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Using genetic tools for sustainable management of kelps: a literature review and the example of *Laminaria digitata*

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Abstract: Kelp forests are threatened by human activities that result in habitat loss or deplete natural stocks, but little is known about genetic diversity, importance of gene flow and effect of population fragmentation on genetic structure. We reviewed the literature to characterize the patterns of connectivity and scales of population structure in kelps. In all, 44 papers have been published on the patterns of genetic differentiation in 17 kelp species, using various kinds of molecular markers. Our literature review showed that population connectivity depends mainly on species' dispersal abilities and habitat characteristics (intertidal *vs.* subtidal), but little on their life-span characteristics. Data on within-population gene diversity were found for only seven species and reflect differences in effective population sizes. In addition, we focused on the Brittany populations of *Laminaria digitata*, one of the most commonly harvested species in Europe, and re-sampled populations studied seven years prior. Our analyses of spatio-temporal variation clearly demonstrate the effect of small population sizes on the genetic instability of isolated *L. digitata* populations and have implications for managing this genetic resource.

Résumé : *Utilisation des outils génétiques pour la gestion durable des grandes algues brunes : synthèse bibliographique et exemple de* Laminaria digitata*.* Les forêts de grandes algues brunes (laminaires) sont menacées par les conséquences des activités humaines telles que la disparition de leur habitat et la surexploitation des populations naturelles, alors qu'on connaît mal leur diversité génétique, l'importance des flux géniques et l'effet de la fragmentation des populations sur leur structure génétique. Nous avons analysé la littérature afin de faire un bilan des données disponibles sur la connectivité et les échelles de différenciation spatiales chez les grandes algues brunes. Nous avons dénombré 44 articles publiés sur ce sujet s'intéressant à 17 espèces de grandes algues brunes étudiées à l'aide de différents types de marqueurs moléculaires. L'analyse bibliographique montre que les modalités de la connectivité entre populations dépendent essentiellement des capacités de dispersion et des caractéristiques de l'habitat (intertidal *vs* subtidal) des grandes algues brunes mais très peu de leur cycle de vie. Les données sur la diversité génétique intra populationnelle des laminaires n'ont pu être recueillies que sur 7 espèces seulement et reflètent des différences importantes dans la taille efficace des populations. De plus, nous nous sommes plus particulièrement intéressés au cas des populations bretonnes de *Laminaria digitata,* une des espèces les plus

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communément exploitées en Europe, en ré-échantillonnant pour une analyse génétique temporelle, plus de 7 ans plus tard, les mêmes populations que celles qui avaient été analysées par Billot et al. (2003). Nos analyses montrent clairement un effet des petites tailles de populations sur l'instabilité génétique des populations isolées de *L. digitata*, effet qui a des implications importantes pour la gestion des ressources génétiques.

Keywords: Seaweed harvesting ● Spatial and temporal genetic variation ● Population connectivity ● Conservation strategy

Introduction

Genetic diversity represents the essential evolutionary potential for species to respond to changing environments. Large populations are generally characterized by high levels of genetic diversity and are thus expected to better respond to environmental change (Frankel & Soulé, 1981). Human disturbances such as clearing and fragmentation of habitats, overexploitation, pollution and species introductions are reducing the size and distribution of wild populations and thus represent the major cause of species extinction (Diamond et al., 1989). In this context, population genetic tools and molecular genetic data have found widespread application in the identification and conservation of populations with clear implications for fisheries management (Selkoe et al., 2008). In addition, compared to the terrestrial environment, the marine realm remains largely opaque to direct observation of dispersal, and genetic tools are one of the most powerful means available to characterize patterns of connectivity and scales of population structure in the sea.

Marine populations show extreme patterns of spatial and temporal heterogeneity in genetic and demographic factors, such as dispersal distance and settlement rates (Roughgarden et al., 1988; Palumbi, 2004; Navarrete et al., 2008). High levels of intraspecific genetic diversity without pronounced spatial or geographic structure are typical of many marine invertebrates and vertebrates, particularly harvested species. However, this pattern does not hold for many other marine species which are important socially and economically, such as coral reefs, seagrass meadows and kelp beds, and are critical sources of production and biogenic habitat structure (Carr et al., 2003; Palumbi, 2004). In particular, the limited dispersal potential of many macroalgae (Santelices, 1990) suggests a system of self-sustaining, "closed" populations that contrasts with the ''open'' populations of invertebrates, in which larvae are likely to be dispersed from local parental populations to replenish distant populations (Carr et al., 2003; Kinlan et al., 2005). Consequently, the high resilience of fish populations to habitat destruction and overfishing can be attributed to the fact that they can effectively decouple local offspring production and replenishment of the parental population (Roughgarden et al., 1988). This decoupling of local fertility and recruitment cannot be generalized to the whole marine realm and genetic data are needed for other harvested marine resources.

Kelp forests, stands of large brown algae, are the dominant feature of many temperate coastlines and are often viewed as the marine equivalent to terrestrial rain-forests in terms of complexity of community structure and biodiversity (e.g. Steneck et al., 2002; Christie et al., 2009). Besides being a strong trophic link (see Duggins et al., 1989 and Leblanc et al., 2011), kelps are considered as foundation species because removing them can profoundly disturb the whole ecosystem and modify community structure (Estes et al., 1989 but see Foster & Schiel, 2010). Kelps are also of considerable commercial interest: they are harvested or cultivated worldwide as a source of alginate, a biopolymer widely used in food and cosmetics industries (Vásquez, 2008; Bixler & Porse, 2011; for Brittany: Alban et al., 2011). Various studies have demonstrated that kelp forests are threatened by human activities, such as habitat loss, depletion of fish stocks, reduced water quality, and global warming (see for review Steneck et al., 2002). While some authors (e.g. Carr et al., 2003) consider that habitat restoration has lead to less concern in kelps compared to terrestrial plants since kelps have been shown to recover quickly after even extreme disturbance events (perhaps due to latent microscopic stages in these species: Barradas et al., 2011; Engelen et al., 2011; Pereira et al., 2011; Destombe & Oppliger, 2011); others (e.g. Connell et al., 2008) argue that pre-emptive competition may determine kelp recovery. Kelp harvesting is currently managed so as to maximize the net harvest of kelp biomass (Arzel, 1998; Frangoudes, 2011). However, two recent studies (Lorentsen et al., 2010; Wernberg et al., 2010) warn not to rely solely on inventories of distribution and abundance, but to evaluate ecosystem function and resilience to harvesting and global warming. In addition, kelp beds are probably characterized by self-sustaining, "closed" populations, but very little is known about genetic diversity, importance of gene flow and effect of population fragmentation on genetic structure in kelps.

Population genetic structure is related to reproductive traits, including reproduction mode and dispersal ability. Kelps are characterized by an obligatory alternation of large diploid sporophytes and microscopic dioecious gametophytes during their life cycle. Biflagellate meiospores germinate and give microscopic dioecious gametophytes. At maturity, male gametes are released into the water column and fertilize female gametes. After fertilization, the egg remains attached to the benthic female gametophyte and subsequently develops into a new sporophyte. Although this heteromorphic life cycle was described 100 years ago in *Laminaria digitata* (Hudson) J.V. Lamouroux (as *Laminaria flexicaulis*) by Sauvageau (1918), the consequences of this multiphase life history on population dynamics and genetic structure is still poorly known (Schiel & Foster, 2006). For example, in annual species, population persistence will strongly depend on successful gamete encounters and the persistence of the microscopic gametophyte stages from year to year (Destombe & Oppliger, 2011; Barradas et al., 2011; Pereira et al., 2011). Likewise, the re-establishment of harvested kelps probably depends greatly on the stock of microscopic gametophytes.

The main goal of this paper was to consolidate knowledge on kelp genetic resources to enhance their management. We performed a cursory review of the existing literature to characterize patterns of connectivity and scales of population structure in kelps. In addition, we focused on Brittany populations of *Laminaria digitata*, one of the most commonly harvested species in Europe. We supplemented the previous study of Billot et al. (2003) by surveying the genetic structure of the same populations more than seven years later, thereby providing data to be able to discuss patterns of spatio-temporal genetic variation.

Materials and Methods

Data compiled from the literature survey

We compiled data on genetic diversity and population differentiation within kelps by selecting, from the Web of Science, papers published in international journals on these topics. The search was performed using the complete database (ALL DATABASES) including all years, but excluding meeting abstracts and patents. Only papers published in English were considered. Terms entered in the "Topic" search box were "species AND molecular AND kelp" and "species AND genetic AND kelp". For some genera that were particularly well studied genetically (such as *Laminaria*, *Undaria* and *Saccharina)*, we refined the search and modified the terms as follows: "*Undaria* AND molecular AND genetic", "*Undaria* AND kelp", "*Saccharina* AND kelp", "*Laminaria* AND kelp". Finally, we completed our exhaustive literature survey by cross-checking the references cited in each selected paper, and also by searching for papers citing the selected papers.

We selected different members of the order Laminariales (Phaeophyceae) and also the Tilopteridales, interpreting the term 'kelp' in the large sense, i.e. the common name for a group of large brown algae. First, we considered studies that report on patterns of genetic differentiation within species using various kinds of molecular markers. Second, we only included studies that investigated genetic diversity at the population level (i.e. with samples greater than 20 individuals per population) and connectivity at various spatial and temporal scales using single-locus genetic markers.

Spatio-temporal genetic analyses of Laminaria digitata

Laminaria digitata is a relatively short-lived perennial alga (3-5 years, Werner & Kraan, 2004) that forms continuous stands along the Brittany coast where it is commonly harvested. To study patterns of spatio-temporal genetic structure within the kelp *Laminaria digitata*, we re-sampled 7 to 9 years later some of the populations that had been genotyped in a study by Billot et al. (2003). Although generations overlap, this time interval was considered sufficient to avoid re-sampling the same generations as the ones included in the initial study. Eight populations were selected based on the results of the previous genetic analysis (Table 1). We contrasted situations of populations located in large continuous stands ('core' populations, SB3, NB1, NB2, NB3, Table 1) against fragmented, isolated beds delimited by unsuitable sandy substrate, as found at Locquirec and Saint Malo (NB4 and SM1 respectively, Table 1) or populations of the southern coast of Brittany located at the southern limit of the range distribution of this species (SB1, SB2, Table 1). However, as a background effect, the core populations (SB3, NB1, NB2, NB3) even if not directly harvested themselves, were located in areas that undergo harvesting in contrast to the other four, more marginal populations that are not in harvesting areas (Table 1).

A total of 222 individuals (i.e. 24 to 30 individuals per population, Table 1) were sampled in 2005 or 2006 and were genotyped and compared to 222 individuals sampled in 1997 or 1998 (Table 1) using the same seven micro - satellite loci as in the Billot et al. (2003) study. The geopositions and sample sizes of populations selected for both sampling periods are given in Table 1. We used the same population codes as those in Billot et al. (2003) to facilitate comparison. The population locations are given in Fig. 1. Within the northern or southern Brittany regions, adjacent populations were separated by about 30 km, whereas populations of the two regions were separated by more than 100 km. The marginal population of Saint Malo (SM1) was isolated from all other populations by more than

Table 1. Location and characteristics of *Laminaria digitata* samples. N: sample size. *Data from Billot et al. (2003).

Tableau 1. Position géographique et caractéristiques de l'échantillonnage de *Laminaria digitata*. N : nombre d'individus échantillonnés. *Données de Billot et al. (2003).

Region	Sites	Codes	Latitude	Longitude	Year t1*	N (t1)	Year t2	N (t2)	Harvested area	Small isolated stands
Southern	Le Pouldu	SB1	47°45'58"N	3°33'29"W	1998	25	2005	25	No	Southern Limit
Brittany	Rospico	SB2	47°47'28"N	3°45'39"W	1998	25	2006	28	No	Southern Limit
	Eckmühl	SB3	47°47'59"N	4°22'59"W	1998	30	2006	30	Yes	No
Northern	Pospoder	NB1	48°31'11"N	4°46'45"W	1997	30	2005	28	Yes	No
Brittany	Plouescat	NB2	48°40'23"N	4°12'58"W	1998	30	2005	30	Yes	No
	Ile de Sieck	NB3	48°42'40"N	4°03'37"W	1997	27	2005	24	Yes	No
Not	Locquirec	NB4	48°41'11"N	3°37'06"W	1997	30	2005	30	No	Yes
connected	Saint Malo	SM1	48°41'48"N	1°55'07"W	1998	25	2006	27	No	Yes

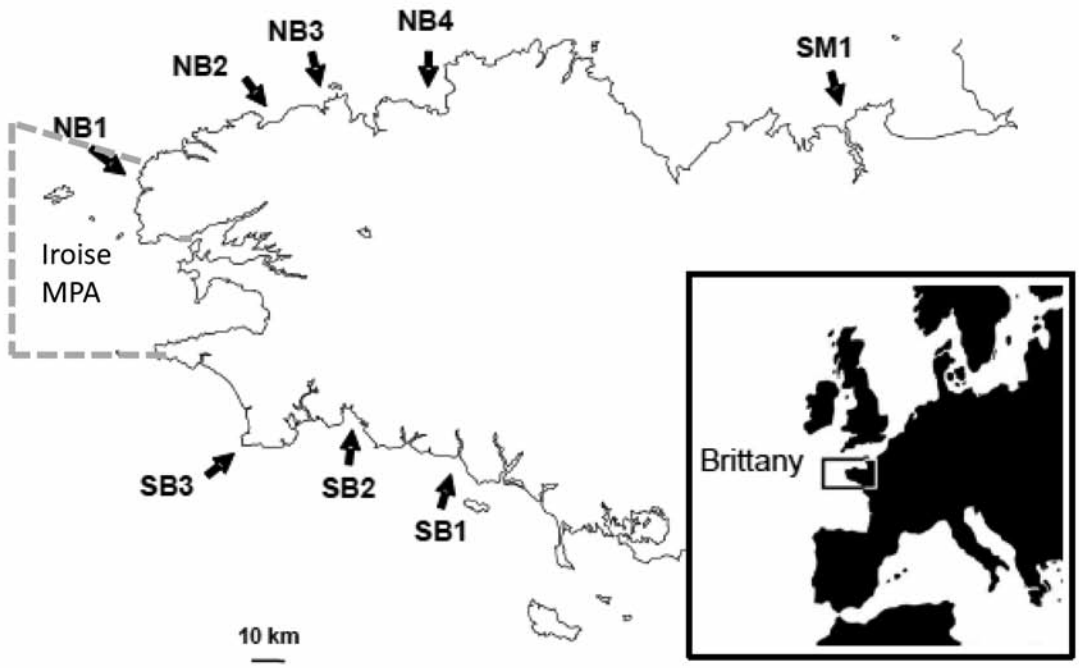

Figure 1. Location of the study sites. The Iroise Marine Protected Area is indicated by a grey dotted line.

Figure 1. Situation géographique des sites étudiés. La délimitation du Parc Marin d'Iroise est figurée par la ligne pointillée grise.

100 km while the other marginal population of Locquirec (NB4) was located within the northern Brittany region at about 30 km from the closest population, NB3 (Fig. 1).

DNA extraction and PCR amplifications of seven microsatellite loci (Ld1-124, Ld2-148, Ld2-158, Ld2-167, Ld2-371, Ld2-531 and Ld2-704) were performed using the same protocols as those described in Billot et al. (1998). PCR products were electrophoresed on 6% polyacrylamide denaturing gels using an automated DNA sequencer (Li-Cor 4200™) along with a DNA sequence of known length to estimate allele sizes to ensure that allele sizes corresponded exactly to those estimated using a VISTRA sequencer in Billot et al. (2003).

Genetic polymorphism in each population was measured as the mean number of alleles per locus (*N*a) and gene diversity (*He*, sensu Nei, 1978) using the *GenAlEx - Genetic Analysis in Excel* software package (Ver. 6.3; Peakall & Smouse, 2006). To test for genetic independence of the microsatellite loci, genotypic linkage disequilibria between the 21 pairs of loci were tested in each sample by

performing 6720 permutations using FSTAT software (Ver 2.9.3; Goudet, 2001). *F*is estimates of the average deviation from random mating within populations were computed for each locus and heterozygote deficiencies and excesses were tested using 1 000 randomizations of alleles among individuals within each population. Multilocus *F*st estimates of genetic differentiation between all pairs of populations and sampling periods were also calculated and the significance of population differentiation was tested by permuting alleles among samples (12000 permutations). Both *F*is and *F*st estimates were computed using FSTAT software. Four-way analyses of variance (ANOVA) were performed to test for effects of population category (core *vs.* marginal populations), sampling period, population identity (nested within the factor 'population category') and the congruence among loci on genetic diversity (*N*a and *H*e) or *F*is estimates. The 'locus' and 'population identity' factors were declared random while the other two factors were fixed. General linear model procedures were used. Data were transformed when necessary to meet assumptions of normality and homogeneity of variance. All statistical analyses (as well as variable transformation) were done using MINITAB version 13.2 (State College, PA, USA).

Results

Connectivity and genetic diversity in kelps

Our literature review revealed 44 papers that provide data on the patterns of genetic differentiation within species, using various kinds of molecular markers (Annex 1). These analyses of population differentiation involve 15 species of Laminariales (Table 2), or about 13% of the 112 species described in this order (Bolton, 2010). Most of these studies have been conducted on species of economic value (Table 2), with approximately one-third (15 studies) focusing on the two most cultivated kelp species in the world (*Undaria pinnatifida* (Harvey) Suringar and *Saccharina japonica* (Areschoug) C.E. Lane, C. Mayes, Druehl & G.W. Saunders, as *Laminaria japonica*) and another one-third (17 studies) on the main harvested species (*Laminaria digitata*, *Lessonia* sp., *Macrocystis pyrifera* (Linnaeus) C. Agardh, *Postelsia palmaeformis* Ruprecht). Different kinds of highly polymorphic markers have been developed for these species (Table 2). The three most frequently used include co-dominant single-locus microsatellite loci (or single sequence repeats, SSR), dominant multi-locus random amplified polymorphic DNA (RAPD) and sequence polymorphism analyses of nuclear or cytoplasmic coding or non-coding DNA regions. The genetic differentiation among populations varied considerably between kelp species, but also according to the kind of marker used. Almost half of the species (5/12: 43%) showed significant patterns of genetic differentiation at the smallest spatial scale of less than 1 km: *Alaria marginata* Postels & Ruprecht, *Ecklonia radiata* (C. Agardh) J. Agardh, two species of *Lessonia nigrescens* Bory de Saint-Vincent, *Undaria pinnatifida, P. palmaeformis*). These kelps are mainly located in intertidal habitats (Table 2). In contrast, species characterized by morphological structures favoring long-distance dispersal (i.e. air bladders) showed, as expected, the lowest level of genetic structure since differentiation is observed only between populations separated by hundreds of kilometers (Table 2). Finally, no clear relationship with the other life-history traits considered (perennial *vs.* annual species, basal *vs.* distal reproductive structures) and patterns of genetic differentiation emerged from this literature review (Table 2). Note that only two papers have addressed the issue of genetic variation in time (Kusumo & Druel, 2000 in *A. marginata,* and Kusumo et al., 2006 in *P. palmaeformis*), and show that, at the scale of a single shore, genetic variation did not vary significantly in time.

Only six publications (for a total of seven species) corresponded to two selection criteria: use of microsatellites as molecular markers and study of within-population diversity as the relevant scale for genetic analyses (Table 3). Gene diversity varied greatly among species, from 0.065 to 0.795 (Table 3). Three out of the seven kelp species are characterized by relatively low levels of within population genetic diversity ($He < 0.346$ for *E. radiata*, $He < 0.370$ for the northern species of *L. nigrescens* and $He < 0.434$ for *U. pinnatifida)*, while populations of the southern species of *L. nigrescens and M. pyrifera* appear the most genetically diverse with $He > 0.610$ and 0.740, respectively. Comparatively, populations of *Laminaria digitata* show average levels of genetic diversity ($0.475 < He < 0.696$). Finally, in *P. palmaeformis*, huge variation in *H*e between populations from 0.065-0.790 are reported.

Estimations of the inbreeding coefficient (*F*is) were highly variable among populations for most species except for *Laminaria digitata* and *M. pyrifera* (Table 3). In *Laminaria digitata*, *F*is values are close to zero, suggesting the occurrence of random mating. Heterozygote deficiencies leading to high positive values were revealed in all populations of *M. pyrifera* and *P. palmaeformis*. Finally, highly fluctuating positive and negative values across populations are reported for *E. radiata* and *U. pinnatifida*.

The scales at which genetic differentiation among populations were analyzed differed greatly among papers, precluding a comparative analysis (Table 3). For most species, the maximum distance between populations varied from 10 to 60 km, whereas for *E. radiata* and *Laminaria*

Table 2. Result of the survey of 44 papers reporting population genetic differentiation within kelp species. The list of the papers selected for literature review is given in Annex 1. **Order, Family and Species:** According to AlgaeBase (Guiry & Guiry, 2010). *AlgaeBase*. **Habitat**: Intertidal (I), Subtidal (S), Deep Subtidal (DS). **Dispersal structures**: AB: Air bladders. **Life span**: Annual (A) or Perennial (P) sporophytes. **Reproductive type**: Distal or Basal. *Postelsia palmaeformis* has a particular reproductive strategy: although the reproductive structures are found on blades, spores are generally released along the stipe. **Molecular markers**: For microsatellites (or single sequence repeats, SSRs) and microsatellites from expressed-sequence tags (EST-SSR), number of loci indicated in brackets. Other markers include sequences (seq), amplified fragment length polymorphisms (AFLP), restriction fragment length polymorphisms (RFLP), minisatellites (M13), random amplified polymorphic DNA (RAPD), inter-simple sequence repeats (ISSR). **Genetic differentiation**: +++ when significant differentiation between populations was detected over sites separated by less than 1 km; ++ for sites separated by less than 10 km and + for sites separated by more than 100 km; nd: no data. **No. studies:** number of studies drawn from the literature survey (see Material and Methods for the criteria used). ***** Only 2 studies report on temporal genetic variation

Tableau 2. Résultat de l'analyse bibliographique des 44 articles portant sur la différenciation génétique intraspécifique chez les grandes algues brunes. La liste des articles sélectionnés dans la littérature est donnée dans l'Annexe 1. **Ordre, Famille et Espèce :** suivant la classification donnée dans AlgaeBase (Guiry & Guiry, 2010). *AlgaeBase*. **Habitat**: Intertidal (I), Subtidal (S), Subtidal Profond (DS). **Structure de dispersion** : AB: flotteurs. **Cycle de vie** : Sporophytes annuels (A) ou pérennes (P). **Type de reproduction** : Distal ou Basal. Remarque : *Postelsia palmaeformis* présente une stratégie de reproduction particulière: bien que les structures de reproduction soient localisées sur les lames, les spores sont généralement libérées depuis le stipe. **Marqueurs moléculaires** : Pour les microsatellites (ou simples séquences répétées, SSRs) et les microsatellites développés à partir des EST (EST-SSR), nombre de locus indiqué entre parenthèses. Les autres marqueurs incluent des séquences (seq), du polymorphisme de longueur de fragments amplifiés (AFLP), du polymorphisme de longueur des fragments de restriction (RFLP), des minisatellites (M13), du polymorphisme d'ADN amplifié aléatoirement (RAPD), des répétitions simples de séquences inter-géniques (ISSR). **Différenciation génétique** : +++ quand une différence significative entre populations a été détectée entre sites séparés par moins de 1 km; ++ entre sites séparés par moins de 10 km et + pour des sites séparés par plus de 100 km; nd: pas de données. **Nb d'études:** Nombre d'études pris en compte dans la revue bibliographique (voir le Matériel et Méthode pour les critères utilisés).***** Seulement 2 études ont analysé la variation génétique temporelle

digitata, the largest spatial scales were greater than 500 km. Nevertheless, even at comparable spatial scales, global *F*st

Order, Family, Species	Life-history trait				Molecular markers	Genetic differentiation	No. studies
	Habitat	Dispersal structure	Life span	Location of reproductive structures			
LAMINARIALES							
Alariaceae							
Alaria esculenta (A. grandifolia)	I-S-DS	-	A-P	basal	RFLP	nd	1
Alaria marginata f nana	I	-	A	basal	SSR (8)	nd	1
Alaria marginata	I	-	A-P	basal	AFLP	+ / +++	1*
Undaria pinnatifida	S	-	A	basal	SSR (20)	+/++/+++	6
Costariaceae							
Costaria costata	I-S	-	A-P	distal	RFLP	nd	2
Lessoniaceae							
Ecklonia radiata	S-DS	-	P	distal	seq, SSR (14)	++ / +++	3
Egregia menziesii	I-S	AB	P	distal	seq	+	1
Eisenia arborea	S	-	P	distal	M13	+	1
Lessonia nigrescens							
Northern and Southern species	I	-	P	distal	seq, SSR (9), RAPD	+++	6
Lessonia trabeculata	S	-	P	distal	seq	+	1
Laminariaceae							
Macrocystis pyrifera	S	AB	P	basal	seq, SSR (16), M13, RAPD	++/+	4
Pelagophycus porra	DS	AB	A-P	distal	RAPD, RFLP	++	1
Postelsia palmaeformis	I	-	A	basal	SSR (14), AFLP, M13, RAPD	+++	4*
Saccharina (Laminaria) japonica species complex	S	-	P	distal	SSR (18), EST-SSR (9), AFLP, ISSR	+	9
Laminaria digitata	S	-	P	distal	seq, SSR (10), RAPD	++	2
TILOPTERIDALES							
Phyllariaceae							
Saccorhiza polyschides	S	-	P	basal	SSR (10)	nd	1

estimates of genetic differentiation over all populations varied from 0.02 for *M. pyrifera* to 0.533 for *P. palmaeformis* (Table 3). Patterns of genetic differentiation were also very variable between pairs of comparisons within species, the most extreme cases being observed for *E. radiata* and *U. pinnatifida* (from 0 to more than 0.4, Table 3). Finally, estimation of minimal distances between differentiated beds ranged from 5 m to 14 km.

Spatio-temporal genetic analyses of Laminaria digitata

There was no evidence of linkage disequilibrium between any pair of loci (data not shown). Numbers of alleles, gene diversity and *F*is estimates are given for each microsatellite locus, each population and each sampling period in Table 4. The total number of alleles observed over all samples ranged from 5 to 24 for the least to the most polymorphic locus (Ld2-158 and Ld2-371, respectively, Table 4). Significant different levels of variability in terms of mean numbers of alleles and gene diversity were revealed among loci (ANOVAs, Table 5A & B), while in contrast, no significant deviation from random mating was consistently observed over loci (only one value showed a significant

Table 3. Patterns of genetic diversity within kelp populations and connectivity among sites at different scales using microsatellite (SSR) molecular markers. He: multilocus non-biased expected heterozygosity or gene diversity averaged among loci (Nei, 1978); Fis multilocus estimates of the average deviation from random mating and Fst multilocus estimates of the genetic differentiation between pairs of populations. The table reports minimum and maximum values of these genetic indices calculated for each population (or pair of populations). In addition, the global Fst values calculated over all sites are given. *Note that when not available, minimum and maximum geographic distances among pairwise sampling sites were estimated from graphs and/or maps. £: Spatial and temporal Fst values (no significant genetic differentiation over time within site). nd: no data

Tableau 3. Diversité génétique intra population et connectivité entre sites à différentes échelles spatiales chez les grandes algues brunes, estimées par les marqueurs moléculaires de type microsatellites (SSR). He : hétérozygotie attendue multilocus et non-biaisée ou diversité génétique moyenne calculée sur l'ensemble des locus (Nei, 1978); Fis : estimation multilocus de l'écart à la panmixie et Fst : estimation multilocus de différenciation génétique entre paires de populations. Le tableau présente les minimum et maximum de ces différents indices génétiques calculés pour chaque population (ou paire de populations). De plus, les valeurs du Fst global calculées sur l'ensemble des sites est donnée. *Quand les données n'étaient pas disponibles, les distances géographiques minimum et maximum entre paires de populations ont été estimées à partir des graphes ou des cartes. £: Les valeurs de Fst spatiaux ou temporels (pas de différenciation génétique significative entre dates intrasite). nd: pas de données.

Species	**Number of loci**	**Sample size (Number of sites, mean sample size per populations)**	***H*e (min-max)**	***F*is (min-max)**	**Geographic distance* (min-max)**	**Global *F*st (min-max)**	**Minimum distance between differentiated plots**
Ecklonia radiata (Coleman et al., 2009)	6	320 (10, 32)	0.216-0.346	-0.358-0.142	1 - 700km	0.211 (0.006-0.434)	few km
Laminaria digitata (Billot et al., 2003)	7	438 (18, 25)	0.475-0.696	-0.011-0.191	0.05 - 800km	0.068 (0.000-0.166)	10 km
Lessonia nigrescens (Northern species) (Tellier et al., 2011)	4	118 (6, 20)	0.277-0.374	nd	1 - 30km	(0.000-0.250)	7.5 km
Lessonia nigrescens (Southern species) (Tellier et al., 2011)	4	130 (6, 21)	0.612-0.816	nd	1.5 - 25km	(0.000-0.169)	14 km
Macrocystis pyrifera (Alberto et al., 2010)	12	411 (9, 45)	0.740-0.795	0.121-0.215	2.5 - 60km	0.021 (0.001-0.050)	< 2.5 km
Postelsia palmaeformis (Kusumo et al., 2006)	6	245 (9, 27)	nd	0.354-0.625	0.05 - 11km	0.533£ (0.278-0.658)	5 m
Undaria pinnatifida (Grulois et al., 2011)	9	955 (30, 32)	0.204-0.434	-0.158-0.479	0.05 - 20km	0.099 (0.000-0.469)	< 0.2 km

Table 4. Gene diversity within populations for each locus, population and sampling period. *A*: total number of alleles observed over all samples, *N*: sample size, *N*a: Number of alleles, *He*: expected heterozygosity. Bold *F*is values indicate that Hardy-Weinberg equilibrium was rejected at the 5% level after correction for multiple tests.

Tableau 4. Diversité génétique intra population pour chaque locus, population et date d'échantillonnage. *A* : nombre total d'allèles observé sur l'ensemble des populations ; *N* : Nombre d'individus analysés, *N*a : Nombre d'allèles, *He*,: hétérozygotie attendue, les valeurs de *F*is en caractères gras indiquent que l'hypothèse d'équilibre de Hardy-Weinberg a été rejetée avec un seuil d'erreur de 5% après correction pour tests multiples.

		1997-1998								2006-2007							
		Southern Brittany			Northern Brittany			Isolated stands		Southern Brittany			Northern Brittany			Isolated stands	
		SB1	SB2	SB3	NB1	NB2	NB3	NB4	SM1	SB1	SB2	SB3	NB1	NB2	NB3	NB4	SM1
Ld1-124	***N***	22	24	29	30	30	27	29	25	24	28	30	28	29	24	30	27
A = 7	***Na***	4	3	4	5	5	6	4	4	2	2	5	4	4	3	3	4
	He	0.450	0.598	0.195	0.545	0.635	0.570	0.522	0.660	0.042	0.070	0.219	0.534	0.586	0.526	0.532	0.695
	Fis	0.070	0.360	-0.077	-0.120	-0.121	0.006	0.194	0.135	-0.021	-0.037	-0.082	-0.021	0.102	-0.052	0.235	0.023
Ld2-148	***N***	23	24	28	30	30	27	28	24	25	28	30	28	30	24	30	27
A = 12	***Na***	4	5	4	8	9	6	5	3	5	4	7	6	8	7	5	3
	He	0.588	0.589	0.563	0.754	0.794	0.773	0.684	0.678	0.568	0.547	0.645	0.688	0.787	0.737	0.671	0.666
	Fis	0.094	-0.012	0.096	-0.079	0.018	0.121	0.203	-0.004	-0.078	0.070	-0.208	-0.110	0.052	0.076	0.141	-0.020
Ld2-158	***N***	10	11	27	30	30	27	24	18	25	28	30	28	29	24	30	27
A = 5	***Na***	5	4	2	5	4	3	4	3	4	4	4	4	4	4	4	
	He	0.442	0.398	0.230	0.606	0.603	0.322	0.389	0.500	0.258	0.532	0.445	0.572	0.537	0.538	0.436	0.400
	Fis	-0.190	-0.196	0.179	-0.287	-0.012	0.063	0.016	-0.143	0.051	0.043	0.085	-0.144	0.085	-0.107	-0.244	-0.131
Ld2-167	***N***	23	19	29	30	30	27	30	24	25	28	30	28	30	24	30	27
A = 12	***Na***	6	7	8	7	5	7	4	2	8	6	8	9	7	7	3	5
	He	0.630	0.758	0.799	0.677	0.685	0.685	0.562	0.422	0.800	0.686	0.785	0.730	0.789	0.629	0.505	0.535
	Fis	0.153	0.073	0.033	-0.102	0.209	-0.102	-0.147	-0.008	-0.122	-0.114	0.137	0.053	0.055	-0.083	0.261	0.084
Ld2-371	***N***	24	21	30	30	30	27	25	25	25	28	29	28	30	24	30	27
A = 24	***Na***	10	9	12	13	14	17	8	8	11	11	14	14	16	15	8	8
	He	0.785	0.805	0.888	0.889	0.872	0.913	0.791	0.716	0.814	0.749	0.869	0.905	0.889	0.904	0.665	0.726
	Fis	0.132	**0.394**	0.083	0.199	0.106	0.049	-0.032	-0.026	0.047	0.126	0.031	-0.044	-0.144	-0.035	-0.172	-0.143
Ld2-531	***N***	22	24	30	29	30	27	30	24	25	28	28	28	30	24	30	27
A = 7	***Na***	5	5	6	4	5	4	3	2	5	6	6	6	3	5	3	3
	He	0.735	0.763	0.742	0.633	0.570	0.702	0.386	0.503	0.722	0.774	0.528	0.660	0.549	0.667	0.389	0.561
	Fis	-0.013	-0.171	-0.005	-0.163	-0.130	-0.022	0.123	0.407	0.040	-0.128	0.036	0.009	-0.112	-0.340	0.042	0.059
Ld2-704	***N***	23	23	30	30	30	27	28	19	24	28	30	27	30	24	30	27
A= 7	***Na***	3	2	5	6	4	3	2	2	2	4	4	7	4	4	4	2
	He	0.553	0.449	0.516	0.687	0.526	0.388	0.321	0.309	0.454	0.459	0.553	0.655	0.514	0.378	0.427	0.352
	Fis	0.357	0.110	0.014	0.359	0.162	-0.070	-0.018	0.124	-0.125	-0.109	0.265	-0.037	-0.188	-0.014	-0.033	-0.071

Table 5. Results of four way ANOVAs: effect of variation between sampling period, locus, population category and populations was tested on genetic diversity (*N*a and *H*e) or *F*is estimates. **A.** *N*a (transformed in (| log (1/Na) |) to meet the assumption of ANOVAs). **B.** *H*e. C: *F*is.

Tableau 5. Résultats des ANOVAs à quatre facteurs : effet des variations entre dates d'échantillonnage, locus, catégories de populations et populations a été testé pour les deux indices de diversité génétique (*N*a et *H*e) et pour le *Fis*. **A.** *N*a (les valeurs ont été transformées en (| log (1/Na) |) pour respecter les hypothèses des ANOVAs). **B.** *H*e. C : *F*is.

A:				
Source of Variation	**df**	***Adjusted Mean Square***	***F***	***P***
Sampling period	1	0.00913	0.68	0.411
Locus	6	0.53331	39.88	**< 0.001**
Population category	1	0.65251	16.38	**0.007**
Population (Population Category)	6	0.03984	2.98	**0.010**
Error	97	0.01337		
Total	111			
B:				
Source of Variation	**df**	***Adjusted Mean Square***	***F***	***P***
Sampling period	1	0.00715	0.52	0.472
Locus	6	0.31439	22.89	**< 0.001**
Population category	1	0.18558	8.27	**0.028**
Population (Population Category)	6	0.02245	1.63	0.146
Error	97	0.01373		
Total	111			
C:				
Source of Variation	**df**	***Adjusted Mean Square***	***F***	***P***
Sampling period	1	0.10646	5.43	**0.022**
Locus	6	0.02324	1.18	0.321
Population category	1	0.03525	3.43	0.113
Population (Population Category)	6	0.01027	0.52	0.789
Error	97	0.01962		
Total	111			

heterozygote deficiency, Table 4). Mean numbers of alleles and gene diversity were significantly reduced in marginal compared to core populations (Table 5A & B). These two estimates of genetic diversity did not vary significantly with time, although spatial variation was significant among populations for the mean number of alleles. Figure 2 shows that populations from northern Brittany (and more specifically population NB1) were characterized by the highest genetic diversity with a mean number of alleles per locus twice as great as the marginal population of Saint-Malo (SM1). The same pattern was observed for multilocus *H*e with values varying from 0.5 to 0.7, corresponding to the marginal and core population categories, respectively. Significant variation in time was only observed for *F*is values with smaller values for the second sampling period (Tables 4 & 5C).

There was significant population differentiation over all samples ($Fst = 0.07$, $p < 0.01$). Multilocus *F*st estimators of genetic differentiation (and their associated p-values) are given in Table 6 for each pair of samples. The pattern of genetic differentiation was highly dependent on spatial distances between populations. *F*st values were small and generally non-significant for pairs of populations belonging to the same region (from 0.010 to 0.039 among southern Brittany populations and from 0 to 0.037 among northern Brittany populations), while values were higher and significant for population pairs belonging to different geographic regions (from 0.016 to 0.071 between northern and southern populations, Table 6). In these two regions, genetic differentiation was small and non-significant across time (Table 6). In contrast, high (from 0.059 to 0.156) significant values across time and at both small and large spatial scales were always observed for the two isolated populations Locquirec and Saint Malo (NB4 and SM1, Table 6) indicating that fragmentation has a major effect on the pattern of population differentiation in this species.

Discussion

This study outlines many important elements that can be useful for sustainable kelp management. Although only 17 kelp species were found in the population genetic literature, patterns of population connectivity were shown to be highly variable between species and mainly dependent on

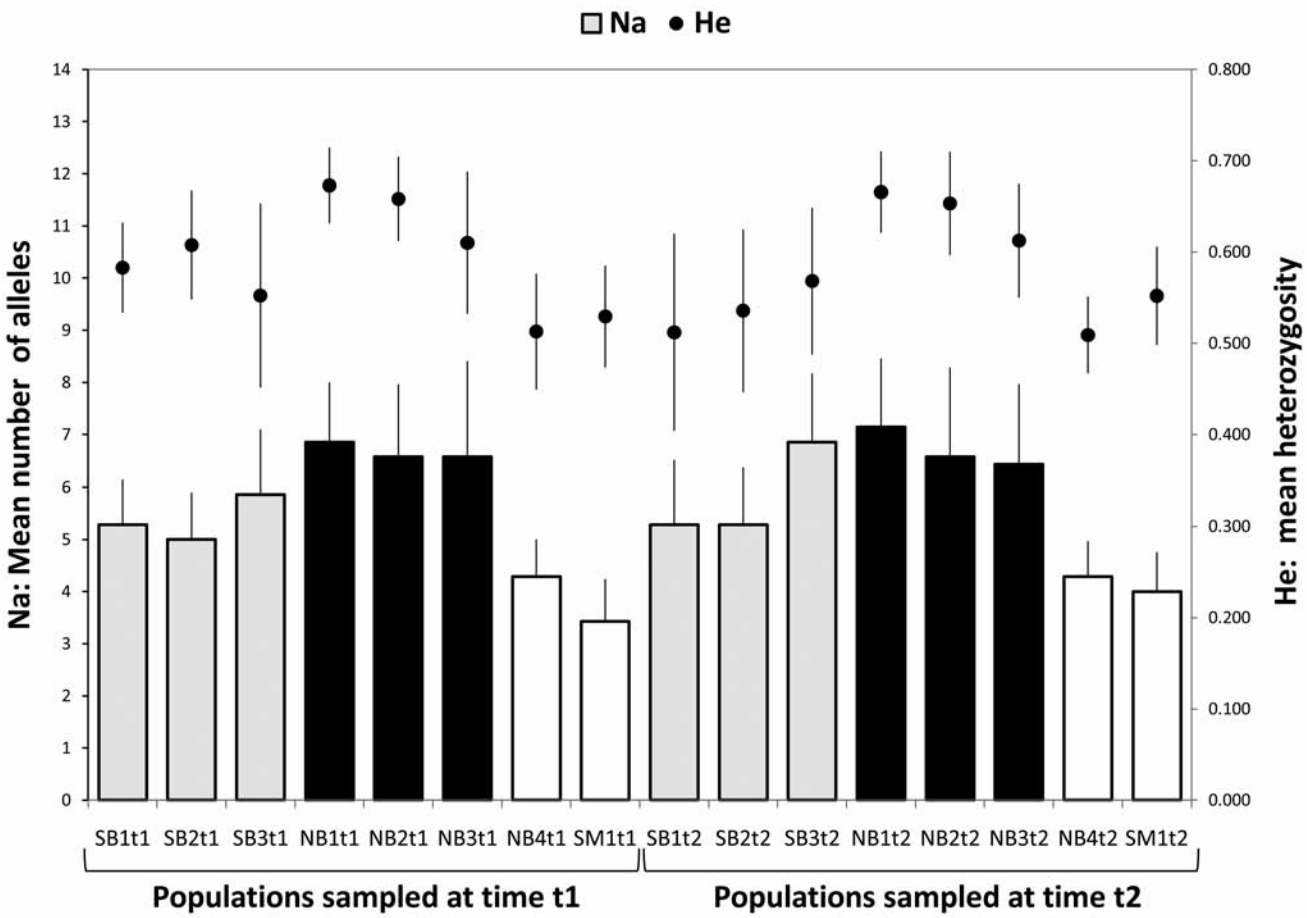

Figure 2. Spatial and temporal variation in genetic diversity. The mean number alleles (*N*a) and the mean expected heterozygosity (*H*e) over loci and their standard errors were computed for each population (Southern Brittany in grey, Northern Brittany in black and non-connected isolated populations in white) and for the two sampling periods t1 and t2 (see Table 1 for the population codes).

Figure 2. Variation spatiale et temporelle de la diversité génétique. Le nombre moyen d'allèles (*N*a) et l'hétérozygotie moyenne attendue (*H*e) calculés entre locus ainsi que leurs erreurs standards ont été calculés pour chaque population (Sud Bretagne en gris, Nord Bretagne en noir and populations isolées non connectées en blanc) et pour chaque date d'échantillonnage t1 et t2 (voir Tableau 1 pour les codes des populations).

their dispersal abilities and habitat characteristics, but little on their life span.

Dispersal distances of spores and gametes are generally reported to be very limited in macroalgae (Santelices, 1990) and more specifically in kelps. For example, in *P. palmaeformis*, *Alaria esculenta* (Linnaeus) Greville, and *M. pyrifera*, it has been shown experimentally that sporophytes recruit within a few metres of the parental sporophyte (Sundene, 1962; Anderson & North, 1966; Dayton, 1973). However, the importance of rare events of long-distance dispersal has recently been highlighted because they are often sufficient to maintain genetic homogeneity (Kinlan et al., 2005; Waples et al., 2008). Our compilation of genetic data revealed that the three species showing morphological structures that may promote long distance dispersal (such as *Egregia menziesii* (Turner) Areschoug, *M. pyrifera* and *Pelagophycus porra* (Léman) Setchell, all of which have air bladders) showed relatively low genetic differentiation in comparison with other kelp species.

Kelp forests form continuous, dense stands on shallow rocky coasts with a sequence of different species from the lower intertidal to deep subtidal zones. Our analysis showed that intertidal species - whatever their reproductive mode - were more genetically structured than subtidal species, probably because spore or gamete dispersal is limited along the shore at low tide. In the red alga *Gracilaria gracilis* (Stackhouse) M. Steentoft, L.M. Irvine & W.F. Farnham, the effect of the intertidal landscape on genetic structure has been demonstrated: self-recruitment increases significantly

Table 6. Analysis of genetic population differentiation in space and in time in *Laminaria digitata.* Comparisons including both spatial and temporal differentiation are shaded to focus on the most meaningful comparisons. Cells corresponding to temporal comparisons among samples from the same location are boxed with a double line; cells corresponding to comparisons within regions are boxed with a bold line. *F*st estimators of genetic differentiation for each sample pairs are given below the diagonal. Type I error probabilities of the absence of genetic differentiation between samples are given above the diagonal. The symbols NS, * and ** correspond to p-values adjusted for multiple comparisons: > 0.05, < 0.05, and < 0.01, respectively.

Tableau 6. Analyse de la différenciation génétique des populations de *Laminaria digitata* dans le temps et dans l'espace. Les cellules du tableau correspondant à des comparaisons à la fois spatiale et temporelle ont été grisées. Les cellules correspondant à des comparaisons temporelles à l'intérieur d'un même site ont été encadrées par un double trait, les cellules correspondant à des comparaisons entre régions ont été surlignées par un trait épais. Les estimateurs *F*st de la différenciation génétique entre chaque paire d'échantillons sont donnés sous la diagonale. Les probabilités de type 1 de rejeter Ho (absence de différenciation génétique entre échantillons) sont données au dessus de la diagonale. Les symboles NS, * et ** correspondent aux valeurs de p ajustées pour les comparaisons multiples respectivement > 0.05, < 0.05, et < 0.01.

	Southern Brittany						Northern Brittany						Not connected populations			
	SB1-T1	SB1-T2	SB2-T1	SB2-T2	SB3-T1	SB3-T2	NB1-T1	NB1-T2	NB2-T1	NB2-T2	NB3-T1	NB3-T2	NB4-T1	NB4-T2	SM1-T1	SM1-T2
SB1-T1		NS	NS	NS	NS	NS	NS	NS	*	*	*	NS	**	**	**	**
SB1-T2	0.016		NS	NS	NS	NS	**	**	**	**	**	**	**	**	**	**
SB2-T1	0.035	0.039		NS	*	NS	**	*	*	**	**	**	**	**	**	**
SB2-T2	0.023	0.010	0.038		**	**	**	**	**	**	**	**	**	**	**	**
SB3-T1	0.030	0.010	0.043	0.034		NS	**	**	**	**	**	**	**	**	**	**
SB3-T2	0.030	0.024	0.052	0.051	0.012		**	NS	**	**	**	**	**	**	**	**
NB1-T1	0.035	0.054	0.041	0.062	0.043	0.030		NS	**	**	**	*	**	**	**	**
NB1-T2	0.016	0.037	0.038	0.048	0.023	0.017	0.000		NS	*	**	NS	**	**	**	**
NB2-T1	0.045	0.071	0.062	0.073	0.054	0.050	0.022	0.014		NS	NS	NS	**	**	**	**
NB2-T2	0.037	0.059	0.050	0.073	0.052	0.047	0.030	0.019	0.010		**	NS	**	**	**	**
NB3-T1	0.039	0.048	0.053	0.058	0.034	0.057	0.037	0.026	0.008	0.021		NS	**	**	**	**
NB3-T2	0.048	0.056	0.052	0.060	0.062	0.066	0.031	0.029	0.017	0.011	0.011		**	**	**	**
NB4-T1	0.114	0.127	0.118	0.153	0.110	0.103	0.072	0.072	0.084	0.079	0.078	0.066		**	**	**
NB4-T2	0.109	0.136	0.147	0.142	0.137	0.118	0.087	0.087	0.086	0.093	0.093	0.076	0.091		**	**
SM1-T1	0.123	0.143	0.142	0.152	0.118	0.127	0.114	0.091	0.074	0.067	0.072	0.059	0.134	0.147		**
SM1-T2	0.111	0.142	0.137	0.156	0.125	0.135	0.124	0.093	0.112	0.108	0.096	0.097	0.145	0.146	0.091	

with the duration of emersion time (Engel et al., 2004). Similarly, Pearson & Serrão (2006) highlight that limited dispersal in the intertidal zone may be important in intertidal fucoid species for recruitment assurance and fertilization success. Likewise, based on a data set of 50 nearshore marine invertebrate species, Kelly & Palumbi (2010) stress that significant variation in genetic structure is better explained by adult habitat depth than by duration of the pelagic phase. Together, these results show that the intertidal landscape limits migration between high and low shores, and suggest that restricted gene flow promotes local adaptation to different shore-level ecophysiological conditions. The patterns of genetic differentiation of intertidal species are thus more similar to what is observed in marine broadcast-spawning species or terrestrial plants than in marine animals with long pelagic larval phases (Carr et al., 2003).

From the 17 kelp species reviewed in this paper, no clear relationship was observed between life-span characteristics and patterns of genetic differentiation. In general, the effect of population turnover is expected to shape intra-population genetic diversity rather than among-population differentiation. Recurrent extinction and recolonization of populations is expected to reduce population size and thus genetic diversity within populations. Because *F*st is a ratio of between-population differentiation to total diversity, the genetic effects of these demographic processes may be difficult to interpret only in terms of *F*st. Thus, analysis of absolute measures of diversity within populations, such as the number of alleles (*A*) and gene diversity (*H*e), provides additional required information. A number of empirical studies have shown a correlation between reduced heterozygosity and lowered individual fitness, demonstrating the major role of genetic processes in population extinction (Frankel & Soulé, 1981). Unfortunately, our literature review revealed that data on within-population diversity are rare in kelps, as we found published reports for only seven species.

In a compilation of 307 studies in wild angiosperms and gymnosperms, Nybom (2004) showed that among- and within-population molecular diversity differed significantly when tested against life form, breeding system and successional status. As previously verified with allozyme data (Hamrick & Godt, 1990), RAPD- and microsatellite-based analyses show that long-lived, outcrossing, late successional plant species retain most of their genetic variability within populations while annual, selfing and/or early successional taxa allocate most of their genetic variability among populations (Nybom, 2004). Similarly, marine broadcast-spawning species have been found to demonstrate patterns of spatial genetic structure driven by processes resulting from their life histories (Hellberg, 2009). In kelps, genetic diversity within populations varied greatly among the seven study species and the range of *H*e variation was similar to that of microsatellite DNA in plants and broadcast spawners. These variations probably reflect differences in effective population sizes and have important consequences for management strategies. In species characterized by small population sizes, care should be made to limit any increase in gene flow or connectivity because it could prevent local adaptation, while in species characterized by large populations, connectivity should be maintained to allow recolonization from adjacent populations when natural stocks are over-harvested (Allendorf et al., 2008). In addition, reduced population size due to harvesting can reduce the number of migrants and cause genetic variation to be lost within sub-populations. Knowledge on patterns of gene flow among kelp stands is thus particularly relevant to improve management and conservation of kelp habitats (Billot et al., 2003; Coleman et al., 2009). In this paper, it is noteworthy that the three harvested species *M. pyrifera*, the southern species of *Lessonia nigrescens* and *Laminaria digitata* showed the highest values of gene diversity, suggesting that these species are characterized by large populations. Loss of genetic diversity should not be a crucial problem for these populations unless harvesting of wild populations induces isolation and population fragmentation. Management plans could be considered whereby harvesting is conducted only in certain years or time periods to maintain genetic connectivity in these large kelp stands. In this context, as proposed by Allendorf et al. (2008), genetic monitoring of valuable harvested populations should be used as a standard management tool.

In kelps, population connectivity has been shown to be affected by habitat discontinuity such as long sandy beaches (in *Laminaria digitata,* Billot et al., 2003 and in *Durvillaea Antarctica* (Chamisso) Hariot*,* Fraser et al., 2010) or mine-waste disposal (in the northern species of *Lessonia nigrescens*, Faugeron et al., 2005). In this paper, we confirmed that *Laminaria digitata* populations along the Brittany coast are still strongly influenced by habitat discontinuities (increased genetic differentiation and reduced genetic diversity within populations) when sampled in the same isolated stand seven years later. Moreover, we showed that populations located at the southern limit of the species range distribution have significantly reduced gene diversity, probably due to local demographic effects reducing population size. However, in our study, it was not possible to test the effect of harvesting using spatial analyses since only large, connected and genetically highly diverse populations were located in harvesting areas.

Examination of genetic samples collected over time (i.e. genetic monitoring) is a powerful way to detect genetic changes caused by recent demographic effect such as harvesting (Waples et al., 2008; Allendorf et al., 2008). Our analyses of temporal samples of *Laminaria digitata* did not

reveal significant changes in genetic diversity, probably because heterozygosity is relatively insensitive to the effects of population bottlenecks (Allendorf et al., 2008). The mean number of alleles (*A*) is more sensitive to bottlenecks. However, no significant temporal variation in *A* values was detected. Although *F*is values decreased significantly with time, both sampling periods were characterized by random mating. This significant decrease in *F*is in time was probably due to technical changes in the electrophoresis methods which resulted in a decrease of the frequency of null alleles in the new data set. More interestingly, within-population genetic differentiation varied significantly only for the small, isolated populations of Saint Malo and Locquirec. This temporal variation can most likely be attributed to genetic drift, suggesting a higher turnover of individuals (i.e. macroscopic sporophytes and microscopic gametophytes) in isolated populations compared to core populations. In other words, our results show that when populations are isolated, effective population size is reduced (including both microscopic and macroscopic individuals). This raises the issue of the possible role of the gametophytes as a seed bank analogue in kelp species (Edwards, 2000, and other papers in this volume). Contrary to what has been suggested in other kelp species such as *M. pyrifera*, a local gametophyte "bank" might not be sufficient to prevent genetic changes.

While kelps are economically and ecologically important, only a few studies have attempted to assess genetic variation within kelp populations and on small scales. The majority of molecular studies have been devoted to phylogenetic (for review, see Lane et al., 2006) and biogeographic analyses (for review, see Bolton, 2010), or to solving taxonomic problems of kelp species' delineations (Tellier et al., 2009 & 2011). Connectivity between kelp populations has generally been studied at spatial levels but rarely at temporal levels. For the first time in *Laminaria digitata*, our analyses clearly demonstrate the effect of small population size on genetic stability. These results have important management implications for regulating commercial harvest of *Laminaria digitata* populations, because habitat fragmentation of *Laminaria digitata* stands are likely to be critical. These results also shed light on the importance of preserving isolated populations of this key foundation species.

The reconciliation of conservation actions with harvesting (fishery) strategies has stimulated a large body of literature. Frameworks for the design of networks of marine protected areas (MPA) that meet both conservation and fishery management goals are starting to emerge (Gaines et al., 2010). Setting up marine reserves and other types of MPAs have become key conservation strategies around the world, and during the Eighth Conference of the Parties (COP8) in 2006, most countries have agreed to set aside 10-30% of their waters in MPAs by 2012 (Wood et al., 2008). In France, the first MPA under the Oslo-Paris (OSPAR) convention was created in Brittany (Iroise Natural Marine Park, Fig. 1) in 2007 and several new MPAs are to be created in the coming years. In terms of conservation strategies, given the dissimilarities among sites revealed in our results, a single large MPA is probably not the best option for *Laminaria digitata* compared to a network of smaller MPAs, some of which would require specific conservation measures. Moreover, we provide estimates of the optimal size and connectivity for the kelp *Laminaria digitata* that may be used to design an MPA network. Finally, in addition to sustaining fisheries and enhancing conservation, the success of management plans depends greatly on the response and attitude of the harvesters themselves, and MPAs should be designed to address social and economic considerations as well as ecological ones.

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Annex 1: List of the papers selected for the literature review (Tables 2 & 3)

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