, Portugal. *corresponding author: aengelen@ualg.pt

⁽²⁾ CNRS, FR2424, Service Mer et Observation, Station biologique de Roscoff, Place Georges Teissier, F-29682 Roscoff cedex, France

(3) UPMC Univ Paris 6, UMR 7144, Equipe Biologie Evolutive et Diversité Marine BEDIM, Station Biologique de Roscoff, BP 74, F-29682 Roscoff Cedex, France

(4) CNRS, UMR 7144, Equipe Biologie Evolutive et Diversité Marine BEDIM, Station Biologique de Roscoff, F-29682 Roscoff Cedex, France.

Abstract: To investigate the resilience of *Laminaria digitata* kelp forest to physical disturbance, like human harvesting and storms, we experimentally removed all kelp sporophytes completely and followed the subsequent recovery at two low intertidal locations dominated by *L. digitata* in Brittany, France. Removal was performed in four quadrats per location in Spring and Autumn 2007 and recovery was monitored every 6 months until Autumn 2009. Although total kelp density showed no variation before and 6-30 months after removal, there was a clear increase of the annual kelp *Saccorhiza polyschides* and kelp recruits 6 and 12 months after both spring and autumn removal. Total stipe, blade and total length did not show strong spatial and temporal variation 12 months after removal. However, this lack of strong temporal variation was mainly due to compensated strong decreased *L. digitata* lengths for at least 12 months after removal by increased lengths of *S. polyschides* 6-12 months after removal. *L. digitata* recovery was faster after autumn compared to spring removal but required at least 12 months. However, structural changes in species composition and species size structure took 18-24 months to recover. Conclusions on how long recovery takes, strongly depends on the season of the removal.

Résumé : *Patrons spatio-temporels de restauration de* Laminaria digitata *en zone intertidale inférieure après éradication expérimentale au printemps et en autome*. Pour analyser la résilience des forêts de *Laminaria digitata* aux perturbations physiques, comme la récolte ou les tempêtes, nous avons éradiqué expérimentalement tous les sporophytes des grandes algues brunes de la zone intertidale inférieure, dominées par la présence de *L. digitata*. Afin de suivre la recolonisation, nous avons effectué des éradications expérimentales dans quatre cadrats par site, au printemps et en Automne 2007 dans deux sites Bretons, La recolonisation a été suivie tous les 6 mois jusqu'en Automne 2009. Bien que la densité totale des grandes algues brunes ne montre pas de variation avant et 6-30 mois après éradication, les résultats indiquent une nette augmentation de l'espèce annuelle *Saccorhiza polyschides* ainsi que des recrues de plusieurs autres espèces de laminaires 6 et 12 mois après les éradications. Le nombre total de stipes ainsi que la longueur des stipes et des frondes ne montrent

Reçu le 2 novembre 2010 ; accepté après révision le 4 juillet 2011. Received 2 November 2010; accepted in revised form 4 July 2011.

pas de variation spatio-temporelle significative 12 mois après l'éradication. Cependant, cette faible variation spatiotemporelle s'explique par un effet de compensation : la forte réduction de la taille des individus de *L. digitata* observée un an après l'éradication est contrebalancée par l'augmentation de celle des individus de *S. polyschides*. La recolonisation de *L. digitata* est plus rapide lorsque l'éradication a été faite en automne plutôt qu'au printemps mais elle demande au minimum 12 mois. Quoiqu'il en soit, il faut 18 à 24 mois pour retrouver la même composition en espèces et la même structure en taille qu'avant l'éradication. En conclusion, le temps nécessaire pour retrouver l'état d'origine est fortement dépendant de la saison à laquelle l'éradication a été menée.

Keywords: Laminaria digitata • Sacchoriza polyschides • Kelp composition and structure • Disturbance and recovery

Introduction

In the last 50 years, it has become widely accepted that the eruption of the human population is causing the extinction of much cherished biodiversity and destruction of biomes that we depend on (Costanza et al., 1997; Pimentel et al., 1997). If our greatest achievement in the last century was the collective understanding of what evolution and its products, the biosphere, mean to our own survival, the challenge of the present century is to develop a more predictive science of evolutionary ecology before it is too late to shape a desirable future (Woodruff, 2001). Coastal marine ecosystems are degrading due to a range of human activities threatening their current level of support for human and marine life. The global, widespread ecological decline of coral reefs provides one of the best-known examples of contemporary biome degradation. Although there is still much uncertainty concerning the fate of these communities, there is a growing consensus that perhaps they will change rather than disappear entirely (Hughes et al., 2003), most likely through shifts in species composition (Hughes et al., 2003), with some species even altering their ecological ranges (Precht & Aronson, 2004). There is evidence that suggests that similar changes are taking place in important communities in non tropical marine habitats like kelp forests (Bartsch et al., 2008, Wernberg et al., 2010).

Kelps, i.e. brown algae of the order Laminariales, are important components of coastal ecosystems in polar and temperate waters, in both hemispheres (Steneck et al., 2002). They constitute highly productive kelp forest systems often viewed as the marine equivalent to terrestrial rain forests due to their hosting of a great biodiversity of epiphytic flora and macrofauna (e.g. Lippert et al., 2001; Steneck et al., 2002; Christie et al., 2003 & 2009; Jørgensen & Christie, 2003). In addition, kelps form the basis for commercial kelp harvesting and indirectly coastal fishing industry. These kelps are cool-water species for which elevated temperatures are stressful (Wernberg et al., 2010), so elevated seawater temperatures as predicted under global change scenario might reduce the resilience of kelp forest to other stressors like disturbance.

Kelp has to cope with physical disturbance mainly due to human harvesting and storm events that remove thalli or entire individuals from populations. Traditionally kelp is used for dried food products and as a soil amendment in agriculture in many parts of the world (Chapman & Chapman, 1980; Werner & Kraan, 2004), and is an inexpensive local resource in coastal agricultural areas. Nowadays kelp are harvested worldwide as a source of alginate; a biopolymer widely used in the food and cosmetics industry. In Europe, yearly harvesting for industrial purposes is restricted to Norway (150,000 tons) and France (Brittany 60-80,000 tons; Dauvin, 1997; Arzel, 1998; Werner & Kraan, 2004, Davoult et al., 2011).

In addition, storms are a major cause of physical disturbance and localized canopy loss in most kelp forests (e.g., Dayton & Tegner, 1984). In either case, when the canopy is lost, there are profound changes to local environmental conditions (Wernberg et al., 2005; Irving & Connell, 2006). In order for the canopy to regenerate, either existing recruits must acclimatize to the new canopy-free conditions and grow, or new recruits must establish (Graham, 1997). These recovery processes will become increasingly important to the persistence of kelp forests, and preserving their ecological function, if climate change causes storm intensity to increase as predicted (Harley et al., 2006; IPCC, 2007). Harvesting and storms differ in their timing. The official harvesting season is from May 15th - October 15th. During the winter months, a few boats (2-5) are allowed to harvest seaweeds, in order to sustain a basic supply for the domestic alginate industry. Storms take place predominantly in autumn and winter (Werner & Kraan, 2004).

Management of kelp forests to sustain habitat and resource requires detailed knowledge of how main factors

like physical disturbance influence the spatial and temporal dynamics of kelp species. The main objective of this study was to contribute to this required knowledge by assessing the post-disturbance recovery of *Laminaria digitata* (Hudson) J.V. Lamouroux after a total canopy removal and compare between spring (harvest season) and autumn (storm season) removal over a recovery period of three years. For this purpose we experimentally removed all kelp sporophytes at two low intertidal locations dominated by *L. digitata* in Morlaix Bay, northern Brittany, France. We show that *L. digitata* recovery took at least 12-30 months depending on the criteria used, however colonization by *Saccorhiza polyschides* (Lightfood) Batters during this period compensated part of the loss of *L. digitata* canopy.

Material and Methods

Environment & Site description

The study area of the Bay of Morlaix, located east of Roscoff on the northern coast of Brittany (Fig. 1), covers

approx. 75 km² and faces offshore in a northward direction. The coastal platform is generally less than 17 m deep and the internal relief of the coastal platform is very irregular. Numerous rocky outcrops, shoals and small islands occur in the northwestern and southern part of the bay. Surface water temperature in the bay ranges on average between 8-10°C in February/March and 15-16°C in August/September (Dauvin et al., 1991). Salinity is relatively constant between 34.9-35.5. (Dauvin et al., 1991). The optical transparency is very favorable, 14-26% of radiant energy reaches the 25 m water depth (Sournia et al., 1987) just outside the bay, but there is a gradient from the inner to the outer part of the bay. The amplitude of the semidiurnal tide reaches up to 9.7 m height during spring tide. Maximum tidal current velocities exceed 2 m.s-1 (S.H.O.M., Service Hydrographique et Océanographique de la Marine, Courants de marée dans la Manche et sur les côtes françaises de l'Atlantique, 1953). In the more exposed outer section of the bay, affected by episodically strong storm-wave impact, the rocky seabottom is densely colonized by extended kelp forests of Laminaria



Figure 1. Location of the two experimental sites Duons and Ar Pourven within Morlaix Bay, Brittany, France. Figure 1. Localisation des deux sites d'étude, Duons et Ar Pourven, dans la Baie de Morlaix, Bretagne, France.

hyperborea (Gunnerus) Foslie, *L. digitata* and *S. polyschides* (Wehrmann, 1998). Both study locations are situated in the north-west corner of the bay at a distance of approximately 3 km from each other. Environmental conditions are however rather contrasted. The first site (Ar Pourven, 3°57.55'W-48°42.71°N) is indeed located more inside the bay than the second one (Duons, 3°55.59'W-48°43.66'N). Thus, Ar Pourven is more sheltered from swell and the clarity of water is lower than in Duons. Overall conditions in Duons are slightly more favourable for the development of kelps, and commercial harvesting pressure is higher in this area.

Species

The kelp life cycle consists of a microscopic haploid gametophyte phase, alternating with macroscopic diploid sporophytes. Male and female gametophytes being microscopic, they cannot be observed in the field and consequently only sporophytes were monitored in this study. The model species is *Laminaria digitata*, a relatively short lived perennial seaweed (3-5 years, Werner & Kraan, 2004) and one of the commonly harvested kelp species in Europe. Mature sporophytes can produce blade lengths of up to 2.5 m under suitable conditions. It is a North Atlantic Arctic cold-temperate species restricted to the North Atlantic. The southernmost occurrence of this species in European waters is on the southern coasts of Brittany.

Saccorhiza polyschides is generally described as annual, but would be better described as monocarpic, as the plants which survive to over-winter are those which did not become fertile in their first summer. Life expectancy and age to fertility is 8-10 months for one year and 14-22 months for over wintering individuals. Young sporophytes appear in the spring and grow rapidly. The blades of individual plants may reach lengths of over 3 m and the basal "bulb" may reach a diameter of over 30 cm (Norton, 1970).

Disturbance experiment

A field experiment in each of the two locations, tested the recovery potential of *L. digitata* after complete canopy removal and whether there the recovery differed between spring and autumn removals. At each location, all kelp sporophytes were completely removed from four haphazardly placed plots of 0.25 m² in spring (March) and autumn (September) of 2007. All the removed canopy from each plot was taken to the laboratory where of each individual the species, stipe length (distance from base to meristem), total length, fresh weight (> 5 grams) and reproductive status (presence/absence of sori) was determined. Distinguishing among *L. digitata* and *L. hyperborea* was difficult for small kelp recruits up to a few

centimeter long and therefore these were pooled in the category unidentified recruits. Every six months after removal the same plots were monitored and stipe and thallus (stipe + blade) lengths and reproductive status of all individuals of each kelp species were determined non-destructively. At the end of the experiment, in autumn 2009, all kelp sporophytes were completely removed from all plots and the same variables were determined as after the initial removal of the plots. From spring 2008 to autumn 2009 four untreated permanent plots were monitored in an identical way as the removal plots in each location to function as controls.

Statistics

Data obtained from the initial canopy removal in Spring and Autumn 2007 were analysed using two-way ANOVAs with season (fixed, 2 levels: Spring and Autumn) and location (fixed, 2 levels: Duons and Ar Pourven) to test for temporal and spatial variation in density, stipe length and total length of all kelp per plot as well as for *L. digitata*, *S. polyschides* and unidentified recruits separate. In addition, reproductive *L. digitata* density was analysed.

Monitoring data of both removal seasons was analysed separately using two factor repeated measurement analysis of variance (RM-ANOVA) as the same plots were followed at each census. The two factors involved were time (fixed, every 6 months) and location (fixed, 2 levels: Duons and Ar Pourven). As the initiation of the permanent control plots did not coincide with the initial removals, controls were analysed separately for temporal and spatial variation.

Normality of all data and homogeneity of variances were verified prior to analysis of variance. In some cases data were log10 transformed in order to meet the required criteria. Student-Newman-Keuls pairwise multiple comparisons were used on significant interactions or factors with more than two levels.

Shifts in species composition were analysed using the PERMANOVA module (Anderson, 2001) within Primer 5 software (Clarke & Gorley, 2006). Unlike least squares ANOVA, PERMANOVA can analyse multivariate data and requires no implicit assumptions about the underlying distribution (normality) or spread (variance) of the data. Although observed differences may be because of differences in means or variance, the permutation procedure does not assume either normality or homoscedasticity. Distance based homogeneity of dispersion tests, tests of main effects and pairwise tests on significant factors or interactions were performed as recommended using the permutation of residuals under a reduced model, with 9999 permutations.

Results

Before removal

Kelp densities did not differ significantly between spring and autumn (Two-way ANOVA, Season, p = 0.069, Fig. 2A), but densities were almost 50% higher in Duons compared to Ar Pourven (Two-way ANOVA, Location, p = 0.049, Fig. 2A). Total stipe length was about twice as low in spring compared to autumn (Two-way ANOVA, Season, p = 0.023, Fig. 2B), but did not show significant spatial variation (p = 0.073) although there was a clear trend for a lower total stipe length in Ar Pourven compared to Duons (Fig. 2B). Total thallus length was lower in spring compared to autumn (Two-way ANOVA, Season, p = 0.047, Fig. 2C) and lower in Ar Pourven compared to Duons (Two-way ANOVA, Location, p = 0.018, Fig. 2C). Density of reproductive L. digitata was about 3 times higher in autumn compared to spring 2009 (mean \pm SE: 8.13 ± 1.68 and 2.75 ± 0.41 , respectively; two-way ANOVA, Season, p = 0.003); suggesting that differences in density between locations resulted in spatial total stipe and length differences whereas seasonal differences were predominantly caused by larger and more reproductive individuals in autumn compared to spring.

Effect of Spring versus Autumn removal on changes in all kelp canopy (without distinguishing among species)

Spring removal did not result in spatial and temporal changes in total kelp density, total stipe length, blade length and total thallus length (Fig. 3). After 30 months, kelp densities had more than doubled in Duons compared to Ar Pourven (SNK Test, p = 0.004) and compared to previous census in Duons (SNK Tests, all p-values < 0.003, Fig. 3). With the autumn removal, density showed no significant temporal or spatial variation (RM-ANOVA, all p-values > 0.080, Fig. 3), even though in Duons there was a strong trend of increasing density 6-18 months after removal in some of the plots. Total stipe length was higher 24 months after removal compared to any time before and about twice the total length before removal in Ar Pourven (SNK Tests, all p-values < 0.039, Fig. 3), whereas in Duons, total stipe length was only decreased six months after removal (SNK Tests, all p-values < 0.015, Fig. 3). Total thallus length (RM-ANOVA, Time, p = 0.010) was reduced 6 months after removal (SNK Tests, all p-values < 0.031, Fig. 3), intermediate after 12 months and similar to before removal after 18-24 months of recovery. Total blade length showed no temporal variation in Ar Pourven (SNK, all p-values > 0.223), whereas in Duons, blade length was reduced 6 months after canopy removal compared to before removal (SNK, p < 0.001) and after 24 months of recovery (SNK, p = 0.004, not shown).



Figure 2. Mean (\pm SE) total sporophyte kelp density (A), total stipe length (B) and total length (C) in Spring and Autumn (left) in two locations: Duons and Ar Pourven (right) from removal quadrats. Data are four replicates at each Season x Location combination. Different letters above the error bars indicate groups that are significantly different (Two-way ANOVA, p < 0.05).

Figure 2. Moyennes (\pm erreur type) de la densité des sporophytes de laminaires (A), de la longueur des stipes (B) et de la longueur totale des thalles (C) au printemps et en automne (graphiques de gauche) et dans les deux sites d'étude: Duons et Ar Pourven (graphiques de droite) par cadrat éradiqué. Les données correspondent à quatre réplicats par combinaison Saison x Site. Les lettres différentes au-dessus des barres d'erreur indiquent que les moyennes sont significativement différentes (ANOVA à deux facteurs, p < 0,05).

Effect of Spring versus Autumn removal on changes in community composition

With spring removal, kelp community composition differed spatially and temporally (PERMANOVA, Location x Time interaction, p = 0.045, Fig. 4). In both locations, species composition from before removal differed only from 6 months after removal (Pairwise tests: Ar Pourven p = 0.027, Duons p = 0.029) and the 6 months differed from 18 and 30



Figure 3. Mean (\pm SE) total sporophytes kelp density (top), total stipe length (middle) and total thallus length (bottom) before and after experimental removal of all kelp in Spring (left) and Autumn (left) 2007 in two locations: Duons (black) and Ar Pourven (white). Data are four replicates at each Time x Location combination. Different letters above the error bars indicate temporal groups that are significantly different, * indicates significant differences between locations (SNK, p < 0.05).

Figure 3. Moyennes (\pm erreur type) de la densité totale des sporophytes (en haut), de la longueur des stipes (au milieu) et de la longueur des thalles (en bas) avant et après éradication expérimentale de toutes les sporophytes au printemps (à gauche) et en automne (à droite) en 2007 dans les deux sites: Duons (en noir) et Ar Pourven (en blanc). Les données correspondent à quatre réplicats pour chaque combinaison Temps x Site. Les lettres différentes au-dessus des barres d'erreur indiquent que les moyennes sont significativement différentes entre dates, * indique que la différence est significative entre sites (SNK, p < 0,05).

months after removal in Ar Pourven (Pairwise tests: all p-values < 0.0295) and 24 and 30 months in Duons (Pairwise tests: all p-values < 0.0281). No significant difference between locations was detected at any time (Pairwise tests: p > 0.086). With autumn removal, species composition did not differ temporally before and after removal (PER-MANOVA, Time, p = 0.0522 and Location x Time, p = 0.1695), but there was a consistent difference between Duons and Ar pourven (PERMANOVA, Location, p = 0.0066) with a higher overall abundance of all species in Duons compared to Ar Pourven (SIMPER, Fig. 4).

Laminaria digitata specific changes

Densities of *L. digitata* were not significantly reduced 6 or more months after spring removal, temporal variation depending on location (RM-ANOVA, Location x Time, p < 0.001), was detected due to a fourfold density increase in Duons 30 months after removal (SNK, all p-values < 0.007, Fig. 4). After Autumn removal, densities of *L. digitata* showed temporal variations independent of location (RM-ANOVA, Time, all p-values < 0.026), with higher densities 18 compared to 6 months after removal (SNK, all p-values < 0.045, Fig. 4). Reproductive densities of *L. digitata* showed significant temporal variation (RM-ANOVA, Time, p = 0.002) with lower densities 6 and 12 months after removal compared to before (SNK, all p-values < 0.015) and 18 (SNK, all p-values < 0.047) and 30 (SNK, all pvalues < 0.016) months after removal (not shown).

After spring removal, total stipe length of *L. digitata* did not show any significant change over time in Ar Pourven (SNK, all p-values > 0.069, Fig. 5), whereas in Duons length was reduced 6-24 months after removal compared to before removal (SNK, all p-values < 0.05, RM-ANOVA, Location x Time interaction, p = 0.017). Only after 30 months of recovery total stipe length was returned to before removal levels (SNK, p = 0.121, Fig 5). After Autumn removal, total stipe length of *L. digitata* showed significant change over time independent of location (RM-ANOVA, time, p < 0.001), with strong reductions up to 12 months after removal (SNK, all p-values < 0.05, Fig 5). After more than 18 months of recovery total stipe length was returned to before removal levels (SNK, all p-values > 0.22).

After spring and autumn removal, total blade lengths of *L. digitata* did not vary in Ar Pourven (SNK, all p-values > 0.062 and all p-values > 0.699, respectively), but in Duons blade length was lower 6 and 12 months after removal compared to before (SNK, all p-values < 0.008 and all p-values < 0.026, respectively) and 24 months of recovery after spring removal (SNK, all p-values < 0.007; RM-ANOVA, Location x Time, p = 0.022, Fig. 6) and between 6 months and 24 months of recovery after autumn removal (SNK, p = 0.027, Fig. 6).

Reproductive densities of L. digitata showed temporal

variation depending on location (RM-ANOVA, Location x Time, p = 0.008). In Duons, reproductive densities did not recover during the experimental period to the level before canopy removal (SNK, all p-values < 0.001). In Ar Pourven, reproductive densities were reduced 6 (spring 2008) and 18 (spring 2009) months compared to before canopy (SNK, all p-values < 0.002) and 24 months after removal (SNK, all p-values < 0.002). At the end of the experiment reproductive densities were higher in Ar Pourven compared to Duons (SNK, p = 0.011). Standing wet weight biomass of *L. digitata* showed differences between before removal and at the end of the experiment depending on location according to the RM-ANOVA (p = 0.035), but only temporal differences were detected at Ar Pourven (SNK, all p-values > 0.021, Fig. 7).

Sacorhiza polyschides specific changes

After Spring removal, density of *S. polyschides* did not vary with time in Ar Pourven (SNK, all p-values > 0.05), but in Duons density was strongly increased 6 and 12 months after removal compared to all other sampling dates (SNK, all p-values < 0.003). Total stipe length of *S. polyschides* only changed over time (RM-ANOVA, p = 0.001), with longer stipes 6 and 12 months after removal compared to before and after 18 months (SNK, all p-values < 0.020 and all p-values < 0.036, respectively, Fig. 5). Total blade length of *S. polyschides* only showed temporal variation in Duons with higher blade lengths after 6 and 12 months of recovery (SNK, all p-values < 0.008). Differences between locations were detected 6 and 12 months after canopy removal (SNK, all p-values < 0.014, Fig. 6).

After Autumn removal, densities of S. polyschides did not vary over time in Duons (SNK, all p-values > 0.324), but in Ar Pourven densities were higher 6 months after removal compared to all other sampling dates (SNK, all pvalues < 0.026, Fig. 4). Total stipe length of S. polyschides change over time depended on location (RM-ANOVA, p = 0.001). Although there was a trend of increase 12 and 18 months after removal in Duons, significant differences could only be detected between the two locations 18 months after removal (SNK, p = 0.031, Fig. 5), when about 3 m stipe length was present in Duons and none in Ar Pourven. Total blade length of S. polyschides only showed temporal variation in Ar Pourven with higher blade lengths after 12 months of recovery compared to after 24 months of recovery (SNK, p = 0.021; RM-ANOVA, Location x Time, p = 0.009).

Unidentified kelps specific changes

After spring removal, densities of unidentified kelps did not change in Duons (SNK, all p-values > 0.289), but in Ar



Figure 5. Mean (\pm SE) total stipe length of *Laminaria digitata* (top), *Saccorhiza polyschides* (middle) and unidentified kelp recruits (bottom) before and after experimental removal of all kelp in Spring (left) and Autumn (left) 2007 in two locations: Duons (black) and Ar Pourven (white). Data are four replicates at each Season x Location combination. Different letters above the error bars indicate temporal groups that are significantly different, * indicates significant differences between locations (SNK, p < 0.05).

Figure 5. Moyenne (\pm erreur type) de la longueur totale des stipes de *Laminaria digitata* (en haut), de *Saccorhiza polyschides* (au milieu) et des jeunes sporophytes indéterminés (en bas) avant et après l'expérience d'éradication au printemps (à gauche) et an automne (à droite) en 2007 dans les deux sites: Duons (en noir) et Ar Pourven (en blanc). Les données correspondent à quatre réplicats pour chaque combinaison Saison x Site. Les lettres différentes au-dessus des barres d'erreur indiquent que les moyennes sont significativement différentes entre dates, * indique que la différence est significative entre sites (SNK, p < 0,05).



Figure 6. Mean (\pm SE) total blade length of *Laminaria digitata* (top), *Saccorhiza polyschides* (middle) and unidentified kelp recruits (bottom) before and after experimental removal of all kelp in Spring (left) and Autumn (left) 2007 in two locations: Duons (black) and Ar Pourven (white). Data are four replicates at each Season x Location combination. Different letters above the error bars indicate temporal groups that are significantly different, * indicates significant differences between locations (SNK, p < 0.05).

Figure 6. Moyenne (\pm erreur type) de la lame de *Laminaria digitata* (en haut), de *Saccorhiza polyschides* (au milieu) et des jeunes sporophytes indéterminés (en bas) avant et après l'expérience d'éradication du printemps (à gauche) et de l'automne (à droite) en 2007 dans les deux sites: Duons (en noir) et Ar Pourven (en blanc). Les données correspondent à quatre réplicats pour chaque combinaison Saison x Site. Les lettres différentes au-dessus des barres d'erreur indiquent que les moyennes sont significativement différentes entre dates, * indique que la différence est significative entre sites (SNK, p < 0,05).



Figure 7. Mean kelp (\pm SE) biomass (g wet weight.m⁻²) before experimental removal of all kelp in Spring (left) and Autumn (left) 2007 and after recovery up to Autumn 2009 in two locations: Duons (black) and Ar Pourven (white). Data are four replicates at each Season x Location combination. Different letters above the error bars indicate temporal groups that are significantly different, * indicates significant differences between locations (SNK, p < 0.05).

Figure 7. Moyenne (\pm erreur type) de la biomasse (en g de poids frais.m⁻²) avant éradication expérimentale au printemps (à gauche) et en automne (à droite) et après recolonisation en automne 2009 dans les deux sites: Duons (en noir) et Ar Pourven (en blanc). Les données correspondent à quatre réplicats pour chaque combinaison Saison x Site. Les lettres différentes au-dessus des barres d'erreur indiquent que les moyennes sont significativement différentes entre dates et/ou saisons, * indique que la différence est significative entre sites (SNK, p < 0,05).

Pourven was highest 6 months after canopy removal (SNK, all p-values < 0.003, Fig. 4). Total stipe length of unidentified recruits (very low total lengths) did not show any significant differences (not shown).

After autumn removal, density of unidentified kelps did not change in Ar Pourven (SNK, all p-values > 0.388), but in Duons was higher 6 months after removal compared to before (SNK, p = 0.005) and 24 after removal (SNK, p =0.006, Fig. 4). Six months after removal densities of unidentified kelps was higher in Duons compared to Ar Pourven. *Laminaria hyperborea* was observed in some quadrats in Ar Pourven during the course of the study, but was never observed within the quadrats in Duons. Total stipe lengths of unidentified recruits did not show any significant differences (not shown).

Discussion

Physical disturbance events in the form of storms and harvesting result in local kelp canopy loss that can have profound consequences for environmental conditions and ecosystem functioning. Recovery depends on the remaining microscopic recruits or on completely new recruitment (Graham, 1997; Toohey & Kendrick, 2007). Resilience of kelps is expected to depend more and more on these recovery or recolonisation processes as storm frequency is expected to increase under global change (IPCC, 2007) and harvesting pressure is increasing due to an ever increasing demand. Our experimental results suggest that L. digitata kelp forests are resilient to small scale canopy removing events. Conclusions on how long recovery takes, strongly depends on the criteria used and the season of the removal. After spring removal, total kelp density, stipe length and thallus length was recovered within the first six months, whereas after autumn removal total stipe length was recovered within 6 months and thallus length within 12 months. However, structural changes in species composition and species size structure took at least 18-24 months to recover. The results obtained in our study on L. digitata are similar to those previously reported by Pérez (1971) and Smith (1985). In Porspoder Brittany, Pérez (1971) demonstrated that after destruction of about 60% of the visible sporophytes in the field, 18 months were required to recover the pre-harvest levels. Similarly, in Nova Scotia, Smith (1985) reported that recovery of L. digitata canopy took about 2 years after experimental removal. Because the extent of complete life history of L. digitata from meiotic spores to mature sporophyte was estimated to 27 months (Pérez, 1971), the rapid recovery observed in these different studies should be at least partially explained by the microscopic stages of the life cycle remaining after removal.

Moreover, our results show that removal of L. digitata can on the short term cause a shift in kelp species composition to a dominance of S. polyschides. Most recovering kelp forest demonstrate a clear pattern of succession, with initially more opportunistic, shorter lived species as first colonizers (like *S. polyschides* in our study) which get replaced by the less opportunistic species (like L. digitata) (Kitching, 1941; Kain, 1975). Different studies on kelp experimental harvesting have demonstrated a clear succession of species. For example, in Nova Scotia, two years after removal were required for both species Laminaria longicruris (Bachelot de la Pylaie) Kuntze and L. digitata to reacquire pre-harvest population characteristics (Smith, 1985). However, L. digitata recovered more slowly than L. longicruris the first year, probably because of its prolonged sporophytic life span (> 4 years) compared to L. longicruris (2 years). However, during the second season L. digitata gradually replaced Laminaria longicruris (Smith, 1985). Similar observations were made after removal of the two major kelp species Laminaria bongardiana (Postels & Ruprecht) Sekivanova and Laminaria dentigera Kjellman of Bering Island that showed abundances returned to former levels 2-3 years after harvesting (Oshurkov & Ivanjushina, 1993). More recently, experimental removal of native algal canopy in Tasmania, demonstrated that disturbance promoted the establishment of the invasive species Undaria pinnatifida (Harvey) Suringar, whereas the presence of a stable native algal canopy inhibited the installation of the introduced opportunistic kelp (Valentine & Johnson, 2003). However, the density of U. pinnatifida declined significantly during the second year following removal, associated with a native species canopy recovery. The importance of pre-emptive competition inhibiting or delaying recruitment of other species was considered as a major issue for *Phyllospora* comosa (Labillardière) C. Agardh recovery after habitat degradation (Coleman et al., 2008). More than twenty years ago, such a competitive effect was demonstrated in experimental manipulations with native seaweed species inhibiting the establishment of the introduced species Sargassum muticum (Yendo) Fensholt (Deysher & Norton, 1982).

In the present study, *S. polyschides* colonized rapidly just after kelp canopy removal but declined with the development of *L. digitata*. However, the effect of preemptive competition might become a problem since an increasing proportion of *S. polyschides* in *L. digitata* yield was reported in Brittany these last decades (Arzel, 1998) probably due to an increasing disturbance (storm and harvesting). These shifts of species can also be of great importance for the industry. Prices for the raw material are negotiated by the fishermen and the industry before the start of the harvesting season and are valid throughout the season. Prices, however, are re-adjusted for each boat at the dockside to take into account the actual quality in terms of purity of the crop. One of the criteria that determine the dockside price reduction is the proportion of *S. polyschides* within the *L. digitata* harvest. In recent years, the industry has started to reject *Laminaria* crops containing an apparent proportion of *S. polyschides* of over 50% (Arzel, 1998). In extreme cases this has resulted in a discharge of whole boat loads back into the sea. In this respect our results indicate that a fallow period of at least 18-24 months (Figs 5 & 6) would be most efficient for increasing the harvest of *L. digitata* and reducing the proportion of *S. polyschides*.

Since in France there are no official regulations with respect to fallow periods for L. digitata beds the same kelp beds can be harvested year after year. Since at least 15 years, however, L. digitata beds are thought to be declining. In certain harvesting sectors, where only a small number of harvesting boats are operating in a sufficiently large area, local fishermen have introduced self management and fallow periods of 1 - 2 years (Werner & Kraan, 2004). The introduction of fallow periods or a spatial management scheme within sectors would be advisable under the current view of possible L. digitata decline. Another testable option would be to harvest 1 year after L. digitata yield to just remove the S. polyschides canopy, thereby preventing their reproduction and reducing the shading of young L. digitata recruits by the S. polyschides creating better growth conditions for L. digitata. However both the ecological and economical effects would require investigation.

The reasons for the increasing abundance of S. polyschides and declining L. digitata are unclear. Most probably several factors play a role but the importance of each of them is unknown. Harvesting might be involved as S. polyschides rapidly colonises free space created after harvesting. The two locations used were chosen because of their differences in harvesting pressure which is considerably higher in Duons compared to Ar Pourven. In Duons, total kelp densities and total kelp length was higher than in Ar Pourven, the same trend was observed for total stipe length, although not significant (Fig. 2). Overall, temporal dynamics were stronger and the opportunistic S. polyschides was more abundant in Duons compared to Ar Pourven. However, as we don't have replicated harvested and non-harvested study locations we can only speculate whether these differences are linked to harvesting or other factors. Slight differences of seawater temperature between locations or over times as in the reported decline of L. digitata might also have contributed to competitions shifts between L. digitata and S. polyschides to the benefit of the latter as S. polyschides performs better under higher temperatures (Perreira et al., 2011; Delebecq et al., 2011).

Recovery of kelp was expected to differ between spring and autumn removal of canopy. L. digitata shows two peaks of fecundity, one in June/July and a second one in October/November. This is thought to result in two different cohorts appearing in October/November and March-May (references in Werner & Kraan, 2004). As total lengths were higher in autumn than in spring, more biomass was removed during the autumn clearings.

In conclusion, our experimental results suggest that *L. digitata* kelp forests, in terms of kelp species composition and structure, may be regained within 3 years of canopy removal. However, the size of kelp plants and the age structure of the population in the re-grown forest remained different from the untouched forest. In some cases removal of *L. digitata* resulted locally in a species shift by a temporary dominance of *S. polyschides*.

Acknowledgements

We first like to thank the marine service of Roscoff (namely Mathieu Camusat, Yann Fontana, Noël Guidal, Gilles Maron and Wilfried Thomas) for their logistic help to transport people to the study sites and for their participation to the implementation of the sampling design and to the measurements. We will also want to thank all the people that have actively participated to the surveys in the field: Alexandre Geoffroy, Amandine Mear, Andres Ritter, Catherine Leblanc, Cécile Pérez, Cécile Riboux, Claire Daguin-Thiébaut, Daniella Mella-Flores, Daphné Grulois, Denis Roze, Emmanuelle Billard, Florence Tellier, François Thomas, Frédérique Viard, Gaspard Delebecq, Gauthier Schaal, Licinia Gourveia, Margot Calluet, Maria Gracia Bustamante, Marie Vasseur, Marine Robuchon, Mathieu Oriot, Philippe Potin, Sarah Bouchemousse, Stacy Krueger, Stéphane Mauger, Tania Perreira, Valeria Luz-Oppliger, Vasco Vieira. This study was part of the 3 year ANR project ECOKELP (ANR 06 BDIV 012). Collaborative visits between Faro and Roscoff were made possible by FCT-CNRS collaborative funding. AHE was supported by FCT scholarship SFRH/BPD/7153/2001 and SFRH/BPD/63703/2009.

References

- Anderson M.J. 2001. A new method for non-parametric multivariate analysis of variance. *Australian Ecology*, 26: 32-46
- Arzel P. 1998. Les laminaires sur les côtes bretonnes. Evolution de l'exploitation et de la flottille de pêche, état actuel et perspectives. IFREMER, Plouzané, France, 138 pp.
- Bartsch I. Wiencke C., Bischof K., Buchholz C.M., Buck B.H., Eggert A., Feuerpfeil P., Hanelt D., Jacobsen S., Karez R., Karsten U., Molis M., Roleda M.Y., Schubert H., Schumann R., Valentin K., Weinberger F. & Wiese J. 2008. The Genus Laminaria sensu lato: recent insights and developments. European Journal of Phycology, 43: 1-86.

- Chapman V.J. & Chapman D.J. 1980. Seaweeds and their uses. Chapman and Hall, London, 3rd edition, 334 pp.
- Christie H., Jørgensen N.M., Norderhaug K.M. & Waage-Nielsen E. 2003. Species distribution and habitat exploitation of fauna associated with kelp (*Laminaria hyperborea*) along the Norwegian coast. *Journal of the Marine Biological* Association of the United Kingdom, 83: 687-699.
- Christie H., Norderhaug K.M & Fredriksen S. 2009. Macrophytes as habitat for fauna. *Marine Ecology Progress Series*, 396: 221-233.
- Clarke K.R. & Gorley R.N. 2006. Primer v6: Manual/Tutorial, Plymouth.
- Coleman M.A., Kelaher B.P., Steinberg P.D. & Millar A.J.K. 2008. Absence of a large brown macroalga on urbanized rocky reefs around Sydney, Australia, and evidence for historical decline. *Journal of Phycology*, 44: 897-901.
- Costanza R., d'Arge R., de Groot R., Farber S., Grasso M., Hannon B., Limburg K., Naeem S., O'Neill R.V., Paruelo J. et al. 1997. The value of the world's ecosystem services and natural capital. *Nature*, 387: 253-260.
- Dauvin J.-C. 1997. Le bilan. In: Les Biocénoses marines et littorales françaises des côtes Atlantique, Manche et Mer du Nord. Synthèse, menaces et perspectives. (J.C. Dauvin ed), vol. 28, pp. 300-305. Muséum National d'Histoire Naturelle: Paris.
- Dauvin J.-C., Joncourt M. & Birrien J.-L. 1991. Température et salinité de l'eau de mer au large de Roscoff de 1988 à 1990. *Cahiers de Biologie Marine*, **32**: 545-550.
- Davoult D., Engel C.R., Arzel P., Knoch D. & Laurans M. 2011. Environmental factors and commercial harvesting: exploring possible links behind the decline of the kelp *Laminaria digitata* in Brittany, France. *Cahiers de Biologie Marine*, 52: 429-434.
- Dayton P.K. & Tegner M.J. 1984. Catastrophic storms, El Nino, and patch stability in a southern California kelp community. *Science*, 224: 283-285.
- Delebecq G., Davoult D., Menu D., Janquin M-A., Migné A., Dauvin J-C., & Gevaert F. 2011. In situ photosynthetic performance of Laminaria digitata (Phaeophyceae) during spring tides in Northern Brittany. Cahiers de Biologie Marine, 52: 405-414.
- Deysher L. & Norton T.A. 1982. Dispersal and colonisation in Sargassum muticum Yendo Fensholt. Journal of Experimental Marine Biology and Ecology, 56: 179-196.
- Graham M.H. 1997. Factors determining the upper limit of giant kelp, *Macrocystis pyrifera* Agardh, along the Monterey Peninsula, central California, USA. *Journal of Experimental Marine Biology and Ecology*, 218: 127-149.
- Harley C.D.G., Randall Hughes A., Hultgren K.M., Miner B.G., Sorte C.J.B. & Thornber C.S. et al. 2006. The impacts of climate change in coastal marine systems. *Ecology Letters*, 9: 228-241.
- Hughes T.P., Baird A.H., Bellwood D.R., Card M., Connolly S.R., Folke C., Grosberg R., Hoegh-Guldberg O., Jackson J.B.C., Kleypas J. et al. 2003. Climate change, human impacts, and the resilience of coral reefs. *Science*, 301: 929-933.
- **IPCC 2007.** Climate change 2007: the physical science basis summary for policy makers. In: Intergovernmental Panel on Climate Change, WMO/UNEP, IPCC Secretariat, Geneva,

Switzerland, 21 p.

- Irving A.D. & Connell S.D. 2006. Predicting understorey structure from the presence and composition of canopies: an assembly rule for marine algae. *Oecologia*, 148: 491-502.
- Jørgensen N.M. & Christie H. 2003. Diurnal, horizontal and vertical dispersal of kelp-associated fauna. *Hydrobiologia*, 503: 69-76.
- Kain J.M. 1975. Algal recolonisation of some cleared subtidal areas. *Journal of Ecology*, 63: 739-765.
- Kitching J.A. 1941. Studies in sublittoral ecology III. *Laminaria* forest on the west coast of Scotland; a study of zonation in relation to wave action and illumination. *Biological Bulletin*, 80: 324-337.
- Lippert H., Iken K., Rachor E., Wiencke C. 2001. Macrofauna associated with macroalgae in the Kongsfjord. *Polar Biology*, 24: 512-522.
- Norton T.A. 1970. Synopsis of biological data on Sacchorhiza polyschides. FAO Fisheries synopsis, 83: 11-93.
- **Oshurkov V.V. & Ivanjushina E.A. 1993.** Effects of experimental harvesting on kelp regrowth and on the structure of the shallow-water communities of Bering Island (Commander Islands). *Asian Marine Biology*, **10**: 95-108.
- Pereira T.R., Engelen A.H., Pearson G.A., Serrão E.A., Destombe C., & Valero M. 2011. Temperature effects on the miscroscopic haploid stage development of *Laminaria* ochroleuca and Sacchoriza polyschides, kelps with contrasting life histories. Cahiers de Biologie Marine, 52: 395-403.
- Pérez R. 1971. Écologie, croissance et régénération, teneurs en acide alginique de *Laminaria digitata* sur les côtes de la Manche. *Revue des Travaux de Institut des Pêches Maritimes*, 35: 287-346.
- Pimentel D.S., Wilson C., McCullen C., Huang R., Dwen P., Flack J., Tran Q., Saltman T. & Cliff B. 1997. Economic and environmental benefits of biodiversity. *Bioscience*, 47: 747-757.
- Precht W.F. & Aronson R.B. 2004. Climate flickers and range shifts of reef corals. *Frontiers in Ecology and the Environment*, 2: 307-314.

- Smith B.D. 1985. Recovery following experimental harvesting of Laminaria longicruris and L. digitata in southwestern Nova Scotia. Helgoland Marine Research, 39: 83-101.
- Sournia A., Birrien J.-L., Douvillé J.-L., Klein B. & Viollier M. 1987. A daily study of the diatom spring bloom at Roscoff (France) in 1985. I. The spring bloom within the annual cycle. *Estuarine, Coastal and Shelf Science*, 25: 355-367.
- Steneck R.S., Graham M.H., Bourque B.J., Corbett D., Erlandson J.M., Estes J.A. & Tegner M.J. 2002. Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environmental Conservation*. 29: 436-459
- Toohey B.D., Kendrick G.A. & Harvey E.S. 2007. Disturbance and reef topography maintain high local diversity in *Ecklonia radiata* kelp forests. *Oikos*, 116: 1618-1630.
- Valentine J.P. & Johnson C.R. 2003. Establishment of the introduced kelp Undaria pinnatifida in Tasmania depends on disturbance to native algal assemblages. Journal of Experimental Marine Biology and Ecology, 295: 63-90.
- Wehrmann A. 1998. Modern cool-water carbonates on a coastal platform of northern Brittany, France: carbonate production in macrophytic systems and sedimentary dynamics of bioclastic facies. *Senckenbergiana maritime*, 28: 151-166.
- Wernberg T., Kendrick G.A. & Toohey B.D. 2005. Modification of the physical environment by an *Ecklonia* radiata (Laminariales) canopy and implications for associated foliose algae. Aquatic Ecology, 39: 419-430.
- Wernberg T., Thomsen M., Tuya F., Kendrick G.A., Staehr P.A. & Toohey B.D. 2010. Decreasing resilience of kelp beds along a latitudinal temperature gradient: potential implications for a warmer future. *Ecology letters*, 13: 685-694.
- Werner A. & Kraan S. 2004. Review of the potential mechanisation of kelp harvesting in Ireland; *Marine Environment and health Series*, 17: 1-52.
- Woodruff D.S. 2001. Declines of biomes and biotas and the future of evolution. *Proceedings of the National Academy of Sciences*, 98: 5471-5476.