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Regional-scale analysis of subtidal rocky shore community

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Abstract The French monitoring network, REseau BENThique (REBENT), was launched by the Ministry of the Environment in 2003 following the 1999 Erika oil spill. REBENT aimed to acquire baseline knowledge of coastal benthic habitat distributions with a special focus on biological diversity. This study analyzed data from 38 subtidal rocky reef sites collected by a single diving team of marine biologists along the coast of Brittany from 2004 to 2010. At each site, the depth limits of the algal belts were determined between 0 and –40 m Chart Datum (CD); the flora and fauna compositions and abundances were sampled at –3 and –8 m CD. A total of 364 taxa (156 flora and 208 fauna), belonging to 12 phyla, were identified. The results showed that the depth limit and density of kelp beds increased as water turbidity decreased; moreover, several changes in community structure could be related to water turbidity and temperature. Thus, northern and southern Brittany showed strong differences in diversity and structure of the dominant kelp species (*Laminaria hyperborea* and *Saccorhiza polyschides*). The results from this kelp

habitat composition survey (dominant kelp species and indicator species) provided important information for local pressure assessments, like increases in turbidity. The data also provided a reference that could be useful for detecting changes in coastal water temperatures due to global warming.

Keywords Rocky bottom · Monitoring · Subtidal · Northeast Atlantic · Brittany · Kelp bed

Introduction

National marine monitoring programs in Denmark, Sweden, the United Kingdom, and Germany (Marine Environment Monitoring Group unpublished data; Gipperth and Elmgren 2005; Voss 2007) aim to understand the relationships between benthic community structure variability and environmental factors, including temperature, salinity, oxygen content, water current, sedimentation, wave exposure, and pollution (Sandnes and Gulliksen 1980; Gorostiaga and Díez 1996; Kautsky et al. 1999; Martin 1999; Eriksson et al. 2002; Díez et al. 2003; Martin et al. 2003; Schiel et al. 2004). The main objective of these investigations is to deconvolute the natural variability of benthic structures from anthropogenic factors. Monitoring programs may also fulfill international requirements, like the OSPAR convention, the European Union Water Framework Directive, the Natura 2000 network (Habitat and Bird Directives), the Marine Strategy Framework Directive, and Cooperative Monitoring in the Baltic Marine Environment. In France, several studies sought to identify and quantify the impact of the 1999 Erika oil spill on the coastal environment of Brittany; however, the lack of available data made this goal difficult to achieve (Derrien et al.

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unpublished data). Therefore, the need for a coastal perennial monitoring program became apparent, and it was in this context that the REBENT (REseau BENThique) monitoring program was created.

Kelp forests represent one of the most important habitats of northeastern Atlantic sublittoral rocky bottoms. As with terrestrial forests, kelp beds create complex, heterogeneous habitats that are colonized by diverse species of fauna and flora. Kelp forests are inhabited by sessile fauna (Bryozoans, Tunicata, Porifera, Hydrozoa) and flora that grow upon the stipe or blade, and mobile invertebrates (Polychaeta, Crustacea) that shelter in the holdfast. One kelp can support up to 7,000 individual mobile organisms, and 1–2 % of this biomass is exported daily to benthic and pelagic food webs (Jørgensen and Christie 2003). The production of organic matter from a *Laminaria hyperborea* bed was previously estimated to be 3–12 kg m⁻² year⁻¹ biomass (wet weight) (Fredriksen 2003); the major part of this production is exported (Mann 2000). Thus, kelp forests are highly productive systems that play an essential functional role in coastal ecosystems (Kain and Jones 1971; Sjøtun et al. 1995; Abdullah and Fredriksen 2004). Organic matter derived from kelp forests represents a major source of food for many organisms, particularly filter feeders (Fredriksen 2003; Schaal et al. 2010).

Kelp forests also represent a major economic resource for fishing activities (directly and indirectly through nursery functions) (Norderhaug et al. 2005) and for the phycocolloid (alginate) industry (Arzel 1998; Christie et al. 1998; Jensen 1998). Kelp harvesting enterprises produce 50–60,000 tons of kelp in Brittany (Arzel 1998). Alternatively, kelp forests represent potential biosensor systems; for example, in sublittoral rocky benthic communities, sessile species cannot escape environmental disturbances. Some of these species may be particularly sensitive to physical parameters, like temperature or turbidity; these organisms may serve as ecological indicators that could be monitored over the long term.

This study aimed to investigate the species distributions in kelp beds along the Brittany coasts, with the goal of understanding their assemblage into a community typology. We hypothesized that water temperature and turbidity would be the main factors that influenced assemblages of rocky subtidal species. Therefore, we expected to uncover regional-scale differences in macrobenthic communities located in stratified versus homogeneous waters and clear versus highly turbid sites. This study possessed an original design, because it (a) employed a quantitative approach, (b) investigated both fauna and flora communities of subtidal rocky habitats, and (c) covered a broad-scale coastal region (Arroyo et al. 2004; Ford et al. unpublished data; Manage 2008; Raffo et al. 2009). Indeed, assessments of organism abundance are often generated from an estimation of the

percentage of cover or from biomass measurement based on a few taxonomic groups within a rocky subtidal survey. Here, we chose to quantify the numbers of individuals or colonies, because the percentage of cover for several major annual macroalgal species (i.e., *Saccorhiza polyschides*) exhibited extreme between-season variability, due to their annual growth cycles. To our knowledge, no other comprehensive monitoring survey of rocky subtidal communities has been achieved at a regional scale.

Materials and methods

Study sites and sampling design

We studied 38 sites along 2,700 km of the littoral of Brittany (Fig. 1). Environmental data about turbidity and water temperature were collected (Table 1). We included very sheltered sites (estuaries or gulfs), sheltered sites (sea inlets or bays), semi-exposed (coastal water) sites, and exposed (offshore) sites. The level of turbidity was evaluated using KPar. Photosynthetically available radiation (Par) represents the quantity of photons impinging upon a square meter per second in the visible wavelength range. Then, it is key parameter for photosynthetic organisms as macroalgae. Par is affected by any process that absorbs light like presence of suspended matter. KPar is a coefficient that quantifies the rate of decrease in Par and then represents a good indicator of water clarity. Kpar data were derived from SeaWiFS (Sea-viewing Wide Field of view Sensor) measurements. We used the mean Kpar monthly measurement from 2005 to 2009 at a 1 km spatial resolution.

Temperature data were derived from RePHY (Phytoplankton survey program) collected between 2005 and 2012. We used summer (July–August) mean surface (0–1 m) and 0–1 m above bottom (between 6 and 28 m) temperature data. The number of available temperature measurements varied from 2 to 25 with a mean of 12 per sites. The temperature differences between surface and bottom were calculated to represent water stratification. Indeed, during spring and summer, sea surface temperature increases and a strong vertical temperature gradient (thermocline) appears in May–June, resulting in separation of warm surface water and cold bottom water. In south Brittany, temperature can differ by 8–9 °C between surface and 30 m depth (Puillat et al. 2004).

Sampling was conducted by scuba divers at depths of 0–40 m CD during April–July of 2004–2010. Sites were selected randomly from a set of possible sites that met the following prerequisites: (a) the presence of a rocky bottom; (b) diving access with minimal security conditions (tidal current); and (c) depth lower than –8 m CD, if possible. Within each site, the sampled transect was randomly

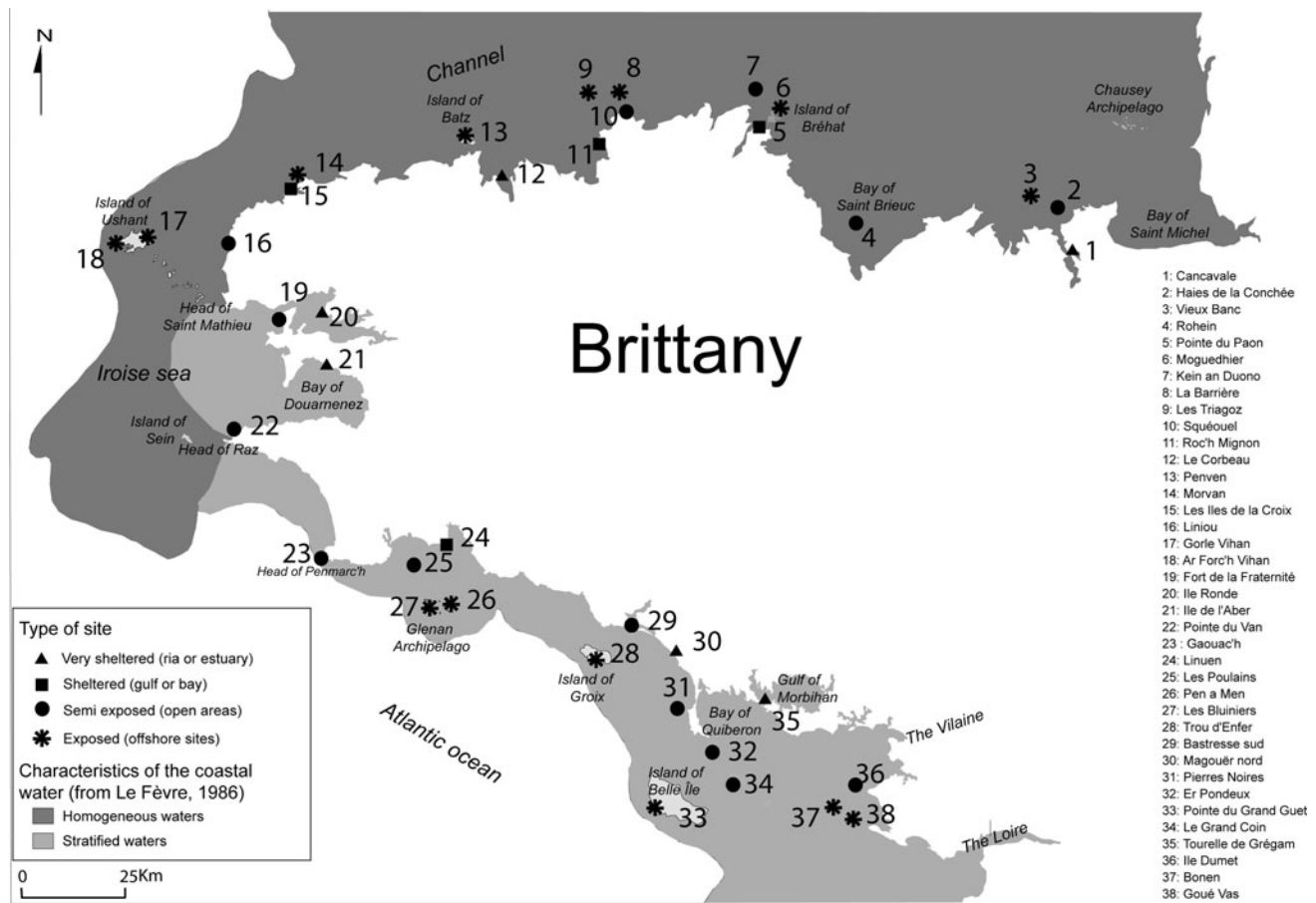


Fig. 1 Map of the 38 littoral sites sampled in Brittany, France. Characteristics of the coastal waters (*bottom left*) are from Lecornu and De Roeck 2009 and Le Fèvre 1986; the list on the *right* gives the site number and its corresponding geographical name

selected from a set of possible line transects. In zones with slopes ($7\text{--}48^\circ$), the transect was positioned perpendicular to the depth gradient. All transects were relatively short in length (≤ 120 m) for diving security reasons. Transects were georeferenced with 2 dGPS (Magellan explorer XL and Humminbird 727), and all useful information (surface photo, bathymetric profile, bottom description) were collected to guarantee finding the same transect over the years.

At each sampling site, a diver swam along the transect on a width of about 10 m (5 m either side of line), looking for the last kelp individual (all species taken together with 1 cm size limit). Then, the end of kelp zone corresponded to the infralittoral–circalittoral boundary (Castric-Fey 1973a, b; Castric-Fey et al. 1973, 1978, 1997, 2001; Connor et al. 2004). Unfortunately, at several sites, it was not possible to determine the depth at which light was insufficient to support kelp development, due to sediment that covered the rocky substratum. In those places, the last observed kelp represented the minimum depth limit of the potential kelp habitat. Then, infralittoral–circalittoral boundary could not be determined, and these data were not included for statistical analysis.

Macrobenthic community composition was assessed with quadrats. The number of organisms was evaluated as the number of individuals, and encrusting species (like encrusting sponges and bryozoa) were evaluated as the number of colonies. The lower size limit was about 5 mm for erect organisms (*Balanus* sp., *Pycnoclavella aurilucens*). Only sessile (attached to the rocky substrate) and semi-mobile (Gastropoda, echinodermata) species were recorded and counted. Thus, epibionts were not recorded. Although determination and counting of small species or colonies (e.g., *Pycnoclavellina aurilucens*, *Clavellina nana*, *Stolonica socialis*, some small hydrozoa, Barnacles) were very time consuming in the field, it was achieved throughout the whole investigation. Moreover, turf algae are not very abundant in Brittany subtidal zone (for example, ectocarpales were recorded in only 42 quadrats of 924 with an average of 14 ind/quadrat) and encrusting bryozoa, didemniidae, and botryllidae form circular small colonies, so it was possible to individualize and count them. Concerning sponges, encrusting common species were massive (like *Cliona celata*, *Tethya aurantium*, *Pachymatisma johnstonia*) and then easy to count. We used

Table 1 Environmental data for littoral sites in Brittany, France, surveyed during 2005–2010

Site number	Site	Exposition	Mean Kpar	Maximum mean summer surface temperature °C	Surface-bottom ΔT °C
1	Cancavale	Very sheltered	0.373	19.56	0.00
2	Haie de la Conchée	Semi-exposed	0.205	18.85	0.00
3	Vieux Banc	Exposed	0.161	17.66	0.00
4	Rohein	Semi-exposed	0.17	17.80	0.07
5	Moguedhier	Semi-exposed	0.319	18.03	0.15
6	Pointe du Paon	Exposed	0.197	17.71	0.15
7	Kein an duno	Semi-exposed	0.202	18.42	0.15
8	La Barrière	Exposed	0.177	16.37	0.65
9	Les Triagoz	Exposed	0.18	16.37	0.65
10	Squéouel	Semi-exposed	0.212	16.95	0.65
11	Roc'h Mignon	Sheltered	0.377	17.86	0.65
12	Corbeau	Very sheltered	0.356	17.11	0.14
13	Penven	Exposed	0.204	16.04	0.14
14	Morvan	Exposed	0.159	14.67	0.14
15	Les îles de la croix	Sheltered	0.172	14.67	0.14
16	Les Liniou	Semi-exposed	0.162	16.28	0.14
17	Gorle Vihan	Semi exposed	0.147	14.86	0.14
18	Ar Forc'h Vihan	Exposed	0.158	16.50	0.14
19	Fort de la Fraternité	Semi-exposed	0.189	18.00	0.27
20	Ile Ronde	Very sheltered	0.416	17.18	0.27
21	Ile de l'Aber	Very sheltered	0.294	18.50	1.20
22	Pointe du Van	Exposed	0.17	17.50	1.20
23	Gauac'h	Exposed	0.182	17.20	2.13
24	Les Bluiniers	Exposed	0.169	16.98	2.13
25	Pen a Men	Semi-exposed	0.199	16.98	2.13
26	les Poulains	Semi-exposed	0.218	16.98	2.13
27	Linuen	Sheltered	0.309	16.98	2.13
28	Trou d'Enfer	Exposed	0.214	17.86	2.73
29	Bastresse Sud	Semi exposed	0.308	19.43	2.73
30	Magouër Nord	Very sheltered	0.474	17.75	0.05
31	Pierres Noires	Semi-exposed	0.254	17.29	2.95
32	Pointe du Grand Guet	Exposed	0.251	16.78	1.44
33	Er Pondeux	Semi exposed	0.315	16.78	1.44
34	Grand Coin	Semi exposed	0.28	16.78	1.44
35	Tourelle de Grégam	Very sheltered	0.409	18.36	0.05
36	Ile Dumet	Sheltered	0.416	18.66	2.00
37	Bonen	Exposed	0.273	18.56	2.00
38	Goue Vas	Exposed	0.29	18.56	2.00

Mean Kpar (coefficient of photosynthetically active radiation) data (2005–2009) was derived from (Saulquin et al. 2013), and temperature data (2005–2012) were derived from REPHY program (extracted from Quadrigé² database of Ifremer)

0.25 m⁻² (0.5 × 0.5 m) quadrats for sampling to maximize accuracy in the quantification of species (Edwards 1998; Kautsky et al. 1999; Martin 1999; Davies et al. 2001; Neto 2001; Eriksson et al. 2002; Mercer et al. 2003; Preciado and Maldonado 2005; Rinde and Sjøtun 2005). This quadrat size allowed the diver to make accurate in situ

qualitative and quantitative readings. Moreover, the quadrat sampling technique is well adapted for sample areas that have a cover of foliose and filamentous algae (as in kelp forests). The diving team was composed of marine biologists that were expert at in situ identification. Direct identification by divers limited the requirements for the

Table 2 Overview of littoral sampling sites in Brittany, France (nk: no kelp)

Site no.	Site	Year of sampling			Available depth			Total number of Kelp and associated flora and fauna quadrats (7 replicates at –3 m C.D and –8 m C.D)	Kelp quadrats (10 replicates at each depth)
		1st	2nd	3rd	–3 m C.D.	–8 m C.D.	–13 m C.D.		
1	Cancavale	2005			x	x	x	21	nk
2	Vieux Banc	2004	2008		x	x	x	42	60
3	Haies de la Conchée	2006	2008		x	x	x	42	60
4	Rohein	2008			x	x	x	21	30
5	Moguedhier	2006	2007	2010	x	x	x	63	90
6	Pointe du Paon	2005	2007	2010	x	x	Sediment	42	60
7	Kein an Duono	2007			x	Sediment	Sediment	7	10
8	La Barrière	2006	2009		x	x	x	42	60
9	Les Triagoz	2006	2009		x	x	x	42	60
10	Squéouel	2005	2009		x	x	x	42	60
11	Roc'h Mignon	2006	2009		x	Sediment	Sediment	7	20
12	Corbeau	2005	2008		x	x	x	42	60
13	Penven	2006			x	Wall	x	14	20
14	Morvan	2005	2007	2010	x	x	Wall	42	60
15	Les Iles de la Croix	2006	2007	2010	x	x	Sediment	42	60
16	Les Liniou	2004	2007	2010	x	x	x	63	90
17	Gorle Vihan	2006	2009		x	x	x	42	60
18	Ar Forc'h Vihan	2006	2009		x	x	x	42	60
19	Fort de la Fraternité	2004	2009		x	x	Sediment	28	40
20	Ile Ronde	2006	2009		x	x	Sediment	28	nk
21	Ile de l'Aber	2008			x	Sediment	Sediment	7	10
22	Pointe du Van	2006	2008		x	x	Wall	28	40
23	Gaouac'h	2008			x	x	x	21	30
24	Linuen	2005	2009		x	x	x	42	60
25	Les Poulains	2005	2008		x	x	Sediment	28	40
26	Pen a Men	2005	2009		x	x	Sediment	28	40
27	Les Bluiniers	2006	2009		x	x	x	42	60
28	Trou d'Enfer	2004	2007	2010	x	x	Sediment	42	60
29	Bastresse Sud	2007			x	x	Sediment	14	20
30	Magouër nord	2006	2007	2010	x	x	x	63	nk
31	Pierres Noires	2008			x	Wall	x	14	20
32	Er Pondeux	2005	2008		x	x	Sediment	28	40
33	Pointe du Grand Guet	2005	2008		x	x	x	42	60
34	Grand Coin	2008			x	x	Sediment	14	20
35	Tourelle de Grégam	2005	2008		x	x	x	42	nk
36	Ile Dumet	2008	2009	2010	x	Wall	Sediment	21	30
37	Bonen	2008	2009	2010	x	x	x	63	90
38	Goué Vas	2009			x	x	x	21	30
	Total							1,274	1,610

collection of organisms and minimized the impact on the studied community; the latter aspect is considered essential for long-term monitoring. Species that could not be identified in the field were gently collected, preserved (fauna were fixed in 5 % formalin and stored in 70 % ethanol;

flora were conserved in a herbarium for flora), and later identified in the laboratory. At each site, 7 quadrats (replicates) were positioned randomly at each depth of –3 and –8 m CD. To focus on the density and composition of kelp beds, we also quantified the kelp in 10 additional quadrats

at each depth of -3 , -8 , and -13 m CD (when available) (Table 2). We sampled 38 sites between 2004 and 2010; this represented a total of 1,274 sampled quadrats for evaluating fauna and flora abundances and an additional 1,610 quadrats for evaluating kelp densities.

Each year, 40,000–230,000 individuals from 200 to 270 taxa were inventoried over 9–12 survey sites, representing 40–70 diving hours per marine biologist per year. It was not possible to sample all 38 sites in only 4 months (April–July); thus, each year, at least one area was visited on coastlines of the Channel, Iroise Sea, and Atlantic Ocean. Several sites were sampled three times during the study period to evaluate inter-annual and inter-site variations.

Data analysis

Habitats classification

We used abiotic parameters (Kpar, mean summer surface temperature, mean summer surface-bottom temperature difference, and level of exposition) to run a cluster analysis, using Euclidian distance and Ward's method which is the most appropriate method according to Clarke and Warwick (2001). Cluster analysis was performed with Xlstat Microsoft 2011.4 software. The statistical significance of the resulting groups was tested with ANOSIM (analysis of similarity) provided in R software.

Kelp beds depth, composition, and density

For each site, the depth limits of the kelp zone (infralittoral–circalittoral boundary) were noted. We used the one-way ANOVA to test differences in the depth limits (sites where sediment covered the rocky substratum were excluded from the analysis)

At each site, the mean density of kelp species (*Laminaria digitata*, *Laminaria hyperborea*, *Laminaria ochroleuca*, *Saccorhiza polyschides*) was extrapolated as the number of individuals per square meter (ind/m^2) at three depths (-3 m, -8 m, and, when available, -13 m CD). In order to test difference in total kelp densities among 2 different levels of turbidity ($\text{Kpar} < 0.25$ or $\text{Kpar} > 0.25$), we used a Mann and Whitney test (Shapiro–Wilk test indicated data did not exhibit normality).

We also determined the relative abundance of *Saccorhiza polyschides* (Sp) to *Laminaria hyperborea* (Lh) and *Laminaria ochroleuca* (Lo), the dominant kelp species in infralittoral in Brittany. We used the *Saccorhiza polyschides* relative abundance to test difference between homogeneous and stratified water sites. The Sp relative abundance data did not exhibit normality (Shapiro–Wilk test). Then, we used a Mann–Whitney test (nonparametric test) to analyze differences between stratified (mean

summer surface-bottom $\Delta T^\circ\text{C} > 1^\circ\text{C}$) and homogeneous (mean summer surface-bottom $\Delta T^\circ\text{C} < 1^\circ\text{C}$) water sites. All statistical tests were performed with Xlstat Microsoft 2011.4 software.

Community analysis

We also evaluated differences in species abundance between sites by examining the abundances of algae and invertebrates in the quadrats at -3 and -8 m CD. The number of species was first reduced by eliminating those that had been recorded less than three times and that accounted for less than 4 % of the total abundance at any sites (Clarke and Warwick 2001; Clarke 1993). Indeed, uncommon species (site-specific species) would tend to confuse the clustering and multivariate analysis, which would prevent detection of the large-scale community structure. The data were arranged in a matrix of 66 sites * year variables described by 142 taxa. Abundances (X) were transformed with the $\text{Log}_{10}(X + 1)$ function.

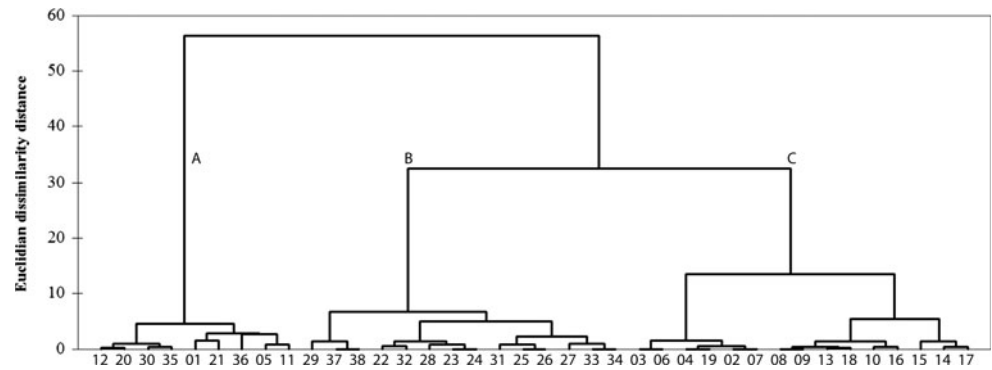
First, we performed a multivariate analysis (correspondence factor analysis; Benzecri 1973) to establish the affinities between survey sites and species and to check the inter-annual variation between sites. Next, we performed a cluster analysis to identify the regional-scale subtidal communities. This classification method used the Bray–Curtis dissimilarity distance and average linkage. Cluster and multivariate analyses were performed with Xlstat Microsoft 2011.4 software. The statistical significance of the resulting groups was tested with ANOSIM (analysis of similarity) provided in R software.

Results

Cluster analysis on abiotic parameters detected 3 groups A, B, and C at a dissimilarity distance of 32.42. (ANOSIM: $R = 0.625$, $p < 0.001$; Fig. 2). Cluster A grouped the most turbid sites (Kpar varied from 0.319 to 0.474) and l'Île de l'Aber which is a moderately turbid site ($\text{Kpar} = 0.294$). Cluster B represented all the clear water sites of South Brittany where a thermocline appears during late spring ($\text{Kpar} < 0.315$ and mean summer surface-bottom $\Delta T^\circ\text{C}$: 1.2 – 2.95°C). The last cluster C consisted of the clear water sites of North Brittany where the water column is homogeneous because of water mixing ($\text{Kpar} < 0.212$ and mean summer surface-bottom $\Delta T^\circ\text{C}$: 0 – 0.65°C).

This study documented a total of 364 taxa (156 flora and 208 fauna), including 120 taxa of Rhodophyta, 26 of Phaeophyta, 10 of Chlorophyta, 23 of Tunicata, 59 of Porifera, 36 of Hydrozoa, 28 of Bryozoa, 18 of Anthozoa, 3 of Crustacea, 17 of Mollusca, 17 of Echinodermata, and 7 of Annelida.

Fig. 2 Dendrogram from a cluster analysis shows the classification of study sites based on abiotic data assessed with the Euclidian dissimilarity distance and Ward's linkage method. The three primary classes correspond to *A* highly turbid sites, *B* clear, stratified sites and *C* clear, homogenous sites. Numbers represent the 38 studied sites (referred to Fig. 1)



The survey of macrobenthic communities (algal bed compositions and depth limits) allowed us to generate a between-site comparison of the lower depth limits of the kelp zone (corresponding to the limit between infralittoral and circalittoral stage; Table 3). When kelp was absent, as at Cancavale, Ile Ronde, Magouër Nord, and Tourelle de Grégam (sites 1, 20, 30, and 35; Fig. 1), other macroalgae were found, including *Cystoseira* spp., *Solieria chordalis*, and *Sargassum muticum*. When the lower depth limit of the kelp bed was observed (in the presence of kelp and the absence of sediment), it varied from -32.2 m CD at the offshore, clear water site of Ar Forc'h Vihan (site 18; Fig. 1) to -1.6 m CD at the sheltered, turbid site of Roc'h Mignon (site 11; Fig. 1). One-way ANOVA results confirmed that the depth limits of kelp zone significantly decreased with turbidity (Table 4).

The total kelp densities showed significant differences between low- and high-turbidity sites (Table 5). The kelp density analysis at -3 m CD revealed that sites with clear water exhibited much higher kelp densities (32.5 ind/m²) than sites with high turbidity (14.8 ind/m²). Indeed, kelp beds were absent from sites located in sheltered areas with high water turbidity (sites 1, 20, 30, and 35; Fig. 2). At -8 and -13 m CD, sites with clear water showed significantly higher kelp densities (26.0 and 13.0 ind/m², respectively) than sites with high turbidity (6.4 and 1.8 ind/m², respectively). The highest kelp densities at -13 m CD were observed at offshore, clear water sites: La Barrière, site 8 (8 ind/m²); Gaouac'h, site 23 (18.4 ind/m²); Ushant island, sites 17 (24.0 ind/m²) and 18 (27.6 ind/m²); Les Bluiniers, site 27 (26.4 ind/m²); and Pointe du Grand Guet, site 33 (22.8 ind/m²).

Kelp composition (Fig. 3), based on the Sp relative abundance, showed high variability; the Sp relative abundance ranged from 0 to 100 %. There were clear differences in the Sp relative abundance at shallow depths between homogeneous (Northern Brittany) and stratified waters (Southern Brittany) (Table 6). At -3 and -8 m CD, the average Sp relative abundances were higher in stratified water sites of Southern Brittany (average Sp relative

abundances of 94.4 and 69.0 %, respectively) than in homogeneous water sites of the English Channel and Iroise Sea (average Sp relative abundances of 5.2 and 15.7 %, respectively). However, there was no significant difference in Sp relative abundance between stratified and homogeneous water at -13 m CD. Indeed, *Saccorhiza polyschides* was generally rare at -13 m CD (average relative abundance of 0.8 and 8.3 % at homogeneous and stratified water sites, respectively) at all sites, replaced by *Laminaria hyperborea* even in stratified water sites.

In the Northern Brittany fairway (Moguedhier site 5 and Les Iles de la Croix site 15), *Laminaria ochroleuca* was the dominant kelp species.

We also performed ordination with correspondence factor analysis (Fig. 4). Axis 1 graphically represented a gradient of increasing turbidity (from left to right). Axis 2 showed the stratified water sites of Southern Brittany on the positive side and the homogeneous water sites of Northern Brittany on the negative side; this can be interpreted as a graphical representation of water masses characteristics. Axes 1 and 2 contributed to the total inertia by 11.35 and 8.77 %, respectively. The distribution of sites on axes 1 and 2 indicated that inter-site variation was more important than inter-annual variation. This made it possible to perform large-scale comparisons of the subtidal communities of the Brittany coasts. The major absolute contributors to the inertia explained by axis 1 were (Table 7), in decreasing order, variables *Aiptasia mutabilis*, *Solieria chordalis*, *Nemertesia ramosa*, *Hydrallmania falcata*, *Bougainvillia muscus*, *Gracilaria multipartita*, *Ulva* sp., *Morchellium argus*, *Ophiothrix fragilis*, *Nemertesia antennina*, *Chondria dasyphylla*, *Aplidium elegans*, *Chondracanthus acicularis*, *Sabella spallanzanii*, Corallinaceae, *Laminaria hyperborea*, *Tethya aurantium*, *Delesseria sanguinea*, and *Polymastia penicillus*. For axis 2, the major absolute contributors were variables *Balanus* spp., *Pterosiphonia complanata*, *Dysidea fragilis*, Ectocarpales, *Asterias rubens*, *Saccorhiza polyschides*, *Plocamium cartilagineum*, *Meredithia microphylla*, *Hypoglossum hypoglossoides*, *Marthasterias glacialis* and *Phyllophora*

Table 3 Depth of infralittoral/circalittoral boundary at sites studied between 2004 and 2010, in Brittany, France

Site n°	Site	Infralittoral/circalittoral boundary depth						
		2004	2005	2006	2007	2008	2009	2010
1	Cancavale		nk			nk		
2	Vieux Banc			−12.6*		−12.7*		
3	Haies de la Conchée			−8.5		−8.4		
4	Rohein					−12.9*		
5	Moguedhier			−11.1	−11.8		−9.9	
6	Pointe du Paon		−9.6*		−9.6*			−9.9*
7	Kein an Duono				−4.0*			
8	La Barrière			−25.6			−24.4	
9	Les Triagoz				−22.7		−22.7	
10	Squéouel		−13.1				−14.7	
11	Roc'h Mignon			−1.6			−2.5	
12	Corbeau		−7.5			−3.9		
13	Penven			−14.0*				
14	Morvan		−22.5*		−22.8*			−22.8*
15	Les Iles de la Croix			−11.5*	−11.9*			−12.0*
16	Les Liniou	−18.5*			−18.3*			−18.3*
17	Gorle Vihan			−32.1			−23.0	
18	Ar Forc'h Vihan			−32.2			−29.2	
19	Fort de la Fraternité	−8.4*					−9.3*	
20	Ile Ronde			nk			nk	
21	Ile de l'Aber					−6.6*		
22	Pointe du Van			−23.9*		−23.7*		
23	Gaouac'h					−24.0		
24	Linuen		−9.0				−10.9	
25	Les Poulains		−10.8*			−11.2*		
26	Pen a Men		−11.2*				−9.9*	
27	Les Bluiniers			−27.8			−23.0	
28	Trou d'Enfer	−9.2*			−8.5*			−8.7*
29	Bastresse Sud				−8.8*			
30	Magouër nord			nk	nk			nk
31	Pierres Noires					−14.7		
32	Er Pondeux		−11.8*			−11.8*		
33	Pointe du Grand Guet		−16.4			−20.2		
34	Grand Coin					−9.1		
35	Tourelle de Grégam		nk			nk		
36	Ile Dumet					−3.5	−4.9	−4.6
37	Bonen					−10.0	−15.5	−12.0
38	Goué Vas						−12.6	

ANOVA was only performed with data without

nk no kelp

* Lower limit of hard substrate enabling kelp growth; below soft sediments

crispa. Then, CFA analysis distinguished three groups of sites: (1) Clear, stratified water sites (top left corner) characterized by *Saccorhiza polyschides* kelp forests that included *Pterosiphonia complanata*, *Hypoglossum hypoglossoides*, the Ectocarpales, *Lomentaria clavellosa*, and

the echinodermata *Marthasterias glacialis* and *Asterias rubens*; (2) clear, homogeneous water sites (bottom left corner) with the kelp *Laminaria hyperborea* and the associated algae *Delesseria sanguinea*, *Phyllophora crispa* *Plocamium cartilagineum*, *Meredithia microphylla* and the

Table 4 Comparisons of infralittoral/circalittoral boundary depth according to the level of turbidity; *p* values based on the one-way ANOVA tests; * *p* ≤ 0.05; ** *p* ≤ 0.01; *** *p* ≤ 0.001

Source	<i>df</i>	Sum of square	Mean square	<i>F</i> ratio	<i>p</i> value
Between groups	1	1,154.290	1,154.290	26.040	<0.0001
Error	20	886.536	44.327		
Total	21	2,040.826			

corallinaceae, the cirriped *Balanus* spp. and the sponge *Dysidea fragilis*; and (3) highly turbid water sites (on the right) defined by the presence of the algae *Solieria chordalis*, *Ulva* sp., *Gracilaria multipartita*, *Chondracanthus acicularis* and *Chondria dasyphylla*., the Cnidarians *Aiptasia mutabilis*, *Bougainvillia muscus*, *Nemertesia ramosa*, *Nemertesia antennina*, *Hydrallmania falcata*, the Ascidians *Aplidium elegans* and *Morchellium argus*, the porifera *Tethya aurantium*, and *Polymastia penicillus* the annelida *Sabella spallanzanii* and the echinodermata *Ophiothrix fragilis*.

Next, the cluster analysis detected three distinct groups of sites (A, B, and C) with a dissimilarity distance of 2.69 (ANOSIM: *R* = 0.603, *p* < 0.001; Fig. 5). Cluster analysis based on species abundances showed the same groups of sites that the cluster analysis performed on abiotic parameters. Then, Cluster A was interpreted to include the clear, homogeneous water sites from Northern Brittany to the Bay of Brest, which were characterized by kelp forests dominated by *Laminaria hyperborea* or *Laminaria ochroleuca*. Cluster B consisted of highly turbid sites where kelp was absent or rare, but high-turbidity water communities flourished (*Sargassum muticum*, *Solieria chordalis*, sciaphilic algae, and filter feeders filterers). Cluster C included sites with clear and stratified water from Southern Brittany, where *Saccorhiza polyschides* dominated the kelp forests. Subgroups could also be distinguished in clusters A, B, and C (dissimilarity index = 1.1). Cluster A was divided into three subgroups: (A.1) northwestern Channel and Iroise sea sites; (A.2.1) most of northeastern Brittany (the “Normano-Breton” Gulf); and (A.2.2) Northern

Brittany fairways sites, characterized by the dominance of *Laminaria ochroleuca*. Cluster B was divided into two subgroups: (B.1) the highly turbid sites of northern Brittany with homogeneous water; and (B.2) stratified water sites in Southern Brittany. Cluster C was divided into three subgroups: (C.1) sites 37 and 38, which are geographically close and characterized by a calcareous substratum; (C.2) two close sites (24 and 26) influenced by sediment input; and (C.3) an assemblage of semi-sheltered sites in Southern Brittany.

Discussion

Our results supported our hypothesis that water temperature and turbidity would be the main factors that influenced assemblages of rocky subtidal species (kelps species and associated fauna and flora). Our correspondence factor analysis indicated that inter-site variation was more important than inter-annual variation. Thus, the regional-scale differences in macrobenthic communities clearly demonstrated the effects of stratified versus homogeneous waters and clear versus highly turbid sites.

Water temperature is a key parameter for macroalgae survival. Western European kelp species are considered to be stenothermal (Birkett et al. 1998), with their geographical ranges directly linked to their temperature range tolerances (Table 8). *Saccorhiza polyschides* lives from Morocco (Ribera et al. 1992) to the western coast of middle Norway and may also be found in a few deep sites (25–110 m) in the Mediterranean (Fredj and Giaccone 1987; Birkett et al. 1998). *Laminaria hyperborea* is a cold-temperate species ranging from Northern Portugal to the northern Norwegian coast (Kain 1967), east to the Bay of Murmansk (Schoschina 1997), and west to Iceland (Kain 1967) and the Faeroe islands (Irvine 1982; Nielsen and Gunnarsson 2001) (for distribution maps, see Lüning 1990). In Brittany, the water temperature is highest on the southern coast, particularly near the surface, in the first few meters of the water column. A thermocline is present in spring and summer, due to water stratification (Le Fèvre 1986). This phenomenon does not occur in the Iroise Sea or

Table 5 Mean total kelp density at different depths in homogenous or stratified water masses

Depth	Low turbidity		High turbidity		Mann and Whitey test results	
	<i>N</i>	Mean	<i>N</i>	Mean	<i>p</i> value	<i>U</i>
–3 m C.M.	22	32.3	15	14.1	0.0009***	272.5
–8 m C.M.	19	26.0	14	6.4	0.0003***	232.5
–13 m C.M.	12	13.0	13	1.8	0.0006***	136.0

N represents the number of data values. *p* values represent the significance of differences between kelp density among the level of turbidity based on the Mann–Whitney *U* test; *** *p* < 0.001

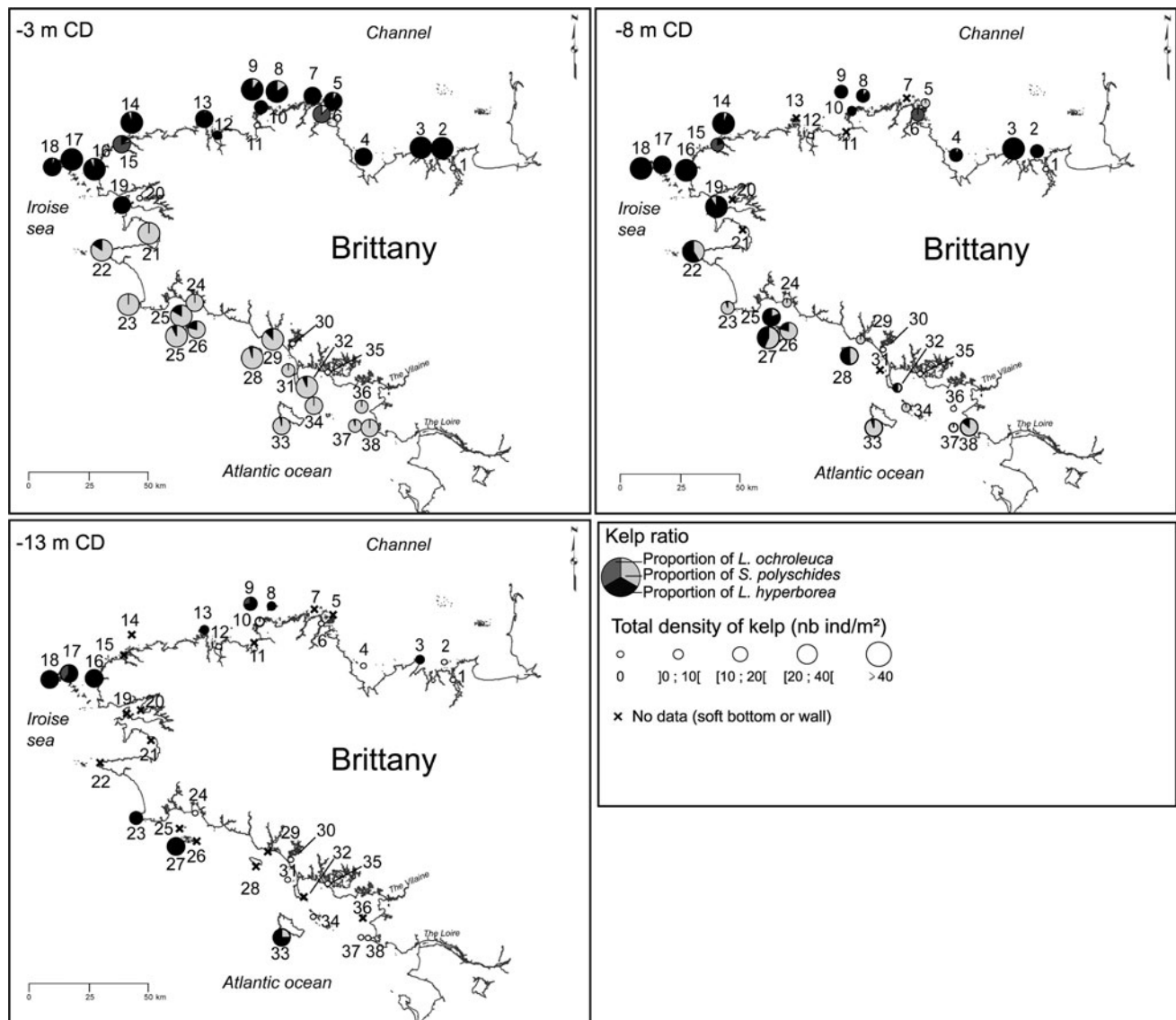


Fig. 3 Map of kelp density and species distributions in 38 littoral sites in Brittany. Panels show measurements at the same sites (numbered) taken at -3 , -8 , and -13 m CD; the mean total kelp density is indicated by the size of the circle; the relative abundances

of *Saccorhiza polyschides*, *Laminaria hyperborea*, and *Laminaria ochroleuca* are shown as a pie chart, with the proportions shown as light, dark, and medium gray areas, respectively; (ind/m²), number of individuals per square meter

Table 6 Distributions of kelp species at different depths in homogenous or stratified water masses

Depth	Homogeneous water		Stratified water		Mann and Whitey test results	
	<i>N</i>	Mean (%)	<i>N</i>	Mean (%)	<i>p</i> value	<i>U</i>
-3 m C.D.	18	5.2	16	94.4	<0.0001***	0
-8 m C.D.	14	15.7	12	69.0	0.0006***	17.5
-13 m C.D.	7	0.8	3	8.3	0.5150	8.0

Sp relative abundance, Abundance of *Saccorhiza polyschides* to total kelp (*Laminaria hyperborea*, *Laminaria ochroleuca* and *Saccorhiza polyschides*) densities; *p* values represent the significance of differences between Sp relative abundance in different water masses based on the Mann–Whitney *U* test; *** $p < 0.001$

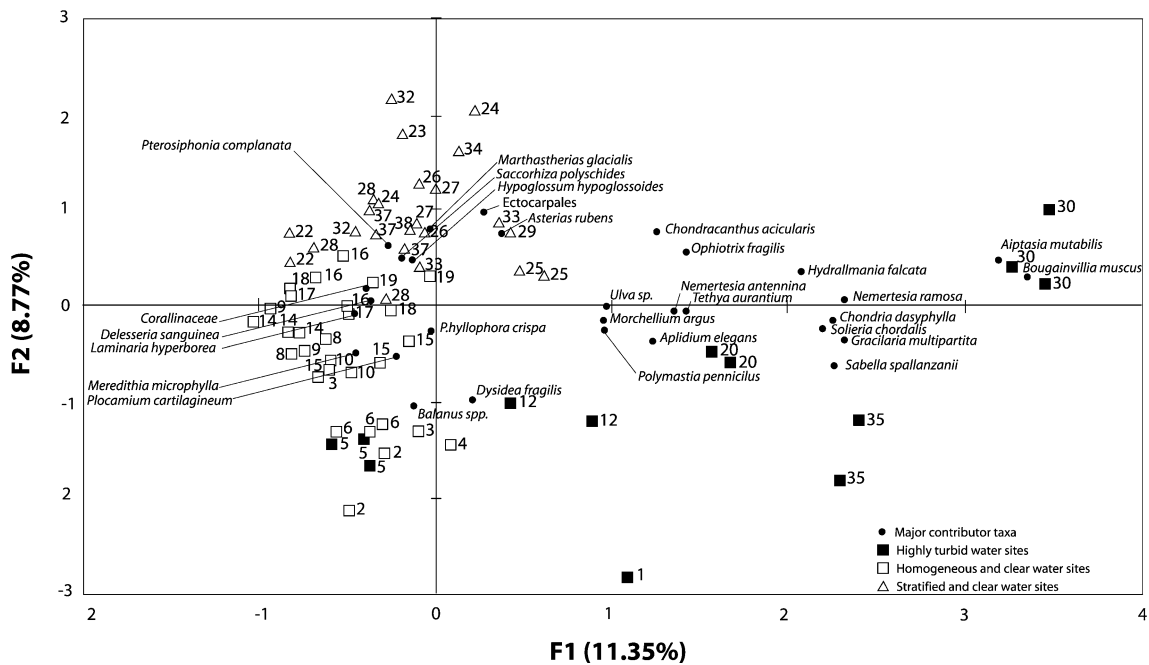


Fig. 4 Correspondence factor analysis, with projections of a variable (main contributor species) and the sampling site. *F1* represents turbidity, from low (left) to high (right); *F2* represents water mass stratification, from homogenous (negative) to highly stratified

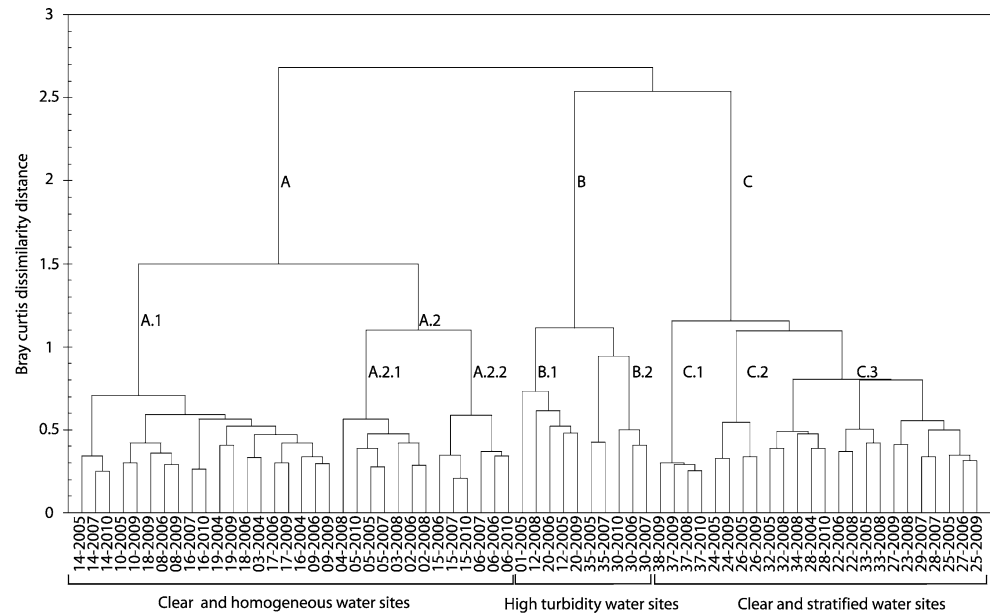
(positive). The contributions of these factors to inertia are shown in parentheses. The same numbers represent results from different years. Site typology was defined according to cluster analysis on abiotic parameters results (Fig. 2; Table 1)

Table 7 Major contributor species to the CFA axis

Correlation type	Axis 1		Axis 2	
	Species	Contribution to the inertia (%)	Species	Contribution to the inertia (%)
Positive	<i>Aiptasia mutabilis f. couchi</i>	7.84	<i>Pterosiphonia complanata</i>	3.05
	<i>Solieria chordalis</i>	7.20	Ectocarpales	2.74
	<i>Nemertesia ramosa</i>	6.07	<i>Asterias rubens</i>	2.70
	<i>Hydrallmania falcata</i>	5.72	<i>Saccorhiza polyschides</i>	2.58
	<i>Bougainvillia muscus</i>	5.05	<i>Hypoglossum hypoglossoides</i>	1.66
	<i>Gracilaria multipartita</i>	4.03	<i>Marthasterias glacialis</i>	1.43
	<i>Ulva spp.</i>	3.05		
	<i>Morchellium argus</i>	2.94		
	<i>Ophiothrix fragilis</i>	2.79		
	<i>Nemertesia antennina</i>	2.65		
	<i>Chondria dasyphylla</i>	2.41		
	<i>Chondracanthus acicularis</i>	1.69		
	<i>Tethya aurantium</i>	1.38		
	<i>Polymastia penicillus</i>	1.47		
	<i>Sabella spallanzanii</i>	1.66		
	Negative	Corallinaceae	1.47	<i>Plocamium cartilagineum</i>
<i>Delesseria sanguinea</i>		1.07	<i>Balanus spp.</i>	9.36
<i>Laminaria hyperborea</i>		1.39	<i>Meredithia microphylla</i>	2.32
			<i>Dysidea fragilis</i>	2.93
Total		59.88	<i>Phyllophora crispa</i>	1.14
				32.36

Retained species were those which exhibit contribution superior to 1/*N* (with *N* = total number of species)

Fig. 5 Dendrogram from a cluster analysis shows the classification of study sites based on correlations of fauna and flora densities assessed with the Bray–Curtis dissimilarity distance and average linkage. The three primary classes correspond to *A* clear, homogeneous sites, *B* highly turbid sites, and *C* clear, stratified sites. Numbers correspond to the site (two numbers; Fig. 1) and sampling year (four numbers)



the Western Channel because water mixing occurs, due to strong tidal currents (Le Fèvre 1986). This regional difference may explain the dominance of *Saccorhiza polyschides* over *Laminaria hyperborea* (the mean Sp relative abundance was 94.4 % at -3 m CD) that we observed in the shallow infralittoral zone of southeastern Brittany. *Laminaria hyperborea* sporophyte cannot tolerate temperatures higher than $22\text{--}23$ °C (Table 7); thus, it grows in relatively deeper water, below the thermocline, or in colder water, like that of the Iroise Sea or the northern coast of Brittany. On the other hand, *Saccorhiza polyschides*, a southern species, is adapted to higher temperatures (tom Dieck (Bartsch) 1993; Birkett et al. 1998); thus, it dominates above the thermocline in stratified waters.

Because temperature controls the growth, reproduction, and survival of macroalgae (Breeman 1988; Lüning 1990), oceanic warming could lead to change in macroalgal composition and abundance (Müller et al. 2009). In a water warming scenario (Parry et al. 2007), complete disappearance of kelp species (especially for *Laminaria digitata* and *Laminaria hyperborea*) may occur under extreme warming conditions (Müller et al. 2009). Moreover, if water column stratification persists, the shallow waters of southern Brittany sites would be affected first by water warming with a steady decrease in the density of *Laminaria hyperborea* above the thermocline. Next, in a perspective of thermal stress, *Saccorhiza polyschides* would disappear (Fernández 2011), and it would be replaced by more temperature tolerant species, like *Halidrys siliquosa* or *Sargassum muticum* (Hiscock et al. 2004; Norton 1977).

Light penetration in the water column is another major factor that influences the distribution of algae (Dring 1987;

Castric-Fey et al. 2001). The lower limit of the kelp bed is considered to receive 1 % of the mean surface light (Hiscock 1985); thus, this limit is a good indicator of water turbidity. In the present study, the lower limit parameter was extremely variable between sites. Kelp beds grew at approximately 30 m below CD in clear water at offshore sites (Ushant island), but they were confined to shallow areas or disappeared in turbid waters. At offshore and semi-sheltered sites, water transparency favored high kelp density. Conversely, in very turbid sites (sites 1, 20, 30, and 35, all grouped in cluster B of the cluster analysis), kelp species were absent; in those places, kelp was replaced by other algae (*Halidrys siliquosa*, *Sargassum muticum*, and *Solieria chordalis*) that were adapted to highly turbid water (Dring 1987; Castric-Fey et al. 2001). In Southern Brittany, the Gulf of Morbihan and the Vilaine and Loire estuaries provide suspended matter and nutrients that also cause increased turbidity (De Roeck unpublished data; Dauvin et al. 2009; Lazure et al. unpublished data); that turbidity may form the basis for the lower kelp density observed in this area, even at open-sea sites. Turbidity measurements (Teissier 2006; Méléder unpublished data; EUSeaMap unpublished data) have demonstrated that the waters around the Vilaine and Loire estuaries contain high quantities of suspended matter, often 10–60 nephelometric turbidity units [NTUs], and sometimes up to 100 NTUs. In contrast, the waters of the English Channel, the Iroise Sea, and southwestern Brittany are less turbid (0.5–10 NTUs, frequently less than 5 NTUs). *Saccorhiza polyschides* is able to grow in turbid sites and is more tolerant to sediment input (Santos 1993; Castric-Fey et al. 2001); these properties could explain its abundance in Southern Brittany

Table 8 Survival and tolerance temperature range for four kelp species found in Brittany (from Belsher and Boyen 1983; Lüning 1984; tom Dieck (Bartsch) 1993; Birkett et al. 1998; Müller et al. 2008)

Species	Survival temperature range of gametophytes		Upper tolerance temperature range (growth/reproduction)	
	Lower survival temperature	Upper survival temperature	Sporophyte	Gametophyte
<i>Laminaria digitata</i>	−1.5	20–24	20 °C/19 °C	Upper : 17 °C/18 °C
<i>Laminaria hyperborea</i>	−1.5	22–23	20 °C/15 °C	21 °C/below 18 °C
<i>Laminaria ochroleuca</i>	1	25	22–23 °C ^a	^a /21 °C
<i>Saccorhiza polyschides</i>	1–>1	23–24	24 °C ^a	25 °C/below 17 °C
<i>Halidrys siliquosa</i>		25	a	a
<i>Sargassum muticum</i>	−9	30	a	a

^a Undetermined

sites. Thus, our results confirmed that water transparency is a fundamental environmental parameter that controlled kelp forest distribution, depth limit, and density (Norton and Milburn 1972; Sjøtun et al. 1993; Méléder et al. unpublished data; Pehlke and Bartsch 2008).

Our detailed analysis provided baseline information about the fauna and flora of subtidal rocky bottoms of Brittany. We identified three distinct communities that were controlled by turbidity and water mass distributions (homogeneous and stratified waters). These communities were as follows: (1) a clear, stratified water community characterized by *Saccorhiza polyschides* kelp forests that included algae of *Pterosiphonia complanata*, *Hypoglossum hypoglossoides* (both described as warm-water species according to Norton and Parkes (1972) Birkett et al. (1998) and Husa (2007), the Ectocarpales, *Lomentaria clavellosa*, and the echinodermata *Marthasterias glacialis* and *Asterias rubens*; (2) a clear, homogeneous water community defined by *Laminaria hyperborea* or *Laminaria ochroleuca* (which replace *L. hyperborea* in sheltered and high current conditions) kelp forests with typical algae of *Plocamium cartilagineum*, *Delesseria sanguinea*, *Phyllophora crispa*, *Meredithia microphylla*, and the corallinaceae. All those algae species were described as typically associated with *Laminaria hyperborea* by Hiscock and Maggs (1984) and Maggs and Hommersand (1993) Castric-Fey et al. (2001) in association with filter feeders that are promoted by strong currents (Gili and Coma 1998), like the cirriped *Balanus* spp. and the sponge *Dysidea fragilis*; and (3) a highly turbid water community, where kelp was rare or absent, and *Sargassum muticum* and *Solieria chordalis* grew in association with the silt cover-tolerant algae *Ulva* sp. (Castric-Fey et al. 2001), *Gracilaria multipartita*, *Chondracanthus acicularis* and *Chondria dasyphylla*. Suspended matter favors filter feeders (Saiz-Salinas and Urkiaga-Alberdi 1999) among which some are typical circalittoral species, like the Cnidarians *Aiptasia mutabilis*, *Bougainvillia muscus*, *Nemertesia ramosa*, *Nemertesia antennina*, *Hydrallmania falcata*, the Ascidians *Aplidium*

elegans and *Morchellium argus*, the porifera *Tethya aurantium* and *Polymastia penicillus* the annelida *Sabella spallanzanii* and the echinodermata *Ophiothrix fragilis*.

In extreme conditions (high temperature or turbidity), the disappearance of kelp forests would represent a loss in habitat function and that might cause a shift in the composition of the understory species (Britton-Simmons 2004). This transition would be marked by the disappearance of species characteristic of kelp forests, like *Plocamium cartilagineum*, *Delesseria sanguinea* (Maggs and Hommersand 1993; Kitching, 1941), Corallinacea, and *Meredithia microphylla* (Castric-Fey et al. 2001; Castric-Fey 1988). Conversely, it might promote the appearance of algae tolerant to turbidity and silt cover, like *Chondria dasyphylla*, *Ulva* sp., and *Gracilaria multipartita* (Cabioc'h et al. 1992; Francis et al. 2010), in association with typical circalittoral fauna (*Nemertesia ramosa*, *Nemertesia antennina*, *Hydrallmania falcata*), which is favored by high concentrations of suspended matter in water.

The present study provided quantitative, multiscale data on kelp bed community structure (algal belt depth limits, biodiversity, interspecific competition, and biogeography) at regional and local scales. Perennial monitoring of these communities would provide an opportunity to study local issues (coastal construction, dredge spoils disposal, marine aggregates extraction) and estimate their impact on subtidal communities. The disappearance of kelp species (for example, due to eutrophication, dredge disposal, surface run-off, the extraction of marine aggregates, harvesting, or climate change) would strongly impact the species associated with the kelp forest (Moore 1973; Sheppard 1976; Edwards 1980; Cowen et al. 1982; Dayton 1985; Breeman 1988; Schultze et al. 1990; Eckman and Duggins 1991; Vadas and Elner 1992; Kennelly and Underwood 1993; Méléder et al. unpublished data; Blight and Thompson 2008). A decline of the kelp biotope would have extensive, dramatic consequences (Müller et al. 2009); for example, it would decrease the exported biomass formed by organic matter from kelp degradation (Thrush 1986), and it would

decrease the number of mobile organisms that inhabit the kelp forest. These changes would dramatically impact other afferent functionally linked coastal ecosystems. Thus, kelp beds, due to their contributions to habitat function and harvesting, require special care. Several kelp species meet their survival temperature limit near Brittany coastline (*Laminaria hyperborea*, *Laminaria ochroleuca*, *Laminaria digitata*, *Alaria esculenta* and *Saccharina latissima*) (Lüning 1990; Birkett et al. 1998) that give interest of such monitoring in this transition region in an oceanic warming scenario (Müller et al. 2009).

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