



Contrasted trends of intertidal macroalgal communities and sharp decline of canopy-forming species across two decades

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ABSTRACT: Macroalgal communities are essential to coastal ecosystems, yet increasing effects of global change and anthropogenic pressures are leading to their global decline. Investigating the long-term dynamics of these communities across different localities appears crucial to better understand their responses to such pressures, as our knowledge of spatial heterogeneities in macroalgal trajectories remains elusive. To fill this gap, the community trajectory analysis framework provides a set of innovative multivariate metrics to characterize and quantitatively compare the temporal dynamics of different communities. Using long-term monitoring data (2004–2022), this method was applied to intertidal macroalgal communities across 10 locations distributed over more than 500 km of coastline in Brittany, France. Three distinct temporal dynamics were identified. High-shore communities exhibited minimal changes over time, while low-shore communities were characterized by a fluctuating understorey species composition but a general stability pattern. In contrast, the mid-shore community dominated by *Ascophyllum nodosum* underwent conspicuous changes in composition and structure. Further analysis of the latter community unveiled clear spatial patterns, with a significant deterioration of the structural state attributed to canopy loss in eastern Brittany, negatively impacting understorey species. This decline may ultimately lead to massive changes in coastal ecosystem functioning and services. This study emphasizes the importance of maintaining long-term ecological monitoring as well as the pertinence of temporal trajectory methods to identify and understand community changes at various spatial scales.

KEY WORDS: Long-term monitoring · Community trajectory analysis · Macroalgal community · Rocky shore · Ecosystem engineer · Intertidal zone · Climate change

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1. INTRODUCTION

Coastal ecosystems are of increasing concern because they combine high ecological and socio-economic importance with high sensitivity to anthropogenic pressures and global changes (Harley et

al. 2006). Within these ecosystems, macroalgal-dominated habitats serve as vital components, delivering a multitude of socio-ecosystem services (Mineur et al. 2015). Macroalgal-dominated ecosystems rank among the most abundant and productive, accounting for a minimum of 20% of coastal pri-

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mary production (Duarte et al. 2022) while serving as an effective carbon sink (Pessarrodona et al. 2022). Additionally, large and perennial macroalgae create a complex 3-dimensional biogenic habitat, facilitating organism settlement and providing refuge and food sources (Teagle et al. 2017). Canopy-forming macroalgae are thus considered as ecosystem engineers, by modulating environmental factors and sheltering high biodiversity (Harley et al. 2012).

In the intertidal zone, chemo-physical gradients, caused by tidal cycles and hydrodynamics (Little & Kitching 1996), create an extremely challenging habitat for rocky shore inhabitants (Bird et al. 2013, Burel et al. 2020). The presence of canopy-forming engineer species exerts a buffering effect, especially by modulating physical disturbance, lowering light intensity, decreasing sub-canopy temperature, maintaining humidity and reducing water movements (Bertness et al. 1999, Bertocci et al. 2010). These modified environmental conditions facilitate the colonization of specific assemblages, leading to the formation of distinct communities (Colman 1940, Hurd et al. 2014). Hence, the facilitative effects of canopy-forming algae will likely play a central role in mitigating the effect of environmental variations on intertidal biodiversity (Bulleri et al. 2018), so that understanding the impact of global changes on their distribution and abundance is of utmost importance (Harley et al. 2006, Wernberg et al. 2024).

In the context of global change, the negative effect of abiotic stress on benthic communities might be exacerbated, altering not only species' geographical ranges but also their vertical repartition (Schonbeck & Norton 1978, Benedetti-Cecchi 2001, Miner et al. 2021). In the past few decades, canopy-forming macroalgae have shown clear regressions worldwide, to varying degrees depending on the structuring species and bathymetric level (Benedetti-Cecchi et al. 2001, Mangialajo et al. 2008, Crowe et al. 2013, Wernberg et al. 2019, Gorman et al. 2020, Muguera et al. 2020, Mieszkowska et al. 2021, Whalen et al. 2023). The loss of canopy-forming species would thus directly impact the associated assemblages by deeply modifying the habitat, leading to strong changes in coastal biodiversity and in the functioning of the ecosystem (Hawkins et al. 2009, Bustamante et al. 2017).

Despite their importance and accessibility, macroalgal communities represent one of the least studied biogenic habitats (Wernberg et al. 2024), and long-term intertidal macroalgal community data remain scarce in Europe (Mieszkowska et al. 2021). Yet, a decline in cold-temperate canopy-forming macroalgae has been documented along the coastlines of Spain

and England, particularly in regions reaching upper thermal tolerance limits of species without the concomitant arrival of functionally equivalent species (Álvarez-Losada et al. 2020, Mieszkowska et al. 2021).

While intertidal macroalgal community changes are thus documented along the coastlines of Spain and England, a critical gap in knowledge persists, especially in Brittany. Brittany offers a macro- to megatidal zone (with tidal ranges from 5 to 15 m) and a mosaic of habitats that fosters the emergence of substantial macroalgal biodiversity and biomass (Gallon et al. 2014). This results in the presence of up to 6 distinct intertidal macroalgal communities, characterized by the dominance of Fucales and Laminariales species, representing among the highest community diversity in Europe (Tittley 2002, Ar Gall et al. 2016, Burel et al. 2019a). Despite its functional and societal importance (Delaney et al. 2016), this rich area faces intense human pressures (Halpern et al. 2015, Bowler et al. 2020), including rapid ocean warming in relation to climate change (Burrows et al. 2011, 2019). Located at the convergence of 2 biogeographical zones (Dinter 2001), Brittany constitutes the range limit of numerous macroalgal species (Dizerbo 1969) and has been identified as a potential zone for substantial loss of Laminariales and Fucales (Jueterbock et al. 2013, Assis et al. 2018). This prompts a need for understanding and predicting the response of its high biodiversity across the past decades and in the future. The natural, scientific and anthropogenic contexts of Brittany provide a compelling setting to assess macroalgal community changes amid global change.

Long-term monitoring offers the opportunity to identify community trends, relate them to environmental variations and predict forthcoming changes (Magurran et al. 2010, Hughes et al. 2017). Most studies on temporal changes in macroalgal communities result in comparisons between several sampling periods scattered over time (e.g. Álvarez-Losada et al. 2020, Barrientos et al. 2020), which can impede our ability to accurately estimate global change impacts (Stuble et al. 2021). Long-term studies focusing on the biodiversity associated with macroalgae are scarce (e.g. Mieszkowska et al. 2021), resulting in an incomplete understanding of how the temporal trajectories of these habitats vary across space and environments. Recently, community trajectory analysis (CTA) has emerged as an innovative multivariate method adapted to the study of temporal community dynamics (De Cáceres et al. 2019). CTA quantifies community changes through the implementation of geometrical analysis on temporal trajectories, thus

enabling the characterization and comparison of temporal patterns in community dynamics.

Based on 2 decades of monitoring at the scale of the Brittany coastline, this study represents an unprecedented opportunity to quantify long-term dynamics of intertidal macroalgal communities, on a large temporal and spatial scale. It aims at detecting long-term trends in diversity patterns within each macroalgal community and comparing these dynamics at different spatial scales (community vs. regional), through trajectory analysis. We tested the 2 hypotheses: (1) strong horizontal variability would be found in community dynamics, expecting greater changes in high shore communities, as they are more exposed to environmental and anthropogenic stressors; and (2) changes in community state would follow a latitudinal gradient, with alterations occurring in southern sites where cold-temperate species reach the limit of their thermal range.

2. MATERIALS AND METHODS

2.1. Study area and communities

The study was carried out at 10 sites, distributed along the coast of Brittany (Fig. 1), that are part of a long-term monitoring focusing on macroalgal communities (REBENT programme, www.rebent.org): Berchis (Be), Bréhat (Br), Le Croisic (Cr), Le Dellec (De), Molène (Mo), Portsall (Po), Quiberon (Qb), Saint-Briac (SB), Sept-Îles (SI) and Trégunc (Tg).

Up to 6 different vertically distributed intertidal macroalgal communities can be found in Brittany (Fig. 2). These different macroalgal communities are characterized by 1 or 2 structuring *Fucales* or *Laminariales* species, arranged as follows: (1) *Pelvetia canaliculata* (Linnaeus) Decaisne & Thuret, 1845 dominates the highest shore level, followed by (2) *Fucus spiralis* Linnaeus, 1753. (3) In the mid-intertidal zone, *Asco-*

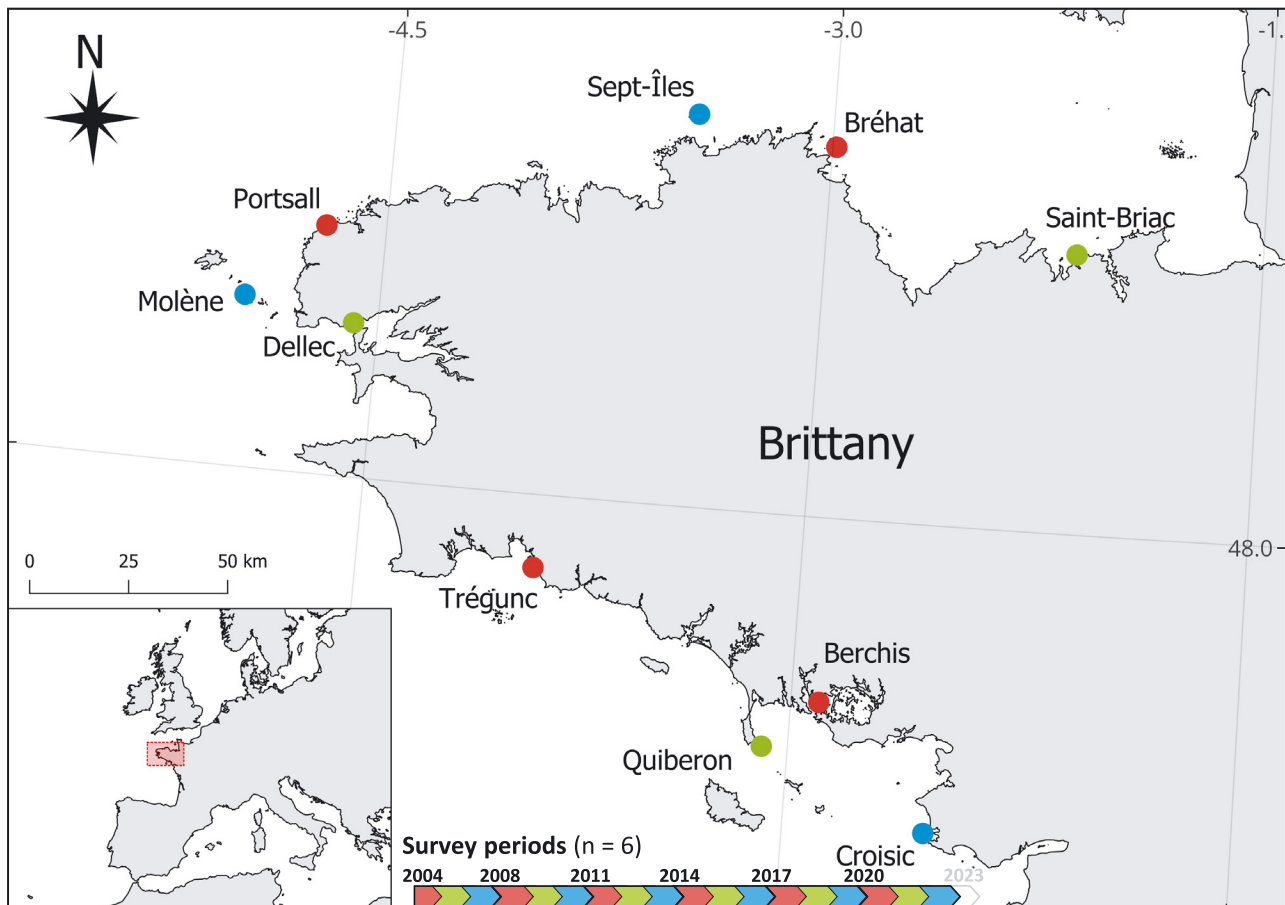


Fig. 1. Spatio-temporal design of the macroalgal community monitoring survey at 10 sites along the coast of Brittany (©IGN-Shom 2009). Each site was sampled 6 times beginning in 2004 with a 3 yr turnover involving 3 sampling series of sites. First sampling series (red): Bréhat, Portsall, Trégunc, Berchis; second series (green): Le Dellec, Quiberon, Saint-Briac; third series (blue): Le Croisic, Molène, Sept-Îles. The shapefile used to plot the maps is European coastlines (<https://www.eea.europa.eu/>)

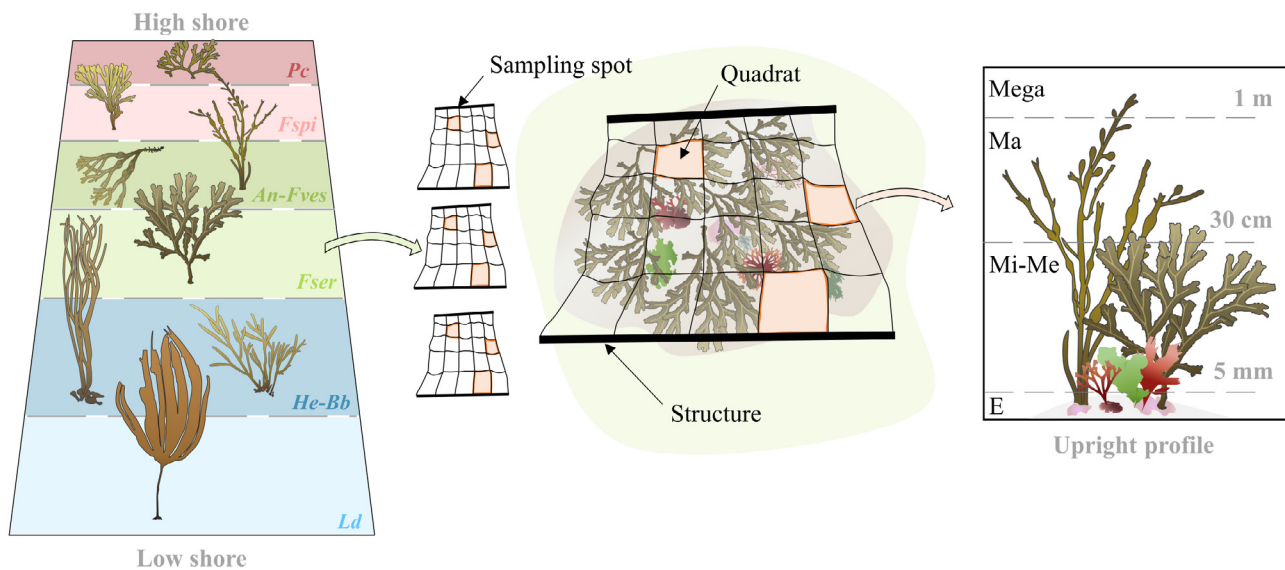


Fig. 2. Description of the sampling method used in the study. Samples were taken in 6 communities that were dominated respectively by *Pelvetia canaliculata* (Pc), *Fucus spiralis* (Fspi), *Ascophyllum nodosum*–*F. vesiculosus* (An-Fves), *F. serratus* (Fser), *Himantalia elongata*–*Bifurcaria bifurcata* (He-Bb) and *Laminaria digitata* (Ld). Three fixed spots were sampled in each community. Upright sampling takes into account the vertical (strata) and horizontal (cover percentage) development of each species and was applied in 3 quadrats of 33 × 33 cm randomly chosen in each sampling spot. Strata were defined as encrusting (E), micro- to meiobiotic (Mi-Me), macrobiotic (Ma) and megabiota (Mega)

phyllum nodosum (Linnaeus) Le Jolis, 1863 and *Fucus vesiculosus* Linnaeus, 1753 co-dominate. (4) *Fucus serratus* Linnaeus, 1753 structures a community also characterized by a large abundance of Rhodophyta species. (5) In the low intertidal zone, *Himantalia elongata* (Linnaeus) S.F.Gray, 1821 dominates in exposed areas and *Bifurcaria bifurcata* R.Ross, 1958 in sheltered areas. (6) The community at the lowest intertidal level is dominated by kelp, notably *Laminaria digitata* (Hudson) J.V.Lamouroux, 1813.

2.2. Sampling

During autumnal spring tides, each macroalgal community has been surveyed at low tide on foot every 3 yr at each site since 2004, when present and accessible (Fig. 1). The *L. digitata* community was absent from 3 sites (Berchis, Bréhat, Quiberon). During the whole study, the same 3 sampling spots (Fig. 2) were surveyed in each community (for a total of 18 sampling spots for each site), identified by photographs and GPS data. Non-destructive sampling was performed using a 1.65 × 1.65 m structure, laid flat on the rocky substratum, subdivided into 25 quadrats of 33 × 33 cm. Three quadrats were randomly chosen for each sampling spot. In each quadrat, all epilithic, epizoic and epiphytic algal species

were visually identified *in situ*. Benthic animal species are not considered in the present study, as their sampling began later in the monitoring process. If necessary, for species requiring microscopical observations, the minimum amount of biological material was collected and brought to the laboratory.

'Upright profile' sampling (Fig. 2) was used to describe both the horizontal and vertical extension of the canopy to mimic the 3D structure of an immersed macroalgal community (Burel et al. 2019b). For each taxon, the erect cover was visually estimated in each quadrat using adapted Braun-Blanquet percentage intervals (Braun-Blanquet 1932), i.e.]0–5[,]5–25[,]25–50[,]50–75[and]75–100]. Each interval is then referred to as its median value, namely 2.5, 15, 37.5, 62.5 and 87.5%, respectively. Individuals were also ranked according to the strata to which they belonged, depending on their size: encrusting, micro- to meiobiotic (<30 cm), macrobiotic (30 cm ≤ height < 1 m) and megabiota (≥ 1 m). For each sampling spot, the average species cover was computed from the 3 replicates and adjusted to the interval median cover. A taxonomic uniformization was performed to ensure a consistent taxonomic resolution: all taxa present in the database were re-evaluated by experts and their associated systematics were checked via AlgaeBase (Guiry & Guiry 2023).

2.3. Statistical analysis

This study uses a combined approach of descriptive analysis and trajectory analysis, enabling a comprehensive understanding of the overall changes in community composition, as well as a detailed examination of the dynamics at a finer scale over time.

2.3.1. Descriptive analysis

Mean species richness (S^*) is defined as the number of species/taxa per sampling spot averaged for each community. The index of community structure (Ics; Ar Gall & Le Duff 2014) was computed for each sampling spot at each sampling period. The Ics assesses the development and structural state of each macroalgal community, considering the cover of taxonomic, functional and size strata groups. Every computed index is presented with standard error ($\pm SE$).

2.3.2. Trajectory analysis

CTA is a statistical method used to quantify temporal changes across multiple variables (e.g. structure and composition of a community). In the CTA framework, each observation, or community state, is represented by its coordinates in a multidimensional space (Ω). This Ω space represents the dissimilarity between pairs of community observations (De Cáceres et al. 2019, Sturbois et al. 2021b). Here, the Ω space was defined using species cover, on which a Hellinger distance coefficient was computed, fulfilling the metric and Euclidean properties (Legendre & Gallagher 2001, Legendre & De Cáceres 2013). The Hellinger distance allows for both dampening the weight of dominant species and not giving excessive weight to the rare ones (Legendre & Gallagher 2001). Principal coordinates analysis (PCoA) was used to display trajectories in the multidimensional space and compute CTA metrics without distortion. A segment connects 2 consecutive observations, with an arrowhead pointing towards the most recent observation. For each community, all consecutive observations linked by different segments represent the temporal trajectory of the community (De Cáceres et al. 2019). Diverse CTA geometrical metrics can then be computed on these trajectories (including all dimensions of Ω) to describe and quantify community dynamics; here, the following metrics were used:

Segment length (SL) is given by the distance between 2 consecutive observations. This metric is rel-

evant to analyse the magnitude of the variability at each step of the community trajectories. It allows gradual or abrupt changes to be described. The maximum value for a segment is equivalent to the maximum of the Hellinger distance, which is $\sqrt{2} \approx 1.41$.

Trajectory path length (L(T)) is given by the sum of segment lengths belonging to a trajectory. This metric informs about the overall temporal variation of the community. With the Hellinger distance, the maximum value of the trajectory path length is $(n - 1) \cdot \sqrt{2}$, with n defined as the number of observations in a sampling unit. Here, 6 observations lead to a trajectory composed of 5 segments, giving a maximum trajectory path length value of $5 \cdot \sqrt{2} \approx 7.07$.

Net change (NC) is given by the distance between the initial state and any subsequent state of the trajectory. This metric allows the difference between the community at each time of the study period and its initial state to be evaluated. With the Hellinger distance, the maximal value remains $\sqrt{2} \approx 1.41$.

Statistical analyses were performed with the R programming language version 4.1.2 (R Core Team 2021) using the packages 'ecotraj' (De Cáceres et al. 2019, Sturbois et al. 2021b, 2022, 2023), 'ape' (Paradis & Schliep 2019) and 'adespatial' (Dray et al. 2021).

3. RESULTS

During the sampling period (2004–2022), 225 taxa were found across the 10 sites. More specifically, we identified 157 Rhodophyta, 37 Phaeophyceae, 27 Chlorophyta and 4 Cyanobacteria species.

3.1. Overall description of communities and associated dynamics

The community mean species richness (S^*) and structural state (Ics) increased along a bathymetric gradient from upper to lower intertidal zones (Fig. 3). High shore communities *Pelvetia canaliculata* (Pc) and *Fucus spiralis* (Fspi) exhibited the lowest mean species richness values ($S^*_{Pc} = 4.3 \pm 0.1$ and $S^*_{Fspi} = 6.7 \pm 0.2$ species per sampling spot) and a reduced structural state ($Ics_{Pc} = 0.63 \pm 0.01$ and $Ics_{Fspi} = 0.78 \pm 0.02$). Mean species richness reached a maximal value for the *Himanthalia elongata*–*Bifurcaria bifurcata* (He-Bb) community with $S^*_{He-Bb} = 19.3 \pm 0.4$ species per sampling spot, while the structural state value was maximal for the *Laminaria digitata* (Ld) community ($Ics_{Ld} = 1.30 \pm 0.03$). The variability in the distribution of mean species richness and Ics values across sites

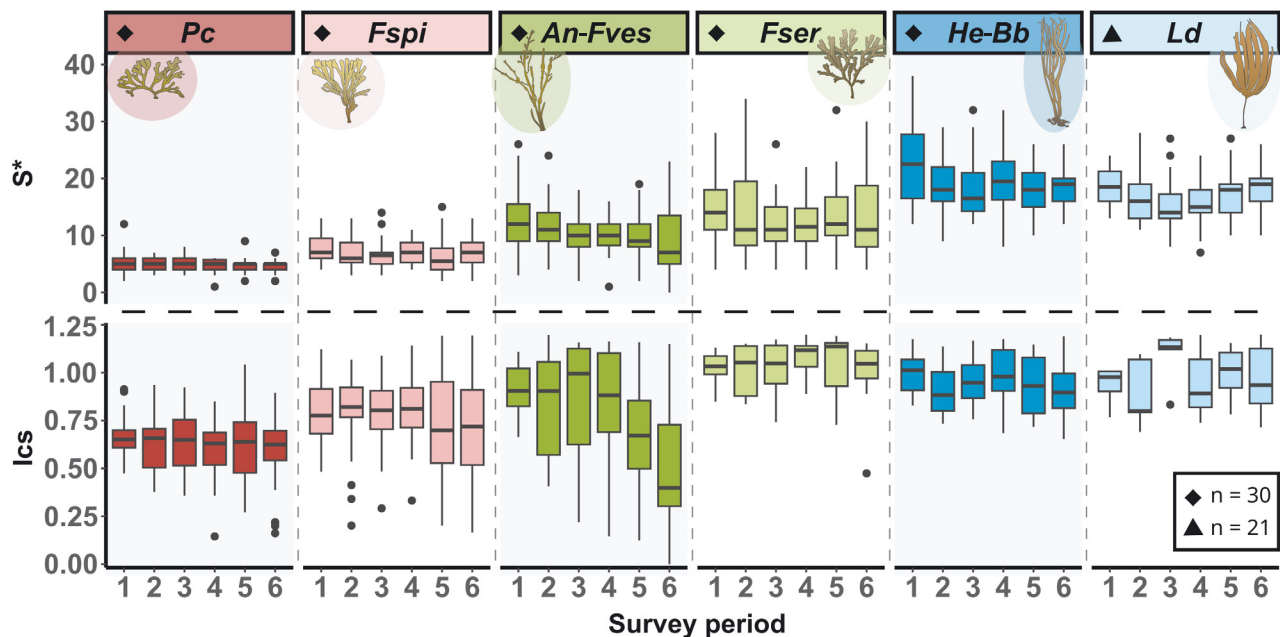


Fig. 3. Mean species richness (S^*) and index of community structure (Ics) per sampling spot for each community during each survey period (1: 2004–2007; 2: 2008–2010; 3: 2011–2013; 4: 2014–2016; 5: 2017–2019; 6: 2020–2022). Boxes represent values of the interquartile range, the thick band is the median value, whiskers represent values within 1.5 of the quartiles, and dots are outliers. Community abbreviations as in Fig. 2

and sampling spots was lower in high shore communities. Considering all communities, no conspicuous temporal trends were observed in the mean species richness. The same pattern was observed when considering the Ics for most communities. However, a strong decrease was observed in the *Ascophyllum nodosum* – *F. vesiculosus* (An-Fves) community from an initial $Ics_{An-Fves} = 1.27 \pm 0.05$ down to 0.78 ± 0.09 in the last sampling period. Over time, this decrease in the mean Ics values was also accompanied by increasing variability across sites and sampling spots.

3.2. Trajectory analysis of community dynamics

Community trajectories were highly variable across communities and sites (Fig. 4; Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m742p073_supp.pdf). High shore communities (*P. canaliculata* and *F. spiralis*) exhibited greater similarity between sites, as their trajectories were intricate (Fig. S1), similarly to trajectories of the mid-shore *F. serratus* (Fser) community. The *P. canaliculata* community, highest on shore, exposed the smallest changes over time (mean trajectory path length below 2.55 ± 0.15). On average, *F. serratus* community trajectories showed low net change (below 0.71 ± 0.03) and trajectory path length (below 3.06 ± 0.12) values.

Low shore communities (*H. elongata*–*B. bifurcata* and *L. digitata*) presented strong differences in community composition between sites (Fig. 4; Fig. S1), characterized by variations in the respective abundance within the prevalent species pool rather than species richness variations. Indeed, *H. elongata*–*B. bifurcata* and *L. digitata* communities presented some of the highest mean net changes across all time periods as well as high trajectory path length at the end of the survey (above 3.73 ± 0.08), indicating substantial community changes. In these 2 communities, however, mean net change values were stable over time at high levels (values ranging from 0.81 ± 0.02 to 0.94 ± 0.03) and even decreased between the second and third survey periods in the *H. elongata*–*B. bifurcata* community and between the fifth and sixth survey periods in the *L. digitata* community.

A discernible dynamic pattern only emerged for the mid-shore *A. nodosum*–*F. vesiculosus* community (Fig. 4; Fig. S1). At the end of the survey, the *A. nodosum*–*F. vesiculosus* community showed the highest mean net change (above 1.07 ± 0.04) and trajectory path length values (above 3.90 ± 0.09) compared to all communities (across both high and low shore). In contrast to *H. elongata*–*B. bifurcata* and *L. digitata*, the *A. nodosum*–*F. vesiculosus* community showed an increasing distance from the initial state over time (with the highest difference

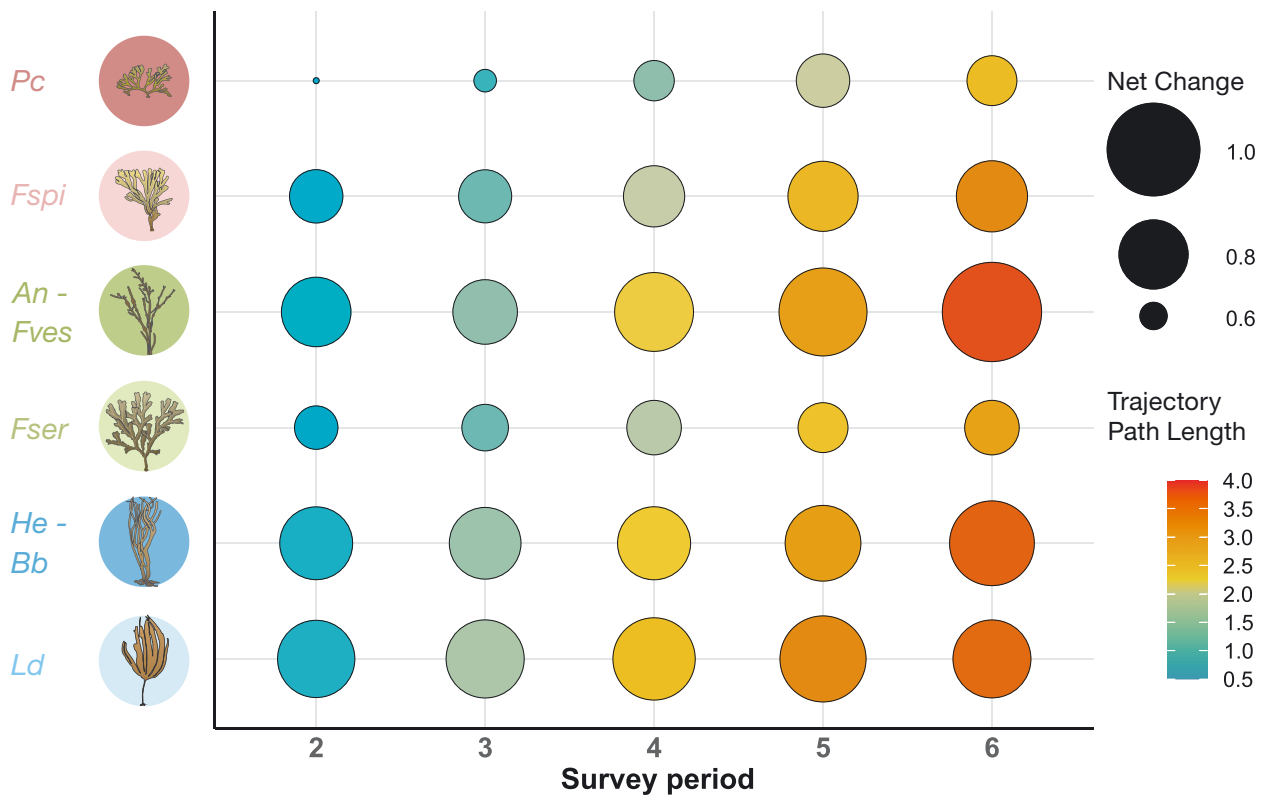


Fig. 4. Net change and trajectory path length mean values for each community computed for each survey period (2: 2008–2010; 3: 2011–2013; 4: 2014–2016; 5: 2017–2019; 6: 2020–2022). Trajectory path length (maximum ≈ 7.07 during the sixth survey period) and net change (maximum ≈ 1.41) are computed between the studied survey period and the initial one (2004–2007). Size of the points represents net change while their colour represents trajectory path length. Community abbreviations as in Fig. 2

between initial and final net change values), indicating departing trajectories. The *F. spiralis* community behaved similarly, albeit with lower magnitude of community change.

3.3. Focusing on the *A. nodosum*–*F. vesiculosus* community trajectory

For the *A. nodosum*–*F. vesiculosus* community, the first 2 axes of the PCoA respectively accounted for 21.6 and 9.6% of the total variance (Fig. 5). The first PCoA axis separates 2 groups of sites based on the dissimilarity between samples, with Sept-Îles and Saint-Briac grouped together on one side (highlighted in green) and Molène, Portsall, Bréhat and Trégunc (highlighted in orange) on the other. These 2 groups correspond to 2 different patterns of canopy-forming species: in Sept-Îles and Saint-Briac, *F. vesiculosus* was dominant, whereas *A. nodosum* was the main species in Molène, Portsall, Bréhat and Trégunc (Fig. S2). Community trajectories of these sites remained within the same dominance pattern from

their initial to their final state. In contrast, 4 sites, namely Berchis, Le Dellec, Quiberon and Le Croisic, all switched from an *A. nodosum* dominance to a community characterized by a total Fucales canopy loss (highlighted in blue in Fig. 5B).

3.4. Spatial variation in *A. nodosum*–*F. vesiculosus* dynamics

When mapped across the surveyed sites, the total trajectory net change and trajectory path length of the *A. nodosum*–*F. vesiculosus* community showed a strong spatial heterogeneity at the regional scale (Fig. 6). Western sites (Trégunc, Bréhat, Sept-Îles and Portsall) showed consistency in their community composition over time and were characterized by low net change values (mean values between 0.86 and 1.01) and low trajectory path length values (between 3.16 and 3.86). In contrast, southeastern sites (Berchis, Quiberon and Croisic) were characterized by the highest net change values (mean values above 1.22), close to the maximal net change value of 1.41. More-

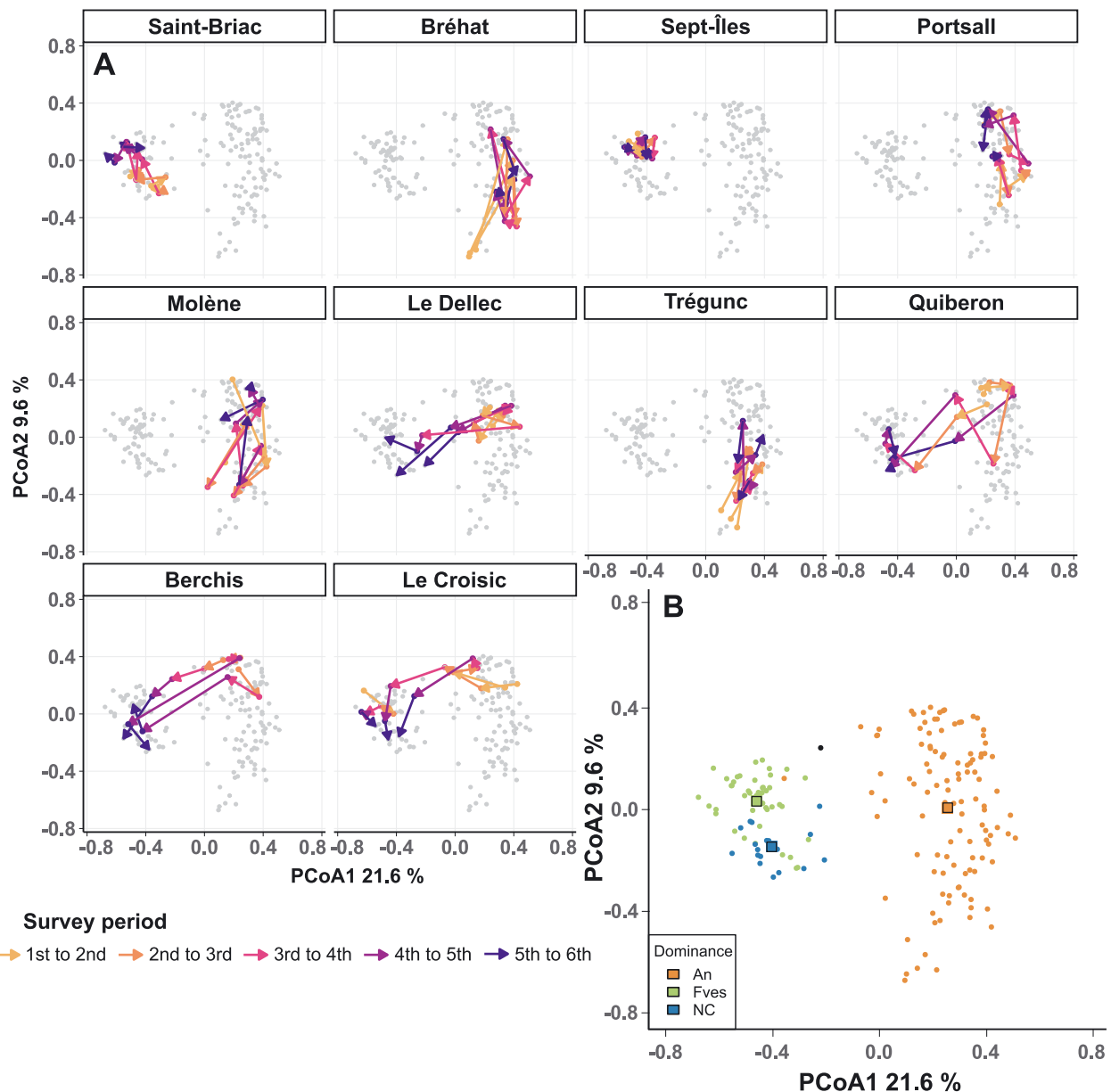


Fig. 5. (A) Community trajectories for the *Ascophyllum nodosum*–*Fucus vesiculosus* (*An*–*Fves*) community, differentiated for each studied site. The 3 sampling spots per site are represented. Trajectory darkens over time, with lighter (yellow) and darker (violet) arrows representing the first and last community state, respectively. (B) Underlying Ω space, namely the principal coordinates analysis (PCoA) of the *An*–*Fves* communities, showing sampling spots dominated by: *A. nodosum* (*An*) and *F. vesiculosus* (*Fves*). NC: total disappearance of *A. nodosum* or *F. vesiculosus* canopy (dominance defined in Fig. S2). The centroids of each group are represented by the squares

over, most of the southeast sites (Quiberon and Croisic), as well as Saint-Briac, a northeast site, and Le Dellec, located in the Bay of Brest, were characterized by high net change (mean values above 1.12) and trajectory path length values (mean values above 4.04), revealing a trajectory departing from their initial community state.

4. DISCUSSION

Biodiversity changes are highly variable across space, time and taxonomic groups (Blowes et al. 2019). Analysing long-term monitoring data on an essential component of coastal ecosystems such as intertidal macroalgal communities (Mineur et al.

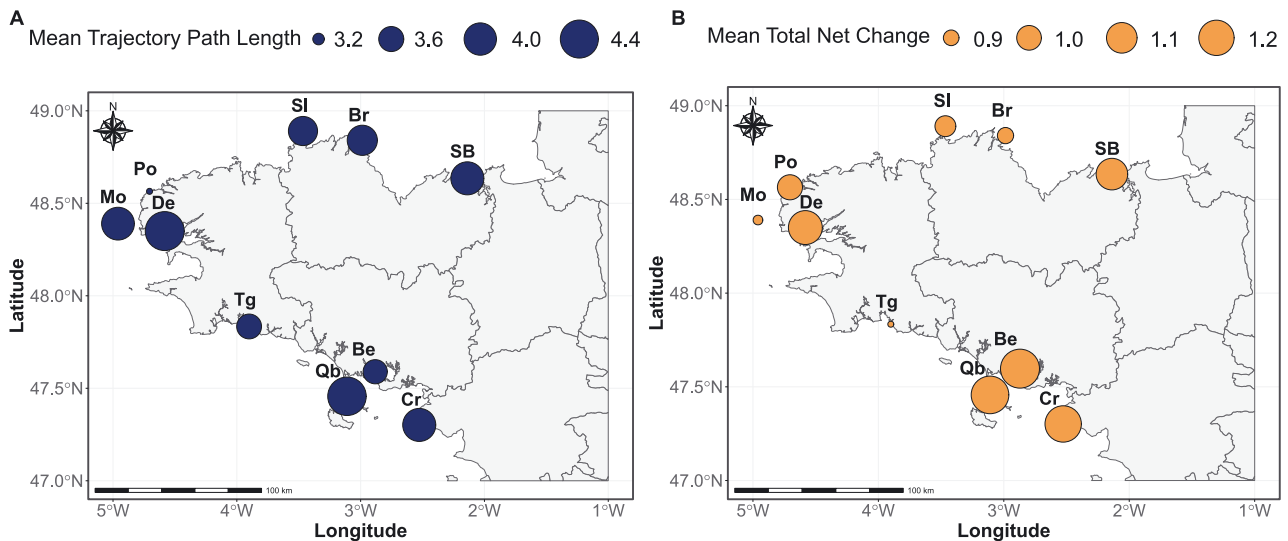


Fig. 6. (A) Mean trajectory path length and (B) mean net change for the mid-shore community co-dominated by *Ascophyllum nodosum* – *Fucus vesiculosus*, computed between the last (2020–2022) and first (2004–2007) community state for each site (mean across the 3 sampling spots). Sites are SB: Saint-Briac; Br: Bréhat; SI: Sept-Îles; Po: Portsall; Mo: Molène; De: Le Dellec; Tg: Trégunc; Qb: Quiberon; Be: Berchis; Cr: Le Croisic. The shapefile used to plot the maps is European coastlines (<https://www.eea.europa.eu/>)

2015) unveils important ecological trends that occurred during the last 2 decades across Brittany, which were never observed for other surrounding intertidal systems (Toumi et al. 2023).

Although the CTA framework has already been applied to various marine and terrestrial communities (e.g. Sánchez-Pinillos et al. 2019, Koshelev et al. 2021, Toumi et al. 2023), this study constitutes the first trajectory analysis for macroalgal communities. While bathymetric analysis revealed an expected gradual increase in community diversity and structural state (Ar Gall & Le Duff 2014, Burel et al. 2019b), the application of this method allowed for the quantification, comparison and illustration of temporal changes in macroalgal communities in Brittany. This method thus revealed 3 distinct temporal dynamics, following strong horizontal variability, consistent with our initial hypothesis:

(1) Both high and mid-shore communities changed little over time. They were characterized by low net changes and trajectory path lengths, with different underlying causes related to diversity and species tolerance. High shore communities (*Pelvetia canaliculata* and *Fucus spiralis*) exhibited clear stability in their community composition in Brittany. At this bathymetric level, communities are less diverse and extensive due to challenging environmental conditions, which prevent the installation of extensive cover of understory species (Floc'h 1964, Denny & Gaines 2007). Therefore, stability might be linked to

the low diversity found in high shore communities, avoiding richness artifacts (Sturbois et al. 2021a, Toumi et al. 2023), resulting in a consistent presence of these species and minimizing the variation between observations. However, decline of the canopy-forming species (*P. canaliculata* and *F. spiralis*) has already been observed in southern localities of the North-East Atlantic (Lamela-Silvarrey et al. 2012, Vodopivec 2013), and future regression might be expected in Brittany.

Even if the mid-shore community dominated by *F. serratus* is structurally and functionally different from high tide communities, it exhibits a similar stability. The overall stability of the *F. serratus* community, despite its lower desiccation tolerance compared to the 2 aforementioned canopy species (Altamirano et al. 2003), might stem from its competitive advantages. These include reproductive capacities, high growth rate and wide genetic diversity, enabling the species to adapt to a large range of conditions (Arrontes 2002, Johnson et al. 2012). Additionally, tidal pressures are weaker at this bathymetric level (Ar Gall & Le Duff 2014). The understory macroalgae, however, are represented by a limited number of species, which are mostly corticated Rhodophyta (Burel et al. 2022). Indeed, corticated rhodophytes, such as *Mastocarpus stellatus* and *Chondrus crispus*, are known to be more resistant to oxidative stress than *F. serratus* (Collén & Davison 1999). These species also present triphasic life cycles (Pereira 2013), high polymorphism (Lub-

chenco & Cubit 1980) and sometimes vegetative propagation (e.g. *Chondracanthus acicularis*, Bulboa Contador et al. 2020), allowing high persistence and resilience even when Fucales canopy is lacking (Álvarez-Losada et al. 2020). The constant occurrence of these abundant species might in our case explain the reduced community changes over time.

(2) Communities that exhibited high variability between survey periods but with stable distance from the initial state were characterized by high segment lengths and low net changes between observations, reflecting a general stability of the community state (Sturbois et al. 2021b, Toumi et al. 2023). Low shore communities (*Himanthalia elongata*–*Bifurcaria bifurcata* and *Laminaria digitata*) were characterized by high diversity and environmental stability, which can be explained by the environmental buffer created by reduced emersion time and species interactions with larger brown canopy-forming species (Floc'h 1964). Yet, this ecological facilitation does not necessarily lead to a static community but rather to a dynamic stability, as observed in other North-East Atlantic intertidal systems (Toumi et al. 2023). As the number of species sharing the same habitat preferendum increases, the probability of observing equivalent community structures across survey periods decreases (theorized by Huston 1979 on general diversity, and by Magurran & Henderson 2018 on fish assemblages). For macroalgae, it can be explained mostly by the growth form of species, described by the Braun-Blanquet sociability scale (Schils 2000): mat-forming species (i.e. *C. acicularis*) cover a large surface and are more likely to be sampled every time while solitary (i.e. *Saccharina latissima*, *Dumontia contorta*) or turf-forming (i.e. Ceramiaceae, Rhodomelaceae) species can either be present or absent from one sampling period to another, creating variability between observations. This effect can obscure long-term trends in canopy-forming species, which have been previously described (Bush et al. 2013).

(3) The *A. nodosum*–*F. vesiculosus* community that presented directional changes from the initial state (Matthews et al. 2013, De Cáceres et al. 2019, Lamothe et al. 2019) was characterized by increasing net change and high segment length. An emphasis on spatial variations in temporal dynamics highlighted a large difference between *F. vesiculosus*-dominated and *A. nodosum*-dominated communities. Only *A. nodosum*-dominated communities showed drastic changes over time, likely linked to the concomitant loss of canopy-forming species at the mid-shore level. The loss of *A. nodosum* canopy, non-replaced by any other functionally equivalent species (Fernández

2016), affected all understorey macroalgal species: altered communities were essentially differentiated from the initial state by the absence of such understorey species (as concluded by Álvarez-Losada et al. 2020, with *F. serratus* loss). Such a decrease has already been reported for the *A. nodosum*–*F. vesiculosus* community in Spain and the UK (Piñeiro-Corbeira et al. 2016, Mieszkowska et al. 2021). Furthermore, no obvious signs of recovery have been observed (Jenkins et al. 2004), which might be attributed to the late maturity of *A. nodosum* reached at 5 yr (Sundene 1973, Pereira et al. 2020). Given that this species presents a unique functional role, distinct from other intertidal large brown macroalgae (Cappelatti et al. 2019), its loss could be irreplaceable with a permanent impact on this community.

In addition to changes at the community level, a strong spatial heterogeneity in dynamics was highlighted between sites by metrics computation. Higher variations were highlighted in south-eastern and north-eastern Brittany, as well as in the Bay of Brest. These heavily changing sites presented trajectories with increasing net change and high trajectory path, resulting in a progressive divergence from the initial state, with apparently no recovery towards the initial state. In the North-East Atlantic, the distribution of *A. nodosum* is mostly governed by hydrodynamics (Burel et al. 2022), as high hydrodynamic conditions lead to high mortality of its zygotes (Vadas et al. 1990) and promote higher grazing pressure (Davies et al. 2007, Le Roux 2008). Therefore, the loss of the canopy-forming species *A. nodosum* might be witness to heterogeneous long-term changes in environmental conditions along the coasts of Brittany. Global warming is a main driver of community changes (Harley et al. 2012, Mineur et al. 2015). Increased wave action, driven by global change (Masson-Delmotte et al. 2021) or artificial defence structures (Martin et al. 2005), can contribute to these community changes (Mrowicki & O'Connor 2015). However, sheltered sites (such as Berchis, which is situated in a semi enclosed bay, the Golfe du Morbihan) presented strong variations in the community structure, whereas much more exposed ones (such as Molène, which is completely open to the Iroise Sea), exhibited high stability (Guillou et al. 2023), highlighting the potential importance of other pressures.

Global warming enhances macroalgal community changes (Harley et al. 2012, Mineur et al. 2015), as temperature has been one of the main factors behind species distribution globally (Breeman 1988). Notably, extreme events, particularly heatwaves, have been identified as significant contributors to damage at the

distribution limits of intertidal communities (Mieszowska et al. 2021, Whalen et al. 2023). Thus, *A. nodosum*, a cold-acclimated species with a low thermal tolerance (Keser et al. 2005), could be more affected by warming compared to *F. vesiculosus*, which is tolerant to a larger thermal range (Haroun et al. 2002). Given the prolonged periods of emersion experienced by organisms on rocky shores, the distribution of intertidal macroalgae is not only governed by sea temperature and hydrodynamics but also by atmospheric temperature (Román et al. 2020), even when considering microtidal systems (Benedetti-Cecchi et al. 2006). The seasonal formation of the Ushant front, a tidal front triggering thermal disparities (Brumer et al. 2020), leads to the creation of a homogeneous water body in north-western Brittany (Derrien-Courtel et al. 2013), gradually reducing both sea and atmospheric temperatures in the region (Le Fèvre & Grall 1970). Therefore, instead of the anticipated latitudinal gradient in macroalgal species, the heterogeneous spatial pattern found in intertidal community variations are more likely accountable for an east–west thermal gradient. As a secondary effect, this warming might also favour the survival rate of grazers (such as molluscs or crustaceans), leading to increased grazing pressures, causing a notable decline in *A. nodosum* (Davies et al. 2007, Lorenzen 2007); the northern extension of herbivorous fishes that feed on *Fucales* might also be expected (e.g. *Sarpa salpa* feeding on *Fucus* spp. in Portugal, Martins et al. 2019).

The regression of the canopy-forming species *A. nodosum* left available space that has not yet been filled by other macroalgal species. The multiplicity and interaction of biotic and abiotic pressures (Mineur et al. 2015) impact the understanding of ongoing changes, and patterns of replacement remain uncertain. As environmental conditions are still predicted to change, with the predicted increase in frequency and intensity of extreme events (Oliver et al. 2018), several potential responses of future Breton intertidal macroalgal communities can be anticipated: (1) a complete replacement by bare rocks and invertebrate-dominated communities (Whalen et al. 2023), (2) a development of species better suited to environmental pressures such as calcareous and turf-forming species (Hay 1981, Díez et al. 2012, Filbee-Dexter & Wernberg 2018), (3) a tropicalization effect (Vergés et al. 2019, De Azevedo et al. 2023), with the expansion of warm-temperate (Fernández 2016, Piñeiro-Corbeira et al. 2016) and non-indigenous species (Katsanevakis et al. 2014).

In conclusion, this study provides valuable insights into the dynamics of intertidal macroalgal commu-

nities, emphasizing the significance of adopting community-based approaches for ecological assessments. This work specifically highlights the long-term loss of *A. nodosum*, and its impact on the associated communities. Such findings suggest that the current decline in *A. nodosum* populations may have far-reaching consequences, leading to the collapse of intertidal communities without obvious short-term recovery, and likely profound changes in the functioning of the coastal ecosystem. Indeed, as canopy-forming species play crucial roles as nurseries, shelters and food sources in the coastal area, it is crucial to evaluate future changes by maintaining the monitoring of these communities. To enhance our understanding of community dynamics, future research endeavours should focus on investigating environmental data to identify key factors driving changes in the community structure and elucidate the factors contributing to community stability. This comprehensive approach will aid in delineating niche areas that warrant conservation efforts, thus facilitating the implementation of targeted protection measures.

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