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Dinard Herbarium: a source of information to infer temporal changes in seaweed communities?

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Abstract – Recent changes in seaweed communities due to rapid shifts of their environment have been largely documented in temperate waters; however, long-term studies are much scarcer. In this study, we investigated the potential of Dinard Herbarium to inform us on temporal changes in seaweed communities of Brittany since the second half of the 19th century. From nearly 3000 specimens collected in France, we identified and, when possible, corrected taxonomic and localisation errors usually encountered in unchecked natural history collections therefore minimising data inaccuracies. This original study aimed to describe the temporal dynamics of this collection and discuss the relevance of Dinard Herbarium in assessing temporal changes in seaweed communities of Brittany. The use of herbaria to assess spatio-temporal changes of seaweed biodiversity is limited, and to our knowledge, this is the first study trying to investigate this potential in the European Atlantic. This work presents new perspectives for inferring temporal changes of seaweed biodiversity.

Macroalgae / natural history collections / community ecology / Brittany / environmental change

INTRODUCTION

While the marine realm has long be considered as having consistent environmental conditions with few variations, research studies, over the past decades, have contributed compelling evidence of climate warming in the ocean. The IPCC (Intergovernmental Panel on Climate Change) has reported an increase of SST (Sea

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Surface Temperature) in the global ocean of 0.13°C per decade; however, the warming is heterogeneous at the surface of Earth and some regions are more affected than others. For instance, SST in the North-East Atlantic has risen at rates ranging from 0.3 to 0.8°C per decade (Lima & Wethey, 2012). Along the European Atlantic coastline, Brittany is at the confluence of two biogeographic provinces, the Lusitanian province in the south and the Northern European Seas province in the north (Spalding *et al.*, 2007). In Brittany, the extent of seawater warming reached 0.36°C per decade over the last twenty years for the whole region and showed uneven warming: the Normano Breton golf and South Brittany were the most affected areas whereas the Iroise Sea was the area where the least warming occurred (Gallon *et al.*, 2014).

Rapid environmental change is a threat to the functioning of marine ecosystems. Increased temperatures are expected to influence the distribution of species, community structure, and ecosystem functioning (Harley *et al.*, 2006; Brierley & Kingsford, 2009; Sunday *et al.*, 2015). Interestingly, seaweeds do not follow the general trends of most of the specific diversity in the intertropical regions but are more diverse in the temperate regions (Kerswell, 2006; Keith *et al.*, 2014). In addition, future changes in SST are predicted to have a particularly important impact on flora in biogeographical transition regions of temperate waters (Bartsch *et al.*, 2012). Algal flora is therefore highly diverse and under threats in temperate waters; over recent years vast numbers of reports have evidenced changes in European seaweeds flora (Fredriksen *et al.*, 2014; Husa *et al.*, 2014; Yesson *et al.*, 2015; Sjøtun *et al.*, 2015), including that of Brittany (Gallon *et al.*, 2014). Most of these studies relied on recently collected floristic data; however natural history collections constitute an alternative source of data that have been accumulated over long periods of time (more than two centuries).

Natural history collections are specimen-based records that describe the spatio-temporal distribution of known taxa and constitute an important source of information regarding the distribution of biodiversity; they have been described as useful to evaluate the dynamics of biodiversity (Ponder *et al.*, 2001). However, the use of natural history collections to infer temporal changes in biodiversity has been criticised for their limitations due to, among other issues, the absence of documented sampling strategies and differences in sampling design among time and space resulting from the *ad hoc* nature of the collection effort (Ponder *et al.*, 2001), addressing the comprehensiveness of those records. Therefore, records from natural history collections can present spatial, environmental, temporal and taxonomic biases in addition to taxonomic and/or spatial errors (Soberón *et al.*, 2000; Graham, 2004). When properly analysed, natural history collections can be an invaluable tool in documenting changes in biodiversity (Shaffer *et al.*, 1998). As such, a few recent studies have emphasised the value of algal herbarium to conduct diachronic studies to infer the dynamic of seaweeds flora (Wernberg *et al.*, 2011; Nelson *et al.*, 2013).

The Muséum national d'Histoire naturelle in Paris is one of the most ancient (established in 1793, formerly 'Jardin du Roy' established in 1635) and important repositories of natural history collections in the world. In particular, it accommodates the National Herbarium which contains more than 8 million of specimens, including seaweeds. Unfortunately the algal "Herbier de France" is not databased yet, therefore hampering the use of this collection to serve as a source of data within this study. However, in light of the importance of marine stations to study local diversity, we have chosen to study the Herbarium from the Dinard Marine Station (Lamy *et al.*, 2016, this issue), which mostly includes specimens from Brittany, to assess its suitability in documenting temporal changes in seaweed communities of this region.

MATERIALS & METHODS

The 2959 specimens of the Dinard Herbarium collected in France were first re-examined to confirm or determine their taxonomic names. For taxa for which we had experts in the laboratory (indicated in Table S2), all specimens were re-examined one by one carefully, under the microscope when necessary. For the other taxa, we trusted the identification indicated on the sheets. In all cases, taxon status was further checked using the ERMS Taxon Match Tool (http://www.marbef.org/data/aphia.php?p=match; accessed on January 7th, 2015) and taxonomic names were corrected where necessary. Then, for each specimen, all information available on the sheet was entered in the MNHN database SONNERAT. Information relevant to this study included taxon's name, collector's name, collection site and collection date. Specimens with no or vague indication regarding the collection site were discarded. For the remaining specimens, the locality corresponding to the collection site was identified and georeferencing was achieved by assigning the GPS coordinates of the locality identified using the GeoNames referential (http://www.geonames.org/) completed by a search on Google Earth when necessary (http://www.google.com/earth/download/ge/) to each specimen. Of the 2959 specimens, 2281 were kept for further analyses, corresponding to specimens collected in the four departments of Brittany (Ille-et-Vilaine, Côtes d'Armor, Finistère and Morbihan) and in one department of Normandy (Manche). For each taxon, we computed the number of specimens collected; we defined common taxa as taxa represented by more than 20 specimens.

In order to investigate the temporal dynamic of the collection, we calculated the cumulated number of collected specimens over time for the 1928 specimens for which a collection date was available. Then, we characterised the Dinard Herbarium at the main collection periods previously identified by i) calculating the number of specimens by taxon and the percentage of common taxa, ii) identifying the different sites of collection and iii) characterizing the collectors.

Finally, the relevance of this collection in assessing temporal changes in seaweed communities of Brittany was investigated using two approaches. First, to allow comparisons of community composition among different periods, we identified spatial units with more than thirty specimens sampled by period. To that purpose, we projected our sites within a grid and tested different spatial resolutions by decreasing pixel resolution: pixel 0.00833*0.00833° (*i.e.* grouping all sites within a pixel of $\simeq$0.6 km * 0.6 km), pixel 0.01666*0.01666° (*i.e.* grouping all sites within a pixel of $\simeq$1.2 km * 1.2 km), pixel 0.03332*0.03332° (*i.e.* grouping all sites within a pixel of $\simeq$2.4 km * 2.4 km), pixel 0.06664*0.06664° (*i.e.* grouping all sites within a pixel of $\simeq$4.8 km * 4.8 km) and pixel 0.13328*0.13328° (*i.e.* grouping all sites within a pixel of $\simeq$9.6 km * 9.6 km). Secondly, we examined the possibility of constructing *a posteriori* distributions of species through time using species distribution models (SDMs). To that purpose, we looked for historical measures of sea surface temperature, an environmental variable highly relevant to characterise the niche of seaweed species (reviewed by Eggert (2012)) which has been used in several SDMs studies (e.g. Martínez *et al.*, 2012, Jueterbock *et al.*, 2013, Raybaud *et al.*, 2013, Gallon *et al.*, 2014) and we checked if they could be used in combination with records from the Dinard Herbarium to build SDMs. The aim of this second approach was to complete the observed distributions of seaweed species by modelled distributions of seaweed species, leading to a thorough representation of spatio-temporal variability in community composition.

RESULTS

The 2281 specimens analysed were collected in 83 sites located in Brittany and Normandy (Fig. 1). The collection effort differed greatly among sites, ranging from one specimen per site (for 28 sites) to 448 specimens collected at Cherbourg (mean ± standard error = 26.6 ± 8.3). Among the specimens 362 taxa were recorded; the mean number of specimens by taxon was 6.3 (± 0.3) and varied from one for 63 taxa to 37 for *Cryptopleura ramosa* (Fig. 2, Table S2). Nine common taxa were defined (Figs 3-11) among which, six Rhodophyta (*C. ramosa*, *Chondrus crispus*, *Plocamium cartilagineum*, *Palmaria palmata*, *Phycodrys rubens*, *Rhodophyllis divaricata*, *Hypoglossum hypoglossoides*), one Ocrophyta (*Fucus vesiculosus*) and one Chlorophyta (*Ulva clathrata*).

The collection effort was not homogeneous through time but concentrated in three main periods (Fig. 12): 1843-1866 (T1), 1910-1931 (T2) and 1949-1967 (T3). Interestingly, the First World War (1914-1918) corresponded to a period of intense collection while no specimens were collected during the Second World War (1939-1945). The number of specimens, the number of species and the number of specimens per species fluctuated among the three main periods of collection (Fig. 13); this last ratio was minimal at T1 (less than two specimens per species), increased at T2 (around four specimens by species) and decreased at T3 (around 2 specimens by species). The relative frequency of common taxa (*i.e.* taxa represented by more than 20 specimens) followed the same trend, with 5.1% of common taxa at T1, 14.1% at T2 and 6.8% at T3 (Fig. 14). The geographic provenance of specimens differed across the three main periods of collection (Fig. 15). Indeed, specimens were mainly sampled in the Manche department at T1, in particular near Cherbourg (orange pixel) and near Saint-Vaast-la-Hougue (green pixels). At T2, specimens were mostly sampled in three zones of Brittany: near Dinard (next to the Dinard and marine laboratory, eastern-most red pixel), Ile-de-Bréhat (orange pixel) and Roscoff (next to the Roscoff marine station, western-most red pixel). Finally, at T3, most specimens were collected near Dinard (green pixel). The collectors involved in specimen collection also varied across time (Table 1): at T1, Gustave Thuret contributed the most to the collection (although there was no indication regarding the collectors for more than 90% of the specimens collected during this period) whereas at T2 and T3, Robert Lami was the main collector.

One site was sampled at both T1 and T2 (Saint-Vaast-la-Hougue, Fig. 1), although with less than 30 specimens by period. Thirteen sites were sampled at both T2 and T3, among which only Saint-Malo (near Dinard and Saint-Servan marine laboratories, Fig. 1) presented more than 30 specimens by period (Table S3). No site was sampled at both T1 and T3. Decreasing spatial resolution from site to pixel 0.13328*0.13328° did not reveal additional spatial units with more than 30 specimens by period. We found historical measures of sea surface temperature and other sea surface related measurements spanning the period 1800-2007 (Woodruff *et al.*, 2011). However, these measures were available at 2*2° resolution which was a far too low resolution to consider doing SDMs in our study area.

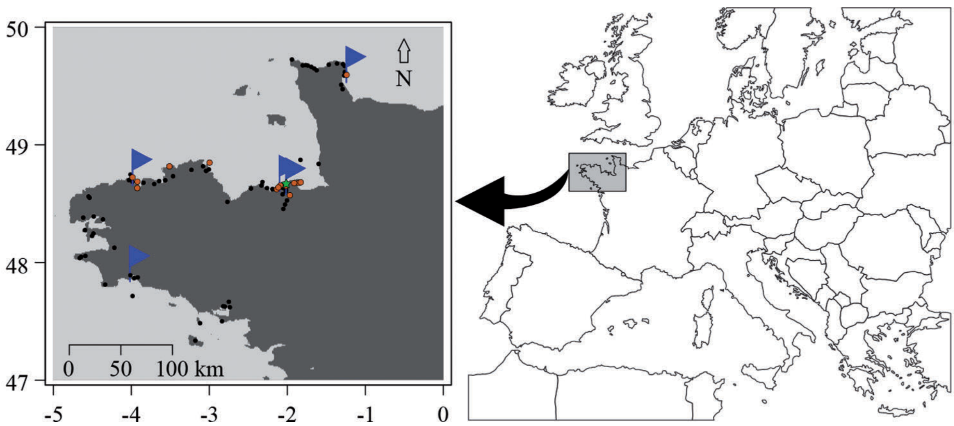


Fig. 1. Map showing the localisation of the 83 sites (black dots) of Brittany and Normandy where specimens from the Dinard Herbarium were collected; orange dots represent sites sampled at several periods, the green star indicates Saint-Malo which was sampled at two different periods with more than 30 specimens by period and blue flags indicate marine stations (from East to West and North to South: Tatihou marine station, Saint-Servan marine laboratory, Dinard marine laboratory, Roscoff marine station, Concarneau marine station).

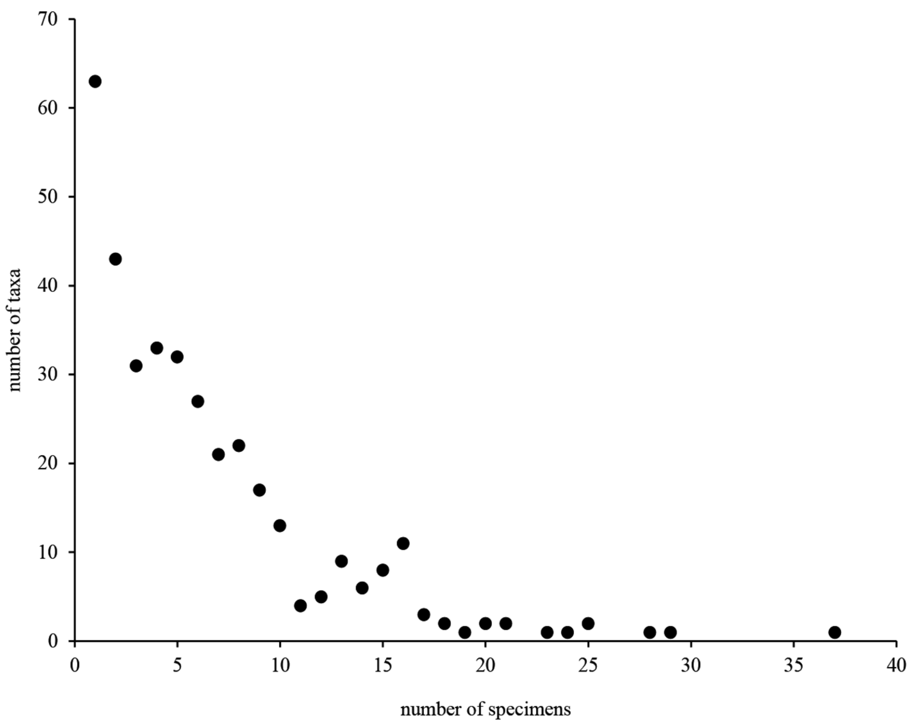
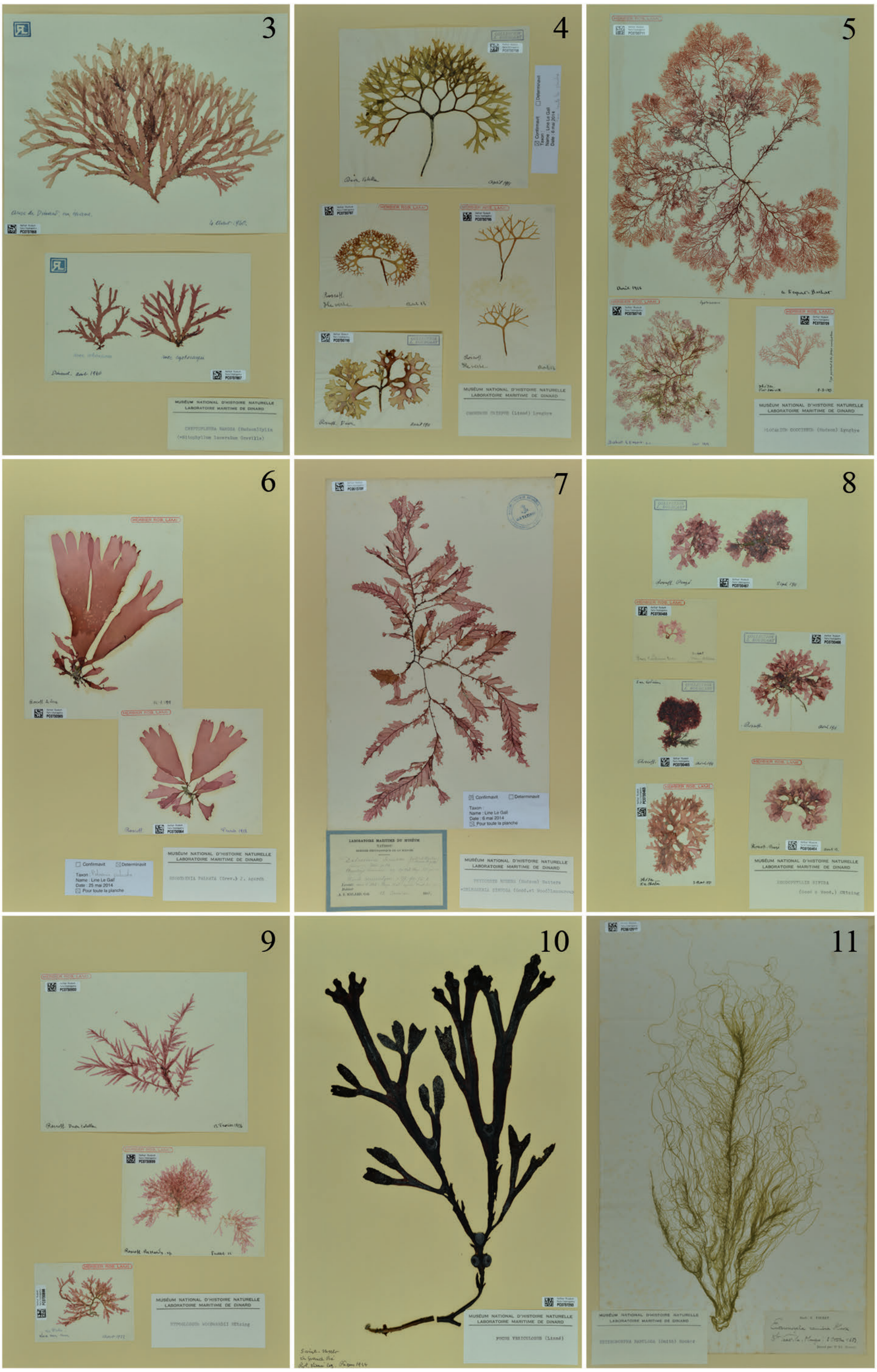


Fig. 2. Graph representing the number of taxa as a function of the number of specimens.

Table 1. Contribution of the different collectors to Dinard Herbarium across the three main periods of collection (in percentage of specimens collected by period); when known, dates of birth and eventually death of the collectors are indicated in brackets

Collector	*T1 1843-1866*	*T2 1910-1931*	*T3 1949-1967*
Bourcart Jacques (1891-1965)	0	0.2	0
Chemin Emile (1876-1945)	0	4.3	0
Chesné	0	0	0.3
Choy	0	0.1	0
Czarnorska	0	0.1	0
de Virville Adrien Davy (1895-1967)	0	0.2	0
Delepine René	0	0	0.3
Delphy Jean (1887-1961)	0	1.3	0
Fischer-Piette Edouard (1899-1908)	0	0.1	0
Gehu Jean-Marie (1930-2014)	0	0	1.0
Hamel Gontran (1883-1944)	0	8.4	0.3
Hamel-Joukow A.	0	0.1	0
Lami Robert (1889-1983)	0	51.1	48.3
LeJolis Auguste (1813-1904)	0.3	0	0
Magne Francis (1924-2014)	0	0	0.3
Mail (unidentified collector)	0	0.2	0
Mangin Louis (1852-1937)	0	3.7	0
Meslin Roger	0	0	1.7
Parriaud Henri (?-2010)	0	0	0.3
Pelletier André (1902-1985)	0	0.1	22.3
Pelvet François Alexandre (1801-18882)	0.5	0	0
Priou Marie-Louise (1916-2012)	0	0	10.1
Quillet Marcel (1898-?)	0	0	1.4
Rayss Tscharna (1890-1965)	0	0.2	0
Thuret Gustave (1817-1875)	4.7	0	0
Unknown	94.5	29.9	13.7

Figs 3-11. Photos of specimens representing common taxa from Dinard Herbarium (*i.e.* represented by more than 20 specimens): **3.** *Cryptopleura ramosa,* **4.** *Chondrus crispus,* **5.** *Plocamium cartilagineum,* **6.** *Palmaria palmata,* **7.** *Phycodrys rubens,* **8.** *Rhodophyllis divaricata,* **9.** *Hypoglossum hypoglossoides,* **10.** *Fucus vesiculosus,* **11.** *Ulva clathrata.* ▶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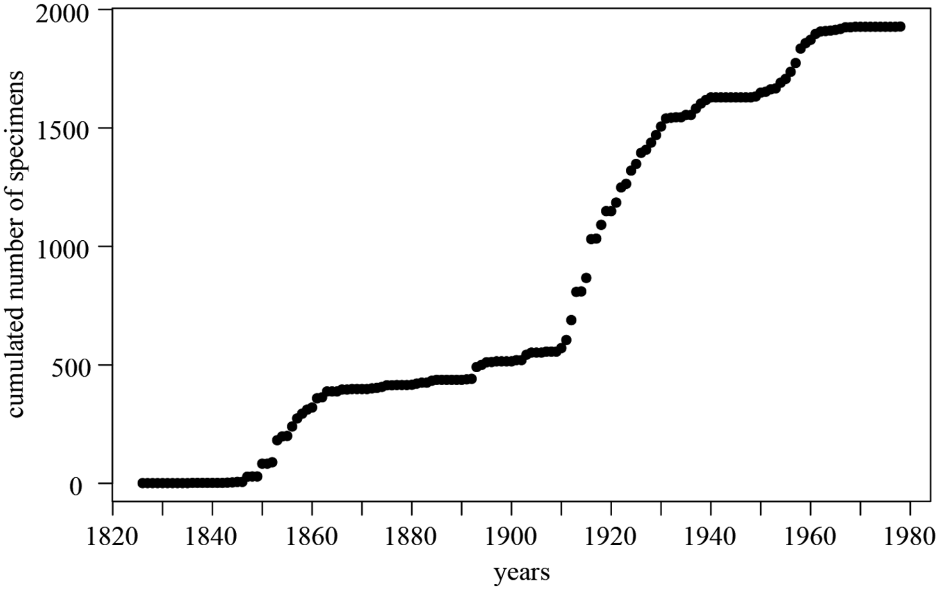

Fig. 12. Graph illustrating the cumulated number of collected specimens from 1826 to 1978.

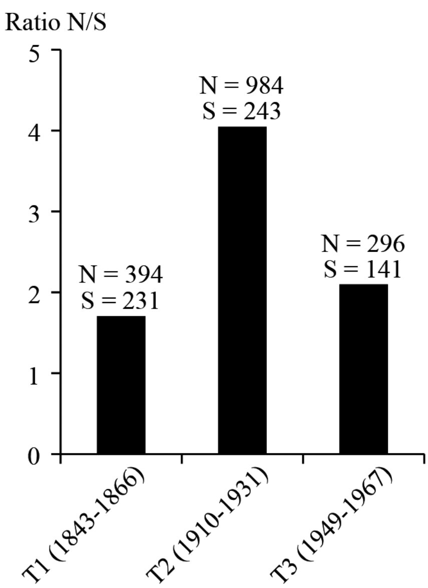

Fig. 13. Variation of the number of specimens (N), the number of species (S) and the number of specimens by species (bars) across the three main periods of collection.

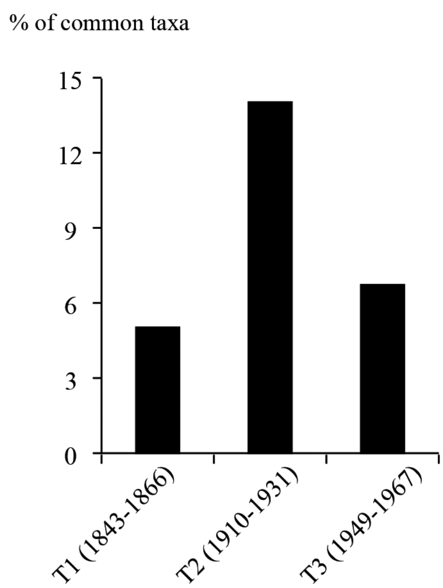

Fig. 14. Variation of the percentage of common taxa across the three main periods of collection.

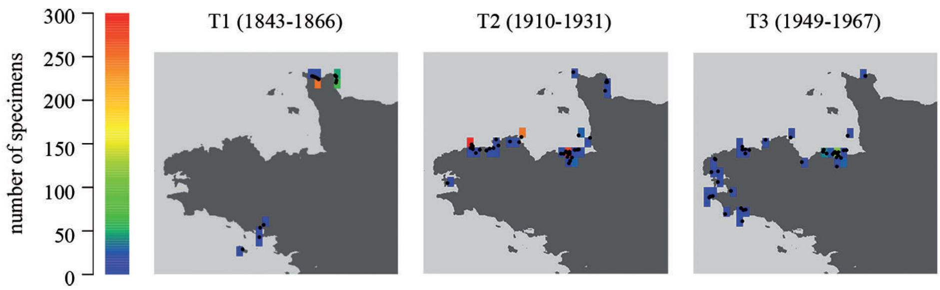

Fig. 15. Maps illustrating the sampling sites (black dots) and the number of specimens sampled in 0.13328*0.13328° pixels (coloured pixels) at the three main periods of collection.

DISCUSSION

Temporal dynamics of Dinard Herbarium: a reflection of the history of phycology?

Specimens constituting Dinard Herbarium were mainly collected during three periods: 1843-1866, 1910-1931 and 1949-1967. The quantity of specimens, the taxa collected, the regions of interest and the collectors involved varied among these three periods and reflect the activity of the "itinerant" marine laboratory which is now in Dinard (see companion paper of Lamy *et al.*, 2016). Between 1843 and 1866, the marine laboratory was not yet created; however, phycologists such as Gustave Thuret and Edouard Bornet produced a comprehensive collection from the Manche department, particularly around Cherbourg and Saint-Vaast-la-Hougue. Their aim was to collect as many taxa as possible, therefore they collected mostly one or two specimens per taxa and showed a limited interest for common taxa. At that time, they did not indicate their names on the collected specimens from this region which were later integrated in Dinard Herbarium: in 1892 Edouard Bornet gave the duplicate specimens he collected in the region with Gustave Thuret to the marine station of Tatihou.

The second period of intense collection occurred afterward the installation of the marine laboratory in Tatihou (1888) and encompassed the move of the marine laboratory from Tatihou to Saint-Servan, at the entrance of the Rance estuary (1923). Between 1910 and 1931, specimens were mainly collected by the phycologist Robert Lami. His collection consists of two periods. During the first period, specimens were mainly collected at Roscoff (around the Roscoff marine station, another well-known marine laboratory belonging at that time to La Sorbonne University, currently Université Pierre et Marie Curie) and in Ile-de-Bréhat. The second period started after the installation of the marine laboratory in Saint-Servan, and specimens were mainly collected around this laboratory, in the Rance estuary. During this second period, the sampling strategy was no longer to get the most taxa possible but rather to characterise species living in different habitats and their temporal variation; this biocenotic approach is reflected in the collection by an increase in the number of specimens per taxa collected as well as a more pronounced interest for common taxa. Between the second and third period of intense collection, only a few specimens were collected and none during the Second World War Two (1939-1945), which can be explained by the proximity of the war zones of Saint-Malo.

Robert Lami was also the main collector during the third period of intense collection (1949-1967), after the transfer of the marine laboratory from Saint-Servan to Dinard, a few kilometres further along the other riverbank of the Rance estuary (1935). He was appointed assistant director of the Dinard marine laboratory in 1957. During this third period of intense collection, specimens were mainly collected in the Rance estuary; the number of specimens collected by taxon and the interest for common taxa appear similar to the first period, perhaps reflecting the teaching activity of the station.

Relevance of Dinard Herbarium to assess temporal changes in seaweed communities of Brittany

Dinard Herbarium presents a high number of specimens over three temporal periods of about 20 years each, together covering the end of the 19th century as well as the first two thirds of the 20th century. Therefore, using Dinard Herbarium as representative of the composition of seaweed communities along the Brittany coastline through the three periods seems feasible, under two conditions. First, community composition must be described by indices that are not strongly sensitive to the biases identified in this study (Figs 13-14). A solution is to use the community temperature index (CTI, Devictor *et al.*, 2008), an index which lies on the thermal niche of species (Julliard *et al.*, 2006). Indeed, there is no reason that collectors preferentially sampled cold or warm species. The use of CTI to describe the evolution of seaweed communities along the Brittany coastline could therefore document the way these marine communities are tracking climate change as has been done for terrestrial taxa (Devictor *et al.*, 2012). The second condition for using Dinard Herbarium as representative of the composition of seaweed communities through time is to find zones that were sampled at different periods with sufficient coverage. Our analysis revealed only one zone corresponding to this second criterion: the Rance estuary, and in particular, in Saint-Malo. One zone is clearly not enough to investigate how seaweed communities have tracked climate change; therefore, we could not go further towards this objective using solely the Dinard Herbarium.

When natural history collections do not comprehensively reflect the actual distribution of species, as is the case for Dinard Herbarium, they can still be used to model species' distributions, an approach which has received growing attention in the last fifteen years (reviewed by Newbold (2010)). In our study, we identified that modelling the distribution of several species and projecting them conjointly along the Brittany coastline at the three main periods of collection could be a solution to following the spatio-temporal evolution of seaweed communities. This second approach is also subject to two conditions. First, data from natural history collections can be used for modelling species distributions only if they do not present an environmental bias, *i.e.* if records come from places with different environments. The second condition for using this approach is to have environmental data that accurately describe the niche of the species. Therefore, both conditions are dependent on the availability of environmental data for the zone and the period corresponding to specimens' collection. In our study, we found measures of sea surface temperature, which has been shown to be a good predictor of species distribution for several seaweeds (e.g. Martin-Lescanne *et al.*, 2010; Jueterbock *et al.*, 2013; Raybaud *et al.*, 2013; Gallon *et al.*, 2014), for the period 1800-2007 (Woodruff *et al.*, 2011). However, we were unable to model this further since these measures were only available at 2*2° resolution, a far too low resolution to consider doing SDMs at the scale of the studied area which only encompasses five degrees in longitude and three in latitude. Furthermore, sea surface temperature in Brittany varies on a much smaller spatial scale (Gallon *et al.*, 2014). Therefore, using records from Dinard Herbarium to build SDMs and follow the temporal evolution of seaweed communities is currently limited by the availability of environmental data at an appropriate spatial resolution for our period of study.

Conclusions

The aim of the present study was to assess whether the Dinard Herbarium could be a source of information to infer temporal changes in seaweed communities. We first highlighted that the temporal dynamics of Dinard Herbarium reflects the history of phycological activities around the marine station. Therefore, records of this collection present inherent spatial, temporal and taxonomic biases. These identified biases do not prevent the study of temporal changes in seaweed communities as long as community composition can be described by indices that are not strongly sensitive to those biases. This implies to either study zones that were sufficiently sampled at different periods or to model the distribution of several species and projecting them conjointly at different periods. Our study of Dinard Herbarium only revealed one zone sufficiently sampled at different periods and modelling species distributions was hampered by the lack of historical environmental data such as sea surface temperature which are not currently available at an appropriate resolution. Therefore, none of the prerequisites were met in our study to assess temporal changes in seaweed communities of Brittany using the sole Dinard Herbarium. However, our study highlights the prerequisites necessary to use herbaria records to document temporal changes in seaweed communities.

Perspectives for inferring temporal changes of seaweed biodiversity in Brittany

Using herbaria to document temporal changes in communities has proven useful in showing that seaweed communities were in retreat from ocean warming in temperate Australia (Wernberg *et al.*, 2011). The main differences between the Australian study and ours are the number of records used and the extent of the period studied: Wernberg *et al.* (2011) used more than 20 000 records covering 70 years (1940-2009) while we used less than 3000 records covering 125 years (1843-1967). This suggests that the number of records is an important determinant of success when studying temporal changes in communities with herbaria records. In the Muséum national d’Histoire naturelle of Paris, numerous herbaria records of seaweeds exist, and they could be used to complete records from Dinard Herbarium in order to follow the temporal evolution of seaweed communities along the Brittany coastline. The main issue regarding these records is that collection data is reported on labels, often hand written, and these still have to be computed on a data base. Given the potential of these records for inferring temporal changes in seaweed communities, we believe that computerising seaweed herbaria records from the Muséum national d’Histoire naturelle of Paris (in addition to the already computerised Dinard Herbarium) should be a priority.

Perspectives also exist regarding the construction of SDMs with herbaria records to follow the temporal evolution of seaweed communities in Brittany. The main limitation is the availability of historical data on sea surface temperature at high resolution. Though these data may not currently be available, there are increasing amounts of downscaled environmental data being made available helping our understanding of the drivers of biodiversity change at local scales (e.g. van Vuuren *et al.*, 2007). An alternative could be to use historical land temperature and/or more recent measures of sea surface temperature, which are available at much higher resolution than currently available measures of historical sea surface temperature.

Finally, while we showed that using records of Dinard Herbarium only to document temporal changes of seaweed biodiversity in Brittany at the community level was limited, we nonetheless produced a list of taxa that were sampled in Saint-Malo during the period 1910-1931 and not sampled again during the period 1949-1967, *i.e.* possibly locally extinct taxa. This area has been affected a lot by different pressures in the second half of the 20th century, notably by important seawater warming (Gallon *et al*., 2014) and the installation of a tidal power station on the Rance estuary (built between 1962 and 1966 and active ever since). This work valorises and makes accessible a list of taxa which constitutes one of the rare existing datasets on benthic community composition before the installation of the tidal power. Therefore, this study can serve as a basis to conduct new taxon-orientated sampling, inluding repeated surveys to estimate detection probabilities (Tingley *et al*., 2009), and possibly document local species extinctions in relation with the different aforementioned pressures.

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