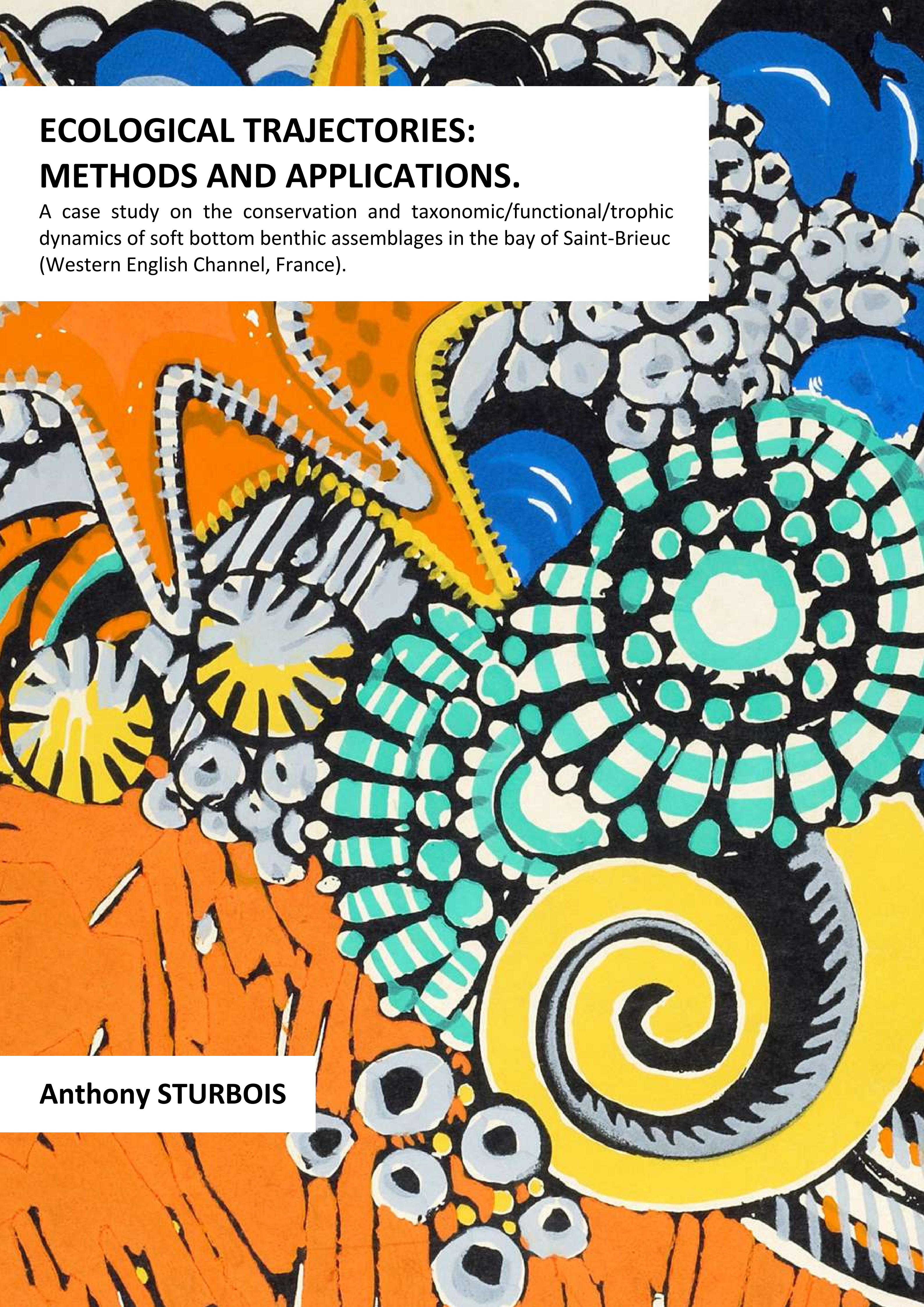

ECOLOGICAL TRAJECTORIES: METHODS AND APPLICATIONS.

A case study on the conservation and taxonomic/functional/trophic dynamics of soft bottom benthic assemblages in the bay of Saint-Brieuc (Western English Channel, France).

Anthony STURBOIS

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Par Anthony STURBOIS

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“Starting out as an amateur is often a good thing in science”

Brian Fry, 2008

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Foreword author presentation

Anthony STURBOIS. Twenty years ago, during my technical and scientific educational pathway, including my first professional experiences as internship student, I identified the lack of permeability that sometimes persists between managers and scientists (and even more stakeholders) and the different fields and disciplines that it includes. From that moment, I made the interface science/management my own professional project with two guiding principles, which progressively emerged and still influence my way of working: openness and transversality. Later, my first professional experiences led me to work at this sometimes very narrow interface, trying to keep the best of both approaches, leaning occasionally to one side or the other. From that point of view, my job at VivArmor Nature as a scientific adviser in the National nature reserve of the bay of Saint-Brieuc since 2009 constitutes a fantastic field to experience the relevance of such science/management interface, its usefulness in decision-making aid processes, and finally confirms my desire to remain at the frontier.

In 2018, this professional project really took shape with the "ResTroph Baie de Saint-Brieuc" research program and the present thesis. Facing the need of knowledge updating about the evolution of benthic soft-bottom habitat and their functioning in the bay of Saint-Brieuc, we worked together, scientists and managers, on funder proposals to build the research program. Lately, playing with data sets and trying to give larger dimensions to local ecological questions, I progressively realized the need of complementary kind of analysis and data visualization concepts, widening the circle of scientific partners involved in the thesis and the ResTroph program, and starting a methodological development that should serve scientist, manager and stakeholders expectations. Even if "*we did not follow strictly the initial plan*", I believe it currently constitutes the strength and among the best feelings of my thesis experience, embedding me strongly at this wonderful interface between science and conservation management.

Abstract

Ecological research focuses on the spatio-temporal patterns of ecosystems and communities. The development of community ecology has historically been influenced by static depictions of inherently dynamic processes, which led to many important insights about the diversity and the structure of communities. Temporal changes in biological assemblages are the sum of local colonisation and extinction events, as well as changes in the biomass and relative abundance of taxa. Climate change and still growing anthropogenic pressures have pointed the pressing need to understand how communities change over time. Understanding ecological dynamics is a challenging task, which requires specific analytical tools devoted to the analysis and the representation of ecosystems changes.

The overall aim of my thesis was to quantify taxonomic and functional changes in intertidal and subtidal benthic communities of the bay of Saint-Brieuc during the last thirty years, and track spatio-temporal patterns in the intertidal benthic food web as part of the ResTroph research program. Answering these questions involved addressing a more general one, which refers to the stability and variability of ecosystems: 'How do ecological states change with respect to an initial reference and/or to a baseline?' In this purpose, the recent *Community Trajectory Analysis* framework considers community dynamics as trajectories in a chosen space of community resemblance and uses geometrical properties of trajectories to compare and analyse temporal changes. Building on this framework, this thesis aims to extend the use of trajectory concepts and metrics in other fields of ecology and beyond community sites*species matrices. New distance- and direction-based trajectory metrics coupled with innovative synthetic data visualizations were proposed. Moreover, with the new *Stable Isotope Trajectory Analysis* framework, I have provided a formal and explicit framework for the analysis and representation of spatial and temporal trajectories in stable isotope ecology. The methodological developments were tested at different spatial, temporal and ecological scales with a diversity of data sets originating from different fields in ecology and specially called in the thesis. These data sets have constantly cross-pollinated with the bay of Saint-Brieuc case study to validate the proposed methods before their local use in the bay of Saint-Brieuc.

Trajectory approaches are coupled with complementary analyses in the specific case study on taxonomic, functional and trophic dynamics of soft bottom benthic assemblages in the bay of Saint-Brieuc (Western English Channel, France). Results show contrasted taxonomic and functional trajectories in intertidal and subtidal benthic assemblages. Whatever the perennial contribution of dominant prevalent species at the site scale in the intertidal area, some species were highly variable over time and space, influencing the structuration of assemblages. Taxonomic changes were not systematically associated to significant changes in the functional properties at local and community scales. The consideration of local changes and variations at the species level explained the differences in composition observed at the scale of assemblages. Observed changes mainly reflected random population changes of structuring species in habitat under strong natural pressures, rather than specific changes of the community. Only few species displayed a dynamic which looked under the influence of green tides in some assemblages. In subtidal habitats, trajectory analyses indicated changes in the structure and distribution of benthic assemblages, with a homogenization of assemblages, and significant functional shifts. Fishing activities and nutrient enrichment are probably strong drivers of the observed changes, as suggested by the higher mortality rate of fragile, flexible, tube-dwelling and burrowing species, and the increase in the abundance of opportunistic species in the assemblages. Some populations of macroinvertebrates seem jointly controlled by climate change and by the aforementioned local factors of disturbance.

The spatio-temporal variability of the intertidal benthic food web was also analysed in terms of composition and structure at the scales of both the whole study area and the different assemblages, which constitute the mosaic of habitats. Inferences on potential sources fuelling the food web were supported by spatio-temporal patterns based on covariations and sources/consumers stable isotope trajectory analysis. Results highlighted that phytoplankton and microphytobenthos support food webs within the different habitats. The trophic connectivity between salt marsh and benthic habitats within the bay was limited to some macrofauna species inhabiting muddy creeks within salt marshes. Unexpectedly, the influence of *Ulva* blooms appeared also limited. Spatial patterns illustrate the constancy of the spatial variability in the benthic pelagic coupling, with a higher influence of microphytobenthos in the upper level compared to low shore assemblages.

This new knowledge must be considered for future governance rounds, in a multi-scale approach involving policy makers and stakeholders, and must make marine habitats, a central part of the conservation process of the study area. Such approaches should not only focus on aggregating local current practices, but also on exploring future visions and potential *scenario.* Overall, this thesis also demonstrates the ability of the *Ecological Trajectory Analysis* framework to quantify and represent changes in a diversity of ecological questions and scales. The new concepts, metrics and data visualizations provided constitute a valuable toolbox for trained ecologists aware of assumptions and limitations of the approach. Trajectory analysis output, coupled with a precise data examination and other statistical approaches, appears as a relevant management and decision-making tool. Accordingly, potential perspectives, as the use of trajectory analysis for the reporting of ecological quality status, are proposed. It implies to deal with the double challenge of the theoretical and practical definition of reference conditions and conservation targets.

Keywords: Ecological Trajectory Analysis, Community Trajectory Analysis, Stable Isotope Trajectory Analysis, Metrics, Data visualisation, Dynamics, Temporal changes, Community ecology, Stable Isotope Ecology, Resources partitioning, Marine habitats, Benthic macrofauna, Functional shift, Trophic connectivity, Conservation, Marine protected area, English-Channel, Bay of Saint-Brieuc.

Résumé étendu

L'analyse des évolutions spatio-temporelles des écosystèmes et des communautés constitue une question centrale en écologie. Historiquement, le développement de l'écologie des communautés a prioritairement été influencé par des représentations statiques de processus intrinsèquement dynamiques, qui ont conduit à de nombreuses découvertes importantes sur la diversité et la structure des communautés. Les changements temporels dans la structure des assemblages biologiques résultent de la somme des événements locaux de colonisation et d'extinction, ainsi que des changements dans la biomasse et l'abondance relative des taxons. Le changement climatique et les pressions anthropiques toujours croissantes ont mis en évidence le besoin urgent de comprendre comment les communautés évoluent dans le temps. La compréhension des dynamiques écologiques est une tâche complexe, qui nécessite des outils spécifiques consacrés à l'analyse et à la représentation des changements dans les écosystèmes. A cette fin, la puissance synthétique des outils d'analyses multidimensionnels a largement été privilégiée pour l'analyse des changements et gradients écologiques. Pour autant, certains auteurs soulignent le besoin d'un cadre explicite plus adaptés à l'étude des dynamiques temporelles.

L'objectif initial de ma thèse était d'analyser les changements taxonomiques et fonctionnels au sein des communautés benthiques intertidale et subtidale de la baie de Saint-Brieuc au cours des trente dernières années, et de caractériser les patrons spatio-temporels du réseau trophique benthique intertidal dans le cadre du programme de recherche ResTroph. Répondre à ces questions m'a amené à aborder une question d'une portée plus générale relative à la stabilité et à la variabilité des écosystèmes: « Comment les écosystèmes évoluent-ils par rapport à un état initial ou de référence ? ». Dans cette optique, l'approche « *Community Trajectory Analysis* » considère les dynamiques au sein des communautés comme des trajectoires dans un espace choisi de similarité et utilise les propriétés géométriques des trajectoires pour comparer et analyser les changements temporels. En s'appuyant sur cette approche, cette thèse vise à étendre l'utilisation des concepts et des métriques de trajectoires dans d'autres domaines de l'écologie, et au-delà des matrices de communautés sites*espèces. De nouvelles métriques de trajectoires, basées sur la distance et la direction, couplées à des modes de représentation des données synthétiques et innovants sont proposées. Je propose par ailleurs, avec l'approche « *Stable Isotope Trajectory Analysis »,* un cadre formel et explicite pour l'analyse et la représentation des trajectoires spatiales et temporelles en écologie isotopique. Ces développements méthodologiques ont été testés à différentes échelles spatiales, temporelles et écologiques avec une variété de jeux de données spécialement utilisés dans la thèse. Les analyses de ces jeux de données ont permis de valider les méthodes proposées avant leur utilisation locale en baie de Saint-Brieuc.

Les approches par trajectoires ont été couplées à des méthodes d'analyses complémentaires dans une étude de cas sur la dynamique taxonomique, fonctionnelle et trophique des assemblages benthiques de fonds meubles de la baie de Saint-Brieuc (Manche occidentale, France). Les résultats mettent en évidence des trajectoires taxonomiques et fonctionnelles contrastées au sein des assemblages benthiques intertidaux et subtidaux.

Dans la zone intertidale (1987 vs 2001 vs 2019, 42 stations), la distribution globale des assemblages benthiques est stable dans le temps et fortement liée à la bathymétrie et au faciès sédimentaire, malgré quelques variations très locales comme l'apparition d'un nouvel assemblage en lien avec des secteurs à forte dynamique sédimentaire. 95,5% de l'abondance totale est représentés par 36 espèces communes aux trois dates d'échantillonnage. Bien que pérennes à l'échelle du site dans la zone intertidale, certaines espèces dominantes présentent des abondances très variables dans le temps et l'espace et influencent la structuration des assemblages. Les changements taxonomiques ne sont pas systématiquement associés à des changements significatifs des propriétés fonctionnelles à l'échelles locale ce qui explique la stabilité observée au sein de la zone d'étude. La prise en compte des changements locaux et des variations au niveau des espèces explique les différences de composition observées à l'échelle des assemblages. Les changements observés reflètent principalement la dynamique aléatoire des populations d'espèces structurantes dans un habitat soumis à de fortes pressions naturelles, plutôt que des changements spécifiques de la communauté. Quelques espèces révèlent toutefois un effet à long terme des marées vertes dans certains assemblages. Les résultats soulignent globalement une persistance taxonomique et fonctionnelle des communautés benthiques à l'échelle de la zone intertidale, avec une difficulté à dissocier l'influence des facteurs naturels et anthropiques dans des habitats dont le caractère dynamique peut être envisagé comme un facteur de stabilité à long terme.

Dans les habitats subtidaux (1987 vs 2019, 38 stations ; 2005 à 2019, une station Rebent suivie annuellement), les analyses de trajectoire indiquent des changements dans la structure et la distribution des assemblages benthiques. Une homogénéisation taxonomique des assemblages est observée suite à l'augmentation importante des effectifs et de la distribution de *Varicorbula gibba,* espèce opportuniste de second ordre connue pour être favorisée dans des contextes de dégradation. En 2019, cette espèce est la plus abondante au sein de deux des trois assemblages benthiques (comprenant 33 des 38 stations échantillonnées). Les changements taxonomiques ont entraîné un glissement fonctionnel avec notamment la diminution des espèces fragiles, flexibles, tubicoles et déposivores, ce qui suggère une perturbation physique des fonds. L'analyse du jeu de données de la station Rebent confirme ces résultats sur les plans taxonomique et fonctionnel et permet de souligner le caractère récent (à partir de 2015) de ces changements. Le régime de houles étant stable au court des 30 dernières années, les changements récents intervenus dans la régulation des activités de pêche à la coquille Saint-Jacques et l'eutrophisation sont probablement des facteurs importants des changements taxonomiques et fonctionnels observés, comme le suggère la mortalité sélective des espèces de certaines catégories de traits liées à la stabilité des habitats, et l'augmentation de l'abondance des espèces opportunistes dans les assemblages. Certaines populations de macroinvertébrés semblent contrôlées conjointement par le changement climatique et par les facteurs de perturbation locaux susmentionnés.

La comparaison des dynamiques temporelles intertidales et subtidales met donc en évidence des différences nettes entre les deux zones. Les résultats observés en zone intertidale traduisent la superposition d'évolutions indépendantes des assemblages associés à des micro-habitats alors que ceux observés en zone subtidale soulignent au contraire une évolution globalement orientée vers l'homogénéisation et la dégradation des habitats résultant de l'impact conjoint de plusieurs perturbations.

La variabilité spatio-temporelle du réseau trophique benthique intertidal a également été analysée en termes de composition et de structure à l'échelle de l'ensemble de la zone d'étude, et des différents assemblages qui constituent la mosaïque d'habitats. Les patrons spatio-temporels du réseau trophique et le rôle potentiel des différentes sources ont été déterminés par des analyses de covariations et de trajectoires des isotopes stables

sources/consommateurs. Le phytoplancton et le microphytobenthos supportent le réseau trophique avec une variabilité dans l'espace et dans le temps. La connectivité trophique entre le pré-salé et les habitats benthiques de l'estran se limite à quelques espèces de macrofaune présentes dans les chenaux vaseux du marais salé. Les patrons spatio-temporels illustrent la constance de la variabilité spatiale dans le couplage pélagique benthique, avec une plus grande importance du microphytobenthos dans les niveaux supérieurs de l'estran par rapport aux assemblages des niveaux inférieurs. De manière inattendue, l'influence des épisodes de prolifération d'*Ulva* semble également limitée. Sans remettre en cause le caractère sanitaire sensibles de ces épisodes de prolifération, la non mise en évidence d'effets majeurs sur les plans taxonomique, fonctionnel et trophique en intertidal à l'échelle de l'ensemble de la Baie de Saint Brieuc peut être mis en relation avec l'exportation régulière des stocks d'ulves par les autorités locales (12680 tonnes en 2021), l'hydrodynamisme de la zone d'étude, et la présence d'autres facteurs potentiels de régulation de l'eutrophisation telle que la mytiliculture (4500 tonnes par an) qui concourt à l'exportation d'une quantité importante de matière organique du système qui viennent s'ajouter à la quantité d'ulves exportée.

Cette thèse souligne également l'importance des suivis à long terme à différentes échelles spatiales et temporelles et vient confirmer l'intérêt de la stratégie de suivi mise en œuvre par les gestionnaires de la réserve naturelle en étendant par ailleurs leur champ d'action à la zone subtidale proche. La difficulté à dissocier l'influence des facteurs naturels et anthropiques appelle en revanche à la mise en œuvre de nouveaux protocoles dédiés à leur suivi à long terme pour compléter cette stratégie de monitoring. Les nouvelles connaissances locales doivent nourrir les processus de gouvernance en impliquant les décideurs politiques et les différents acteurs, et en faisant des habitats marins un élément central de la stratégie de conservation de la zone d'étude et de gestion des différentes pressions identifiées. Ces connaissances pourront également servir les projets d'extension du périmètre de la Réserve naturelle nationale de la baie de Saint-Brieuc et du site Natura 2000 Baie de Saint-Brieuc Est. Une telle démarche ne doit pas seulement se concentrer sur les pratiques actuelles, mais explorer également différents *scenarii* pour le futur. D'une manière générale, cette thèse démontre aussi la capacité du cadre d'analyse « *Ecological Trajectory Analysis* » à quantifier et représenter les dynamiques au travers d'une diversité de questions et d'échelles en écologie. Les nouveaux concepts, métriques et mode de représentation des données constituent une boîte à outils précieuse pour les écologues. Les analyses des trajectoires, couplées à un examen précis des données et à d'autres approches statistiques, constituent un outil pertinent de gestion et de prise de décision. En guise de perspective, je propose des directions potentielles comme l'utilisation de l'analyse des trajectoires pour le rapportage de la qualité des états écologiques, ce qui implique de relever le défi nécessaire de la définition, théorique et pratique, des conditions de référence et des objectifs de conservation.

Mots-clés : Ecological Trajectory Analysis, Community Trajectory Analysis, Stable Isotope Trajectory Analysis, Métrique, Représentation des données, Dynamique, Changements temporels, Ecologie des communautés, Ecologie isotopique, Partage des ressources, Habitats marins, Macrofaune benthique, Variation fonctionnelle, Connectivité trophique, Conservation, Aire marine protégée, Manche, Baie de Saint-Brieuc.

Contents

List of contributions

Methods & applications articles:

I. **Sturbois, A.**, De Cáceres, M., Sánchez-Pinillos, M., Schaal, G., Gauthier, O., Le Mao, P., Ponsero, A., Desroy, N., 2021. Extending Community Trajectory Analysis: new metrics and representation. ***Ecological Modelling***, 440, 109400. https://doi.org/10.1016/j.ecolmodel.2020.109400

II. **Sturbois, A.**, Cucherousset, J., De Cáceres, M., Desroy, N., Riera, P., Carpentier, A., Quillien, N., Grall, J., Espinasse, B., Cherel, Y., Schaal, G., 2021. Stable Isotope Trajectory Analysis (SITA): A new approach to quantify and visualize dynamics in stable isotope studies. ***Ecological monographs***. e1501. https://doi.org/10.1002/ecm.1501

Case study articles:

III. **Sturbois, A.**, Cormy, G., Schaal, G., Gauthier, O, Ponsero, A., Le Mao, P., Riera, P., Desroy, N., 2021. Characterizing spatio-temporal changes in benthic communities: Taxonomic and functional trajectories of intertidal assemblages in the bay of Saint-Brieuc (English Channel). ***Estuarine, Coastal and Shelf Science*** 107603. https://doi.org/10.1016/j.ecss.2021.107603

IV. **Sturbois, A.**, Cormy, G., Le Moal, A., Schaal, G., Broudin, C., Thiébaut, E., Ponsero, A., Le Mao, P., Riera, P., Gauthier, O., Desroy, N., 2021. Using ecological trajectories to track long-term taxonomic and functional changes in benthic shallow soft-bottom communities (Bay of Saint-Brieuc, English Channel). ***Aquatic Conservation: Marine and Freshwater Ecosystems,*** 1-21. https://doi.org/10.1002/aqc.3704

V. **Sturbois, A.**, Riera, P., Desroy, N., Brébant T., Ponsero, A., Le Mao, P., Gauthier, S., 2022. Spatio-temporal patterns in stable isotope composition of a benthic intertidal food web reveal limited influence from salt marsh vegetation and green tide. ***Marine Environmental Research***, 175, 105572.

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CHAPTER I

Introduction

CHAPTER I | Introduction

1.1 | Bays and estuaries in complex eco-socio-systems

Worldwide, marine ecosystems are suffering severe taxonomic and functional changes in response to the cumulative effects of anthropogenic disturbances including overfishing, pollution, climate change, habitat degradation and introduction of non-indigenous species (Gray, 1997; Claudet & Fraschetti, 2010). Human influences induce both acute and chronic effects over various temporal and spatial scales, and can ultimately lead to broad-scale losses of productive habitats, and alteration of community structure and function (Ellis et al., 2000). As a result, 60% of major marine ecosystems worldwide are currently degraded or suffer from unsustainable levels of exploitation, leading to the adoption of conservation policies by many countries (Convention on Biological Diversity, 2010; UNEP, 2011).

Coastal areas are among the most productive marine systems in the world, supporting many ecological processes and ecosystems services (Costanza et al., 1997). While intertidal and shallow subtidal soft-sediments within bay and estuaries make up a small proportion of marine habitats (Snelgrove, 1999, 1997), they are nevertheless highly productive and include a wide variety of communities adapted to such transition areas (McLusky and Elliott, 2004). These ecosystems are highly variable in space and time, notably due to the daily influence of tides and waves, and the seasonal influence of floods/low waters alternation (McLachlan and Brown, 2006).

In bays and estuaries, the productivity is favoured by a wide diversity of primary producers, including phytoplankton seaweeds, algae, seagrass, mangroves, salt marsh plants and benthic diatoms (Bouillon et al., 2011). Benthic invertebrates inhabiting these areas play a central role in benthic and pelagic food webs supporting higher trophic levels such as birds, crustaceans and fishes (Beck et al., 2001; Goss-Custard, 2006). They are key elements in the functioning of intertidal and shallow areas and their contribution to biogeochemical cycles within coastal ecosystems is essential (Grall and Chauvaud, 2002; McLusky and Elliott, 2004).

Benthic macrofauna is considered a relevant descriptor to characterize the biological status of water bodies by the European WFD (Borja et al., 2012, 2009), as this compartment influences nutrient cycling, represents an important food resource for higher trophic levels (McLusky and Elliott, 2004; Snelgrove, 1997), and reacts rapidly to disturbances (Gray, 1997; Claudet & Fraschetti, 2010).

For the assessment of the ecological status of benthic habitat and the definition of potential conservation measures, baseline are crucial, but are in most cases not available or very difficult to compare with more recent datasets. Combining historical data with more recent monitoring in order to inform long-term processes and dynamics is consequently central for research and conservation in marine habitats.

In this context, the European Water Framework Directive (WFD, Directive 2000/60/EC) and the Marine Strategy Framework Directive (European MSFD, Directive 2008/56/EC) require that European Member States implement measures to achieve a good environmental status of their water bodies. The comparison to reference conditions based on pristine or slightly disturbed areas is recommended by the European WFD to track changes in environmental status, although it is generally recognized that non-disturbed marine and estuarine habitats are rare (Borja et al., 2012), and that historical data rarely constitute a pristine state (Bacouillard et al., 2020; Callaway, 2016). In this context, acceptable levels of disturbances can be used to define reference conditions (Borja et al., 2012). Such approach requires repeated and standardized surveys over time and synthetic metrics to:

(1) Track changes with respect to baselines conditions;

(2) Provide up-to-date ecological state to stakeholders involved in the development of management plans for coastal and marine areas.

1.2 | Analysing temporal changes though trajectories

A crucial issue in the analysis of long-term time series is the extraction of major meaningful trends from the underlying unexplained temporal variability. The analysis of dynamics in various communities has received a large attention by scientists, frequently in relation with natural factors or management considerations. This topic became an up warding field in community ecology over the last century (Anderson et al., 2021), and remains a central point of ecological research and conservation. As time series became longer, ecologists often had to deal with high-resolution long-term complex data sets including temporal and spatial replications. Multivariate analyses have been widely adopted for many decades in ecology, embracing all forms of statistical analyses applied to data in which several characters are observed per statistical unit (Kendall, 1958). This efficient tool still constitute one of the primary approach to analyse ecological datasets (Buckley et al., 2021a).

Several statistical frameworks have been proposed and used to test hypotheses on community dynamics (Buckley et al., 2021a; De Cáceres et al., 2019). The analysis of temporal community dynamics is a constantly evolving field at interface of biology, statistics and bioinformatics (Buckley et al., 2021b). It still constitutes a source of methodological innovations with a challenging aim to develop adaptive tools fitting different types of data sets from any fields of ecology. Ordination and descriptive methods based on raw compositional dissimilarities are increasingly used owing to their flexibility and ability to deal with various time series of any length. Recently, Yang (2020) suggested specific and complementary ways to continue building towards a more temporally explicit framework for community ecology, notably, by increasing the representation of temporal changes and developing specific and general insights into event -or factor- driven dynamics. In this way, complementary metrics are needed to document community and environmental changes over space and time.

A common approach is the calculation of dissimilarity indices, which allows differences between a pair of ecological states to be summarized in a single metric. Since community data sets can represent both temporal and spatial variation of ecological states, the resulting dissimilarity matrices can contain spatial, temporal or spatio-temporal information. Then, the use of ecological trajectories in a multivariate space defined by the calculation of a dissimilarity index between all pairs of observations allows representing the dynamics of a system. Ordination methods are therefore often complemented with trajectory analyses, in which changes over time or as a response to natural or anthropogenic pressures are represented by a set of vectors linking consecutive ecological states. These approaches have been previously applied to a wide variety of ecological systems, including plant assemblages (Austin, 1977; Fukami et al., 2005), bird assemblages (Hudson and Bouwman, 2007; Sica et al., 2018; Haig et al., 2019), and freshwater (Matthews et al., 2013; Mathers et al., 2016; Boit and Spencer, 2019; David et al., 2020) or marine ecosystems (Dauvin and Ibanez, 1987; Smith et al., 2010; Legendre and Salvat, 2015; Cimon and Cusson, 2018). In this context, geometric properties of trajectories, defined in the space of an ordination diagram, constitute relevant parameters to study the dynamics of ecological systems, including intermediate transitional states.

The geometric study of community trajectories is generally defined around two or three axes of an ordination space (Boit and Spencer, 2019; Matthews et al., 2013) but this has the drawback of discarding the information contained in additional dimensions. In order to generalize this approach, De Cáceres et al. (2019) considered community dynamics as trajectories in a chosen space of community resemblance, with no limit in the number of dimensions included. In the Community Trajectory Analysis (CTA) framework, trajectories are defined as objects composed of trajectory segments to be analysed and compared using their metrics based on their geometry in a multivariate space. In its original definition, CTA focused on consecutive community trajectory segments and represent trajectories through arrows in ordination diagrams. The framework proposed single-trajectory metrics (length, speed, direction) and metrics for the comparison of trajectories (convergence/divergence, dissimilarity).

Regarding the CTA framework, four aspects deserved further development to quantify temporal changes in biodiversity and ecological shifts due to both natural and anthropogenic drivers:

(1) Comparing current ecological state to an initial state and/or a chosen baseline [goal defined as an ecological state to be achieved (Bioret et al., 2009)] is an overarching topic, which requires repeatedly sampling of communities over time. New metrics are consequently needed to integrate those questions to the analysis of ecological trajectories.

(2) Visualizing concept to favour the graphical representation of ecological dynamics, become relevant for datasets characterised by high temporal and or spatial resolutions. This is especially relevant when dealing with complementary distance- and direction-based metrics.

(3) Defining, when taxonomic changes are pointed in ecological studies, the influence of such changes in species composition and abundance on the functional properties of a community is important. For instance, substantial changes in species composition and structure in space and time may not systematically results in proportional trait-based functional changes (McLean et al., 2019; de Sousa Gomes-Gonçalves et al., 2020). The ability of the CTA framework to integrate functional properties of communities needs to be explored by the use of trajectory concepts and metrics beyond site (sample) by species (taxon) matrices.

(4) Studying ecosystems changes and functioning in response to natural or anthropogenic factors require multivariate times series including a variety of variables to complement taxonomic-based approaches. The concept of Ecological Trajectory Analysis still have to be tested and exported in other fields of ecology (*e.g.* stable isotope ecology in the present thesis).

1.3 | From long term series to conservation: the necessary interface between scientists and managers

Conservation planning, which includes characterizing local biodiversity and identifying spatial priorities, in order to design and implement conservation measures, is a process which may be complex to achieve in practice (Caudron et al., 2012; Margules and Pressey, 2000). « *Bien connaître pour mieux gérer* », literally «*Good knowledge for better management*» is an expression initiated in a research program in applied ecology launched in 1984 (Bioret et al., 2009). Still relevant, it points out the need to build conservation processes on ecosystems knowledge underpinning a strong interface between sciences and managers to allow for a better translation of scientific tools and knowledge into action by managers and stakeholders (Sarewitz and Pielke, 2007; Sutherland et al., 2009).

Conservation is identified as a common goal between scientist and managers, despite some differences exists in their respective aims, methods and spatial and temporal work scales. Even though in the past, multiple examples have illustrated the difficulty of scientist and managers to work together, this time have past, or at least is passing, building on good experiences shared within win-win *scenarii* in collaborations involving both practitioners (Besnard, 2013). Many complementary solutions exists to facilitate these collaboration such as:

(1) co-constructing action research programmes (Caudron et al., 2012);
(2) working with managers right up to the concrete implementation of actions (Arlettaz et al., 2010);
(3) promoting the dissemination of researchers' work (Laurance et al., 2012; Sunderland et al., 2009);
(4) having managers identify research topics first (Braunisch et al., 2012);
(5) internalising scientific expertise within teams of managers of natural areas (Besnard, 2013).

Successful collaborations are also often favoured by two key ingredients inherent to human relationships, perhaps among the most important, the respect of everyone's goals and the desire to work together.

The relationship between managers and scientists is concretely materialised by data from its collection to its analysis. Researches in conservation and ecology make no exception and strongly rely on long term monitoring, the cornerstone of effective environmental policy and management (Lindenmayer and Likens, 2010). Monitoring can be defined as "*the process of gathering information about the state of ecosystems structure, functions and services, at different points in time and space, in order to infer what causes changes in ecosystem state variables*"(Yoccoz, 2012). The knowledge of biodiversity, ecosystem processes and the evolution of their ecological status involves long-term data acquisition strategies and whenever possible data mining (*i.e.* to take the best of potential historic data (Gallant et al., 2016)). While the availability of long-term, large-scale, and high-resolution data is the most limiting factor to study temporal patterns in biodiversity (Dornelas et al., 2013), the choice and the development of methodological approaches to analyze, synthesize, and ultimately represent the dynamics of ecological systems is also an essential issue (Azovsky, 2019; Yang, 2020). Such methodological approaches must provide both synthetic metrics and adapted data representations to facilitate research sharing and their applications with stakeholders.

Intrinsic or extrinsic natural driving factors strongly influence spatio-temporal dynamics. In addition, ecosystems are worldwide suffering severe taxonomic and functional changes in response to cumulative effects of anthropogenic disturbance (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, IPBES, 2019). Accordingly, we are currently facing pressing needs to:

(1) develop and secure long-term, large-scale and high-resolution data sets;
(2) favour the development of methodological approaches to analyse, synthesize, and represent the dynamics of ecological systems;
(3) ultimately transfer knowledge to improve the conservation of ecosystems.

This sequence is obviously conditioned by the fact that long-term monitoring is dependent of long-term financial supports, a point that may potentially become very difficult to ensure, depending on the evolution of political contexts (Wolfe et al., 1987). The recent termination of the unique long term (50 years) time series on intertidal soft-sediment communities in the Dutch Wadden Sea illustrates the Damocles sword that hangs on the perpetuation of such monitoring programs (Beukema and Dekker, 2020). It involves that scientist and managers reinforce their collaboration, when relevant, building researches or long-term monitoring programs and asking together to call for proposals in order to up-date knowledge and find solutions to the assessment of ecological changes. Such collaborations must satisfy both expectations, funder aims and notably the need of assessment for conservation as part of governmental policies or international engagements.

As detailed in Baccouillard et al. (2020), depending on the questions, two main strategies can be used to monitor long-term ecological change:

(1) sampling one or several stations at a regular frequency, often yearly (*e.g.* Clare et al., 2015; Frid et al., 2009; Fromentin et al.,

1997; Warwick et al., 2002), during several decades. It provides valuable information on the dynamics of macrobenthic communities and their drivers, but requires continuous and long-term financial and human support and does not allow consideration of the spatial heterogeneity of environmental conditions or responses of macrobenthic communities ;

(2) sampling a network of stations at lower frequency, generally over a decade, which allows rapid detection of major changes in macrobenthic macrofauna without being able to statistically infer the causes of the observed changes.

The existence of historical data sets on benthic intertidal and subtidal assemblages (Gros and Hamon, 1988) and the natural and anthropogenic contexts of the bay of Saint-Brieuc make it suitable to contribute to the debate about the assessment of changes at spatial and temporal scales and the feasibility of such research. Additionally, the existence of a National nature reserve and a Natura 2000 site devoted to the conservation of marine habitats constitute a breeding ground for the integration of knowledge updating in governance rounds, making marine habitats a central part of the conservation process (Greathead et al., 2020).

1.4 | Scientific context

1.4.1 | The research program ResTroph

In the English Channel, the major bays and estuaries have been the subject of studies supported by various research programmes which, depending on the site, have led to a more or less complete characterisation of their functioning, their functionalities and their food web(s): bay of Somme (Rybarczyk et al., 2003), bay of Seine Bay (synthesis by Dauvin and Desroy, 2005) and bay of Mont-Saint-Michel (Arbach Leloup et al., 2008; Kostecki, 2010; Riera, 2007). The case of the bay of Saint-Brieuc is more singular: until the end of the 1980s, several studies have been conducted, including the Euphorbe (EUtrophisation et PHénomènes d'ORigine BEnthique) program, which aimed to quantify the flows of matter and energy within the bay (Gros and Hamon, 1988), and certain actions linked to the Programme National d'Océanographie Côtière. Despite some more recent studies (Ponsero et al., 2016; Ponsero and Le Mao, 2011; Sturbois et al., 2015), the Bay of Saint-Brieuc has suffered from a relative lack of attention from scientists for the last two decades. Nevertheless, this bay supports an important fishing (scallops) and shellfish farming (bouchot mussels) activity and is characterised by one of the few national nature reserves encompassing marine habitats (over 99% of the surface) and the "Baie de Saint-Brieuc-Est" marine Natura 2000 site. Initially created to ensure the conservation of migratory and wintering birds, the presence of the national nature reserve has encouraged initiatives aiming to document the different biological compartments. The various studies carried out in the marine environment and supported by the nature reserve have in particular highlighted the functional importance of the benthic macrofauna for shorebirds (Ponsero et al., 2016; Ponsero and Le Mao, 2011; Sturbois et al., 2015).

The conservation of this marine protected area requires a better knowledge of the structure and functioning of the ecosystem, and its connections with neighbouring marine environment. Although identified as a major issue in the management plan of the national nature reserve (Ponsero et al., 2019a, 2019b) the ecological functioning has not been addressed yet in a comprehensive manner. After two decades of environmental preservation measures, it is important to conduct an integrated study to enable stakeholders and managers to benefit from an updated knowledge. It is a necessary step for the management of this area and to assess the functional role of protected habitats in relation with adjacent marine habitats.

This “ResTroph - Baie de Saint-Brieuc” research program, which extends beyond the perimeter of the MPA, integrates the historical studies carried out on the benthic fauna and ichthyofauna. The study area encompasses sedimentary habitats located in the south of a line between Saint-Quay Portrieux and Pleneuf Val-André (Figure 1).

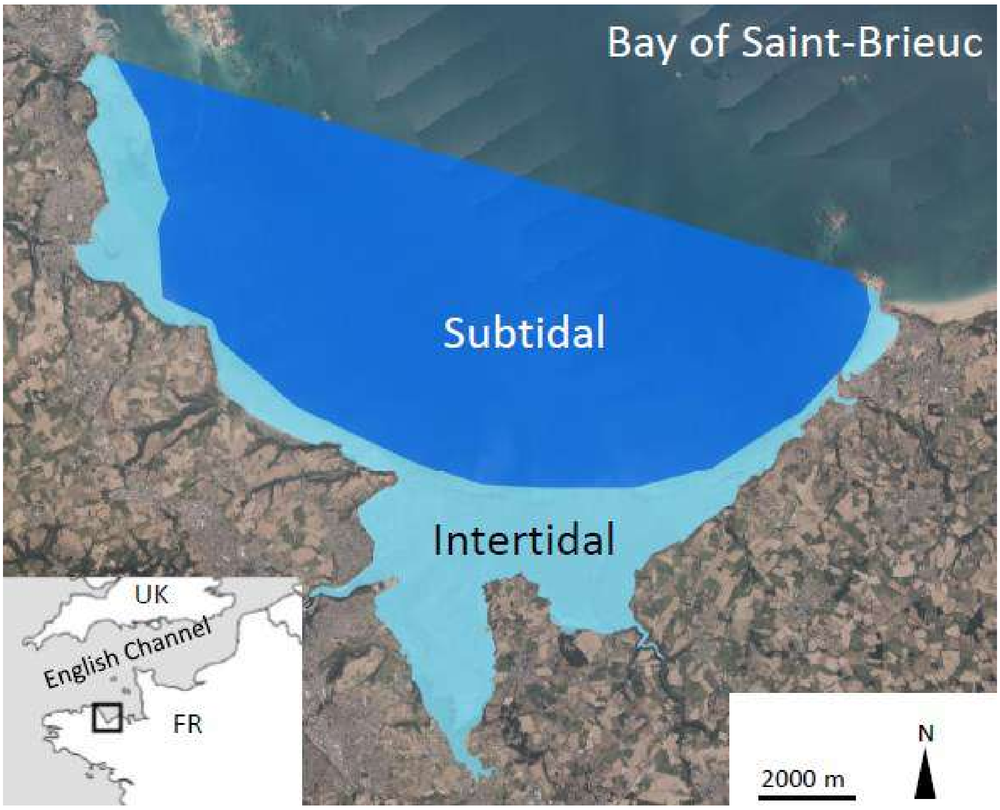


Figure 1: Study area of the Restroph research program within the bay of Saint-Brieuc.

ResTroph is based on four axes (Figure 2) aiming to:

(1) Characterise intertidal and shallow subtidal benthic assemblages and their evolution over the last three decades;
(2) characterise the fish nursery role of the bay;
(3) characterise the benthic marine food web(s) and the potential influence of salt marsh vegetation and green tides events in the trophic functioning;
(4) transfer of the scientific updated knowledge into governance processes

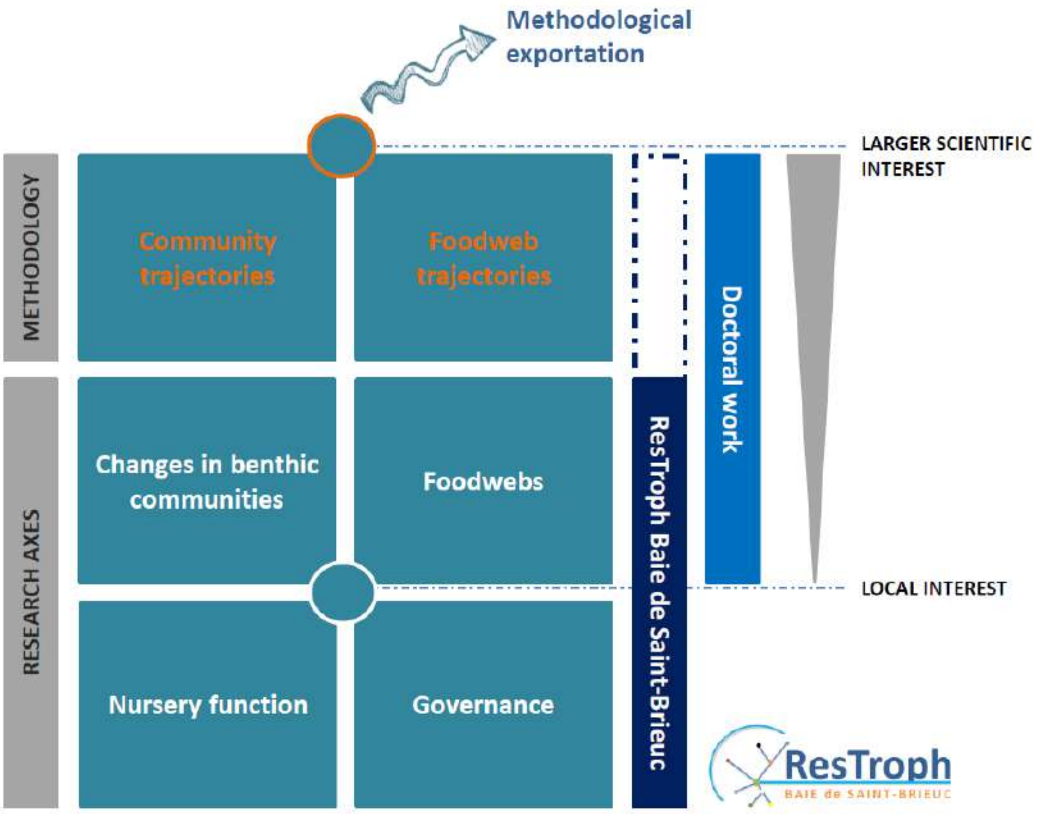


Figure 2: Articulation between the research Program ResTroph Baie de Saint-Brieuc and the doctoral work.

1.4.2 | Thesis aim and goals

Within the ResTroph research program, the overall aim of my thesis was to (1) quantify taxonomic and functional changes in intertidal and subtidal benthic communities of the bay of Saint-Brieuc and (2) track spatio-temporal patterns in the intertidal benthic food web (Figure 2 and 3). I soon realized that answering the question 'How intertidal assemblages changed in 2001 and 2019, with respect to the initial state defined in 1987?' involved addressing a more general one: 'How ecological state changes with respect to an initial reference and/or to a baseline?' This required some methodological development to quantify and represent ecological changes with respect to a chosen baseline state in association with complementary methods. I built on CTA (De Cáceres et al., 2019) to propose an alternative way to calculate trajectory metrics, considering chosen ecological states as central in the analysis. Doing this, I have opened the door of ecological trajectories concepts in a very applied purpose which led to the development of new trajectory concepts, distance- and direction-based metrics, and data visualizations. While this track for new tools was primarily driven by the ecological questions identified in the bay of Saint-Brieuc, I have widened the methodological development to complementary fields, questions and scales of analysis in ecology. Theses propositions had to be validated before they could be used in the Bay of Saint-Brieuc case study. This led me to call ten external data sets from the litterature (Figure 4) to test and validate the interest of these new contributions to bridge a gap in the analysis of ecological changes at different spatial and temporal scales, expending the potential of what we now call 'Ecological Trajectory Analysis' (ETA):

(1) Four data sets from different fields in ecology were used to test ecological trajectory analysis with respect to initial states, and metrics representation in different realms and contexts (Article I).
(2) Six complementary data sets were used to support the development of the Stable Isotope Trajectory Analysis (SITA) framework, which allows the analysis of stable isotope trajectories in two complementary multivariate spaces built respectively to track stable isotope composition dynamics or structural and functional trajectories (Article II).

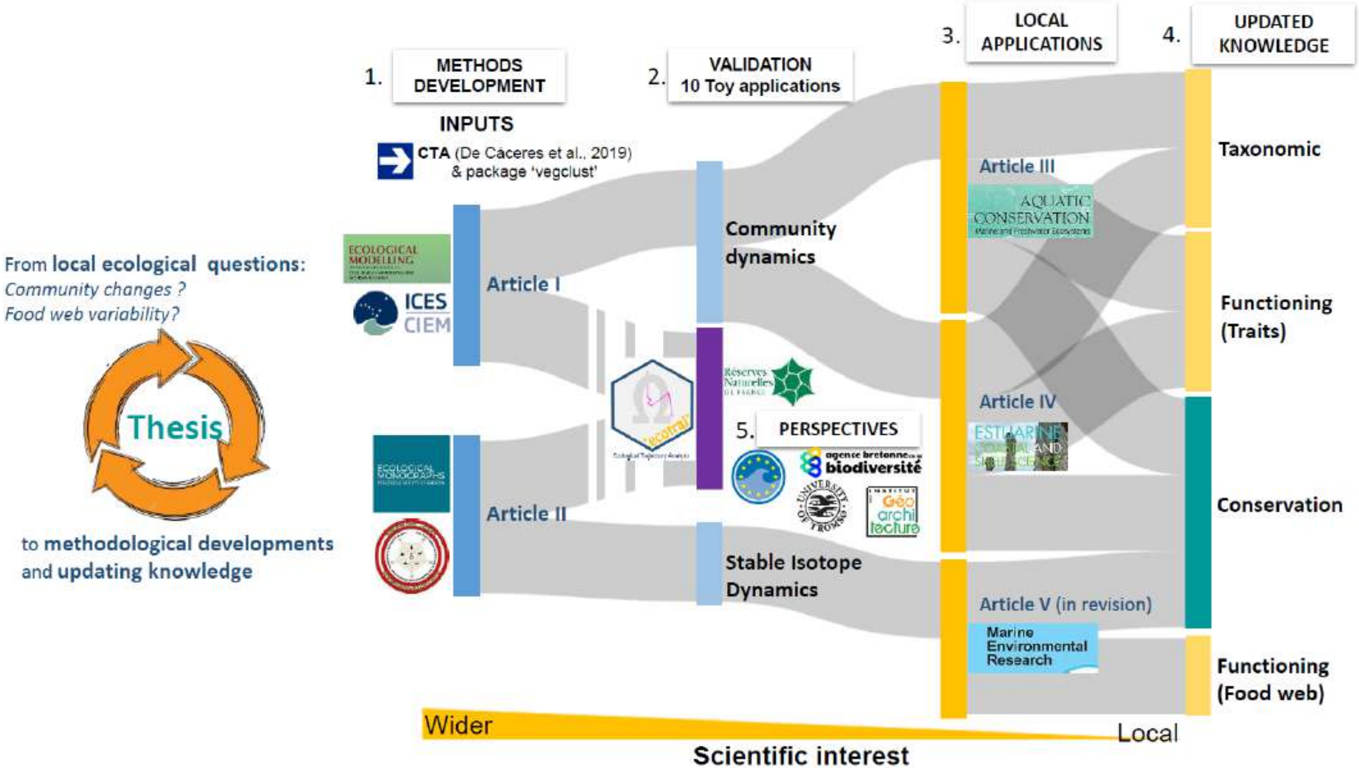


Figure 3: Local ecological questions have required methodological developments building on the Community Trajectory Analysis framework (De Cáceres et al., 2019) and the package 'vegclust'. The thesis articulates around five research articles (see section 'List of contributions'). Ten toy application data sets were called to develop trajectory distance- and direction-based metrics in community ecology (Article I) and stable isotope ecology (Article II), and associated data-visualizations. Ecological Trajectory Analyses were then performed in the bay of Saint-Brieuc to quantify taxonomic and functional changes in intertidal and subtidal benthic communities (Articles III and IV) and analyse spatio-temporal patterns in the intertidal food web (Article V) using the new package 'ecotraj'. Some perspectives have emerged along the doctoral work and concerned: the contribution of Ecological Trajectory Analyses to report ecological status quality within the European Marine Strategy Framework Directive, the development of trajectory analysis training session for managers involved in the Observatoire du Patrimoine naturel littoral and Agence Bretonne de la Biodiversité networks, and Ecological Trajectory Analyses of isoscapes of the North Atlantic with the Artic University of Norway or of Landscape phytosociology with the GéoArchitecture Laboratory.

The methodological development and the 'ecotraj' package designed for ecological trajectories [De Cáceres (2019), Sturbois et al. (Article I)] were used, in a second time, on the bay of Saint-Brieuc data set (Figure 3), to quantify taxonomic and functional changes in intertidal and subtidal benthic communities (Articles III & IV) and to track spatio-temporal patterns within the intertidal benthic food web (Article V).

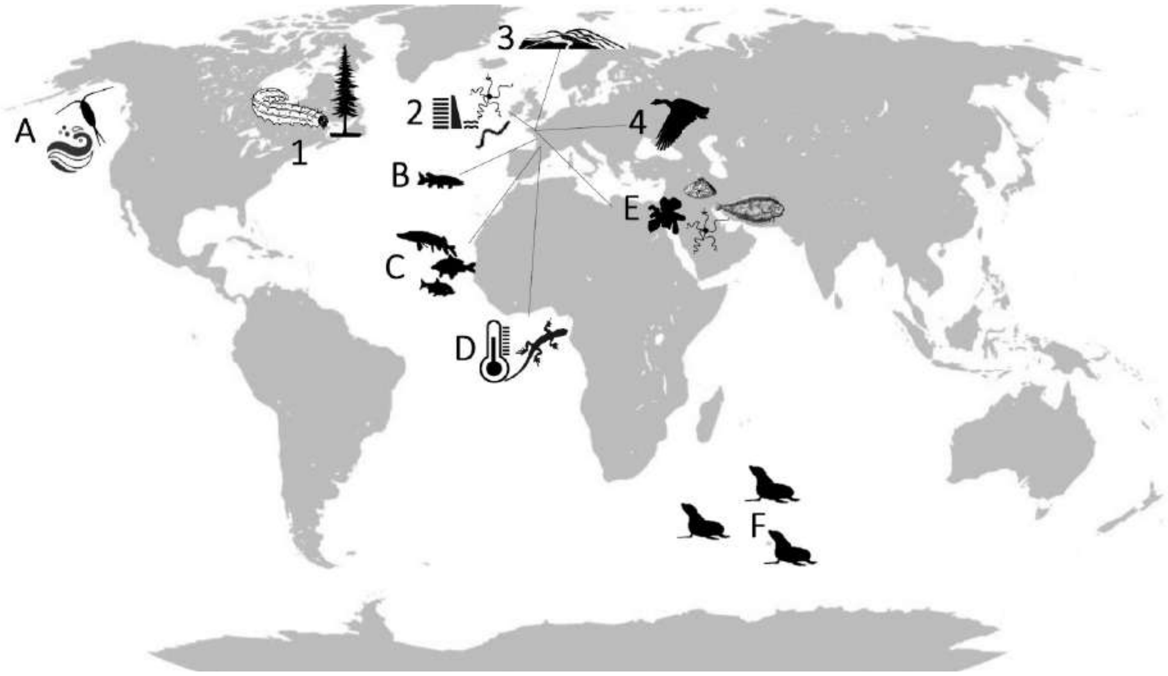


Figure 4: Ecological applications used to explore and test ecological trajectory analysis and representation. *Community Trajectory Analysis* (Article I): 1-Response of boreal forests to insect outbreaks (data set from Sanchez-Pinillos et al., 2019b); 2-Spatio-temporal changes of benthic communities in a modified system controlled for a tidal power station (Desroy and Retière, 2004); 3- Temporal sedimentary variability in a marine intertidal area (Gros and Hamon, 1988; Bonnot-Courtois C. & Dreau A., 2002; Article III); 4- Temporal variability of waterbird communities in a marine protected area (Sturbois & Ponsero, 2019). *Stable Isotope Trajectory Analysis* (Article II): A- Spatio-temporal variability of $\delta^{13}C$ and $\delta^{15}N$ modelled isoscapes in the Northeast Pacific (Espinasse et al., 2020); B- Ontogenic stable isotope trajectories of juveniles fish in a capture-mark-recapture experiment (Cucherousset et al., 2013); C- Trajectory of trophic structure in adult fish food webs of different lakes along the Garonne river (Zhao et al., 2019); D- Responses of Lizard sub-populations under contrasted experimental climatic conditions (Bestion et al. 2019) ; E- Contrasted trajectories in pristine and impacted sandy beaches undergoing green tides events (Quillien et al., 2016) ; F - Spatial and temporal resource partitioning in two species and four populations of fur seals (Kernaléguen et al., 2012).

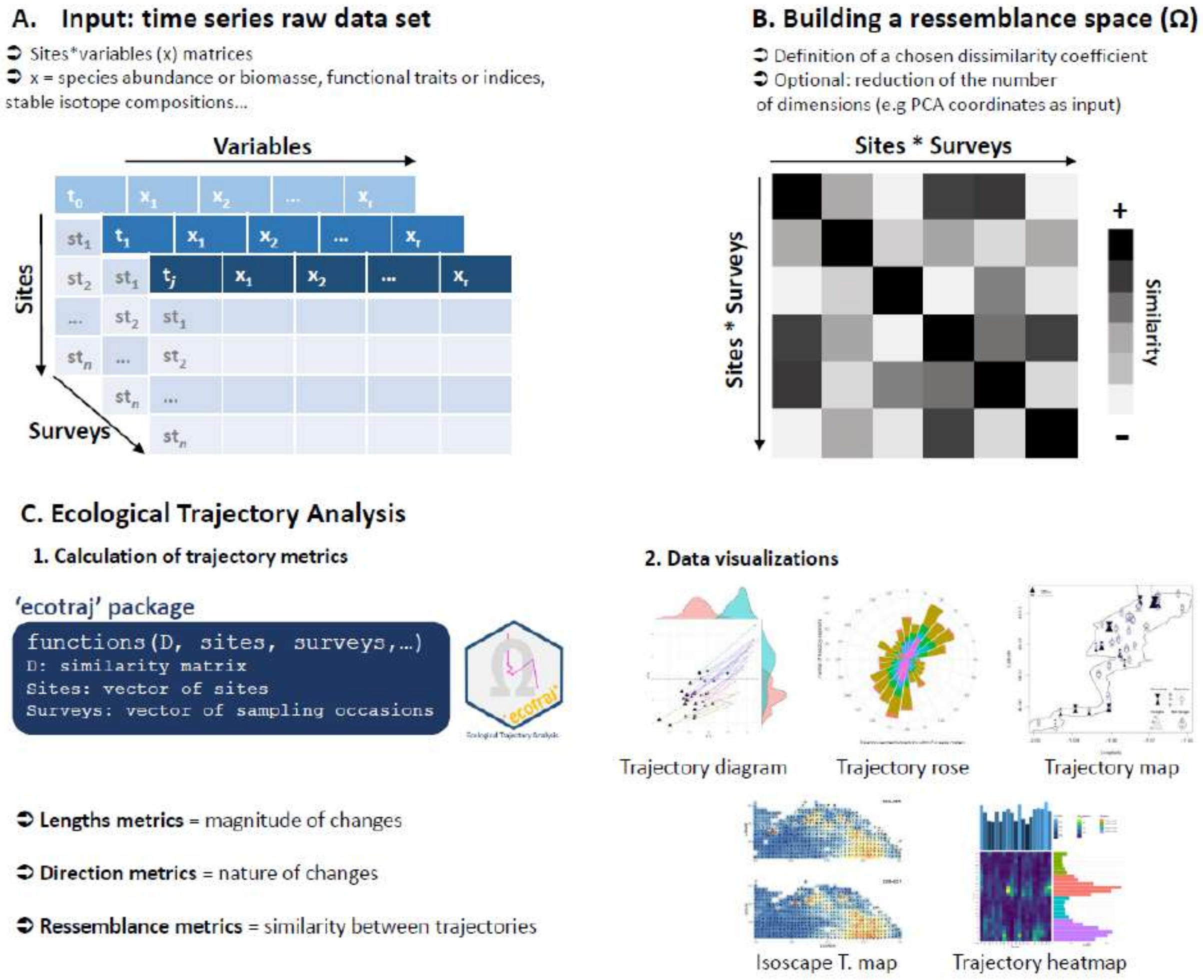
CHAPTER II

Ecological Trajectory Analysis

CHAPTER II | Ecological Trajectory Analysis

2.1 | Introduction

This chapter describes how, building on *Community Trajectory Analysis*, the thesis expands trajectory concepts, metrics and visualisations to an overall integrative *Ecological Trajectory Analysis* framework (Figure 5), by extending the initial CTA framework (section 2.1) and proposing a new framework for stable isotope dynamics (section 2.2).



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functions(D, sites, surveys,…)
D: similarity matrix
Sites: vector of sites
Surveys: vector of sampling occasions
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Figure 5: Main steps and principles of Ecological Trajectory Analysis. A & B: time series raw data sets are used to built a ressemblance space (Ω) supporting trajectory analysis. C. Trajectory-distance and direction-based metrics are calculated with the 'ecotraj' package using three main arguments: D, the distance matrix; Sites, the vector of sampled stations or statistical individual; Surveys, the vector of sampling occasions. Trajectory patterns and metrics are represented through trajectory charts.

2.2 | Community Trajectory Analysis (Article I)

2.2.1 | Introduction

The CTA framework was developed by De Cáceres et al. (2019) to represent temporal changes between $n \geq 2$ consecutives temporal surveys. In the specific case of the intertidal benthic communities of the bay of Saint-Brieuc, the problem arose to know how communities changed in 2001 and 2019, with respect to the initial state defined in 1987? This question refers to a more general one, *i.e.* to know how ecological states change with respect to an initial state and/or to a baseline. To achieve this issue, I suggest an alternative way to analyse trajectories, considering these fixed ecological states as central in the analysis.

This chapter proposes an extension of the CTA to go further than the calculation of lengths and angles between consecutive trajectory segments. It is a complementary tool dedicated to approaches comparing data to an initial state based on distances or distance sequences (Bacouillard et al., 2020; Bagchi et al., 2017; Legendre, 2019; Legendre and Salvat, 2015), differences in cluster classification (Kröncke et al., 2011) or shifts along multivariate axes (McLean et al., 2019).

This chapter section, which refers to article I, focuses on:

(1) the extension of CTA with new distance- and direction-based metrics that notably describe community trajectories with respect to a chosen state;
(2) the synthetic representation of trajectories through three innovative figure concepts: (i) map of changes between ecological states including information about recovering and departing dynamics with respect to a baseline or initial state, (ii) trajectory diagram from initial state to represent trajectory paths and overall changes, (iii) trajectory rose to summarise, in a circular framework, the direction and length of ecological trajectories.

Four data sets were specially called to illustrate the perspectives offered by the extension of the CTA framework (Figure 3). All these ecological applications are presented in article I. In a synthetic purpose, only few aspects are presented in the thesis manuscript to illustrate the CTA extension.

2.2.2 | Concepts, metrics & applications

The terminology used by De Cáceres et al. (2019) was followed for describing and comparing community trajectories in a multidimensional space. Given a target community whose dynamics are surveyed $o_1, o_2, \ldots, o_n$ is an ordered set of n observations ($n > 1$) and $t_1, t_2, \ldots, t_n$, the corresponding set of ordered survey times (*i.e.* $t_1 < t_2 < \ldots < t_n$). For all i in $\{1, 2, \ldots, n\}$, x_i contains the coordinates, or ecological state, corresponding to o_i in a multidimensional space Ω. The geometry of the trajectory T is formalized using a set of $n - 1$ directed segments $\{s_1, \ldots, s_{n-1}\}$, where $s_i = \{x_i, x_{i+1}\}$ is a segment with endpoints (community states) x_i and x_{i+1} (Figure 6, A).

CTA requires the definition of the multivariate space Ω defined by the ressemblance between pairs of observations, measured using a dissimilarity coefficient d [e.g Bray-Curtis, Figure 5, (Legendre and De Cáceres, 2013; De Cáceres et al., 2019)]. Users can choose the scale of CTA by setting the scale at which communities are defined. For example, community trajectories may be studied at the site level, or at larger scales (e.g. landscape or regional level) if community data are aggregated across sites.

Extending distance- and direction-based metrics

CTA allows the calculation of trajectory metrics using geometric trajectory properties. Original CTA metrics relevant for this chapter and new contributions are detailed in the Table I. Distance-based metrics quantify the magnitude of change while direction-based metrics are used for the definition of the nature of change.
The new distance-based metrics developed in the framework of my thesis (Figure 6, B) concern the assessment of:
➲ *Net change*: Community change assessment by the calculation of the distance between any pairs of states with respect to an initial state.
➲ *Net change ratio*: Straightness of recovering or departing processes with respect to an initial state by the calculation of the ratio between the overall net trajectory change and the trajectory path length.
➲ *Recovering or Departing Trajectory*: Definition of recovering and departing trajectory patterns by the calculation of the difference between the two segments lengths including three consecutive states.

The new direction-based metrics developed (Figure 6, C & D) focus on:
➲ *Angle ω*: Linearity of changes with respect to an initial state by the calculation of the direction change of two vectors formed by a triplet of ecological states ordered in time and including an initial state.
➲ *Angle α*: The segment direction in the two dimensions with respect to a reference axis (axis 2 of multivariate space). Angles α can be compared to the influence of the variables used to interpret the two ordination axes.

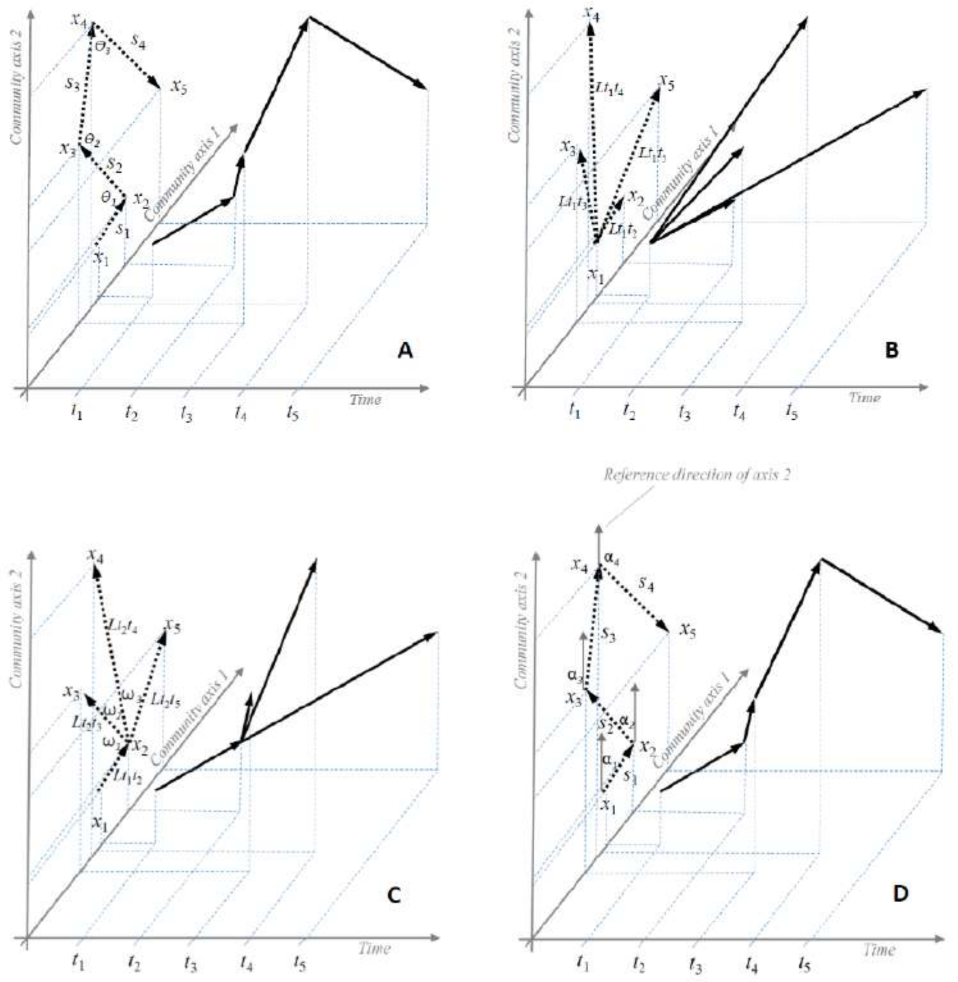


Figure 6: Example of an ecological state trajectory *T* from five observations ($o_1, \ldots, o_5$) at five ordered points in time ($t_1, \ldots, t_5$). Ecological state observations are represented using a corresponding set of states ($x_1, \ldots, x_5$) in a multidimensional space (two principal axes are shown only). The trajectory is represented on the plane formed by community axes and in a three dimensional plot including the time axis (continuous arrows). The trajectory can be also formalized in terms of four directed consecutive segments ($s_1, \ldots, s_4$) in the same space (A). x_i represents positions (coordinates) and s_i are segments, so that the sum of consecutive segment lengths is the total length of the trajectory pathway. One can also consider vectors with respect to the initial state (B,C) with four vectors departing from x_1 (x_1-x_2, ..., x_1-x_5). Lengths Lt_1t_i measure the net change between t_1 and t_i (B). Several spherical angles ($\measuredangle$) can be considered, with different interpretation: $\measuredangle\ \Theta\ (x_i, x_j, x_k)$ is calculated between consecutive segments and defined as the change in direction of vector x_j-x_k with respect to vector x_i-x_j in this plane (A); $\measuredangle\ \omega\ (x_1, x_i, x_j)$ is calculated with respect to the initial state and defined as the change in direction of vector x_1-x_i with respect to vector x_i-x_j in this plane(C); $\measuredangle\ \alpha$ is calculated between each trajectory segment and a chosen direction (here axis 2) in a 2D multivariate space (D).

Table I: Synthesis of distance- and direction-based trajectory metrics. For each metrics, the definition, ecological meaning and equation used for the calculation are detailed. Founder article is also provide to distinguish if metrics were defined within the initial Community Trajectory Analysis framework (De Cáceres et al., 2019), or developed within the thesis (Sturbois et al., 2021, article I).

	Trajectrory metrics	**Definitions / Ecological meaning**	**Equations**	**Founder articles**
Distance-based metrics	*Trajectory segment length*	Distance between two consecutive ecological states ➲ *Magnitude of change between two sampling dates*	$L(s_i)=d(x_i,x_{i+1})$	De Cáceres et al. (2019)
	Trajectory path length	Total of all sites trajectory segments over a study period ➲ *Overall temporal variation of the state of a site within a study period*	$L(T)=\sum_{i=1}^{n-1} L(si)=\sum_{i=1}^{n-1} d(xi, xi+1)$	
	Trajectory speed	Segment length divided by the time interval between observations ➲ *Speed of change*	$S(s_i)=L(s_i)/(t_{i+1}-t_i)$.	
	Net change	Length (i.e. distance) between any pairs of states including an initial state ➲ Changes between the community at the end of a given study period and its initial state	$Lt_1\text{-}t_j=d(x_1,x_j)$	Sturbois et al. (2021) Article I
	Net change ratio	Ratio between the overall net trajectory change and the trajectory path length ➲ Straightness of recovering or departing processes with respect to the initial state	$NCR = Lt_1\text{-}t_{n\ surveys} / L(T)$	
	Recovering or Departing Trajectory	Difference between the two segment lengths including three consecutive states ➲ *Definition of trajectory patterns: recovering (i.e. return to the initial state, RDT>0) or departing (i.e. increasing distance from the initial state, RDT<0)*	$RDT= d(x_1,x_j)-d(x_1,x_k)$	
Direction-based metrics	*Angle θ*	Change in direction of two vectors formed by a triplet of ecological states ordered in time ➲ *Linearity of change (linear when θ = 0°, and opposite in sens when θ = 180°*	$\theta\,(x_i,x_j,x_k)$	De Cáceres et al. (2019)
	Directionality	Assesment of the consistency with which the site is following the same direction ➲ *Distinction between non directional and directional trajectory pattern. DIR(T) is bounded between 0 and 1 where the maximum value corresponds to a straight trajectory*	$DIR(T)=\frac{\sum Wijk * (\frac{180-\theta ijk}{180})}{\sum Wijk}$	
	Angle ω	Change in direction of two vectors formed by a triplet of ecological states ordered in time and including an initial state ➲ *Linearity of changes with respect to an initial sate.* *Recovering when 90°<ω<180°, and departing when 0°<ω<90°*	$\omega\,(x_1,x_j,x_k)$	Sturbois et al. (2021) Article I
	Angle α	Trajectory segment directions with respect to an axe of reference (i.e axis 2 of multivariate space) ➲ *Allows comparing segment direction with respect to the influence of the variables used to interpret the two ordination axes*	$\alpha\,(x_i,x_j,\text{axis } 2)$	

Innovating in the representation of community dynamics

The extension of the CTA framework also includes three chart concepts specially designed for the representation of trajectory metrics.

➲ *Trajectory diagram*: Trajectories are traditionally represented on 2D or 3D ordination diagrams using arrows for segments. I suggest to complete this chart by adding information about trajectory metrics such as net changes (Figure 7). Data point symbols represent the coordinates of each ecological state according to the axes of the ordination diagram and lines represent segments between transitional ecological states. The novelty lies in representing the distance to the initial state (*i.e.* first state of the time series) and time by the dot size and color, respectively. If a single trajectory is represented and one wants to better illustrate the evolution of net changes over time, the trajectory can be centered on the initial state by subtracting the coordinates of the state corresponding to the initial state (x_1) from the coordinates of all ecological states.

Temporal variability of waterbird communities in a marine protected area.

Context and methods - The national nature reserve of Saint-Brieuc (Brittany, France) is a marine protected area designed in 1998 to protect wintering birds. Anatidae populations are monitored each winter as part of the International Waterbird Census (IWC). CTA was performed on the nine most abundant species for which a census has been performed during 21 wintering, from 2000 to 2020. Anatidae monitoring was carried out annually in January, encompassing the whole presumed functional area (*i.e.* intertidal feeding ground). Lengths, angles, and directionality were calculated. The temporal variability of the bird community was illustrated with an ordination diagram centered on the initial survey and representing time and net change using symbol colour and size.

Results and discussion - Lengths of trajectory segments ranged from 2.03 to 6.16 but were quite stable over time (3.46 ± 1.06, total trajectory path= 69.14). At the end of the study period, the distance to the initial state (5.79) was slightly higher than the mean value of net change (4.96 ± 1.28). The ordination diagram (Figure 7) represents the temporal variability of the community with respect to the initial state during the 21 years of sampling. The first axis explained twice as much variance (39%) as the second axis (20%). Different species have influenced the anatidae community. Three species mainly contribute to the first axis and are characterized by a clear decrease in numbers: *Branta bernicla*, *Mareca penelope,* and to a lesser extent *Mareca strepera*. Other species characterised by stable abundances or important interannual variations were mostly expressed on the second axis. The first axis highlights the temporal pattern of the community which is confirmed by the clustering of the most recent sampling occasions on the positive side of the first axis. Alternation of recovering and departing to initial state patterns suggests an ecological turnover in the species involved in ecological change. The small net change ratio between 2000 and 2020 (8.35%) and low directionality (0.375) points out the turnover of species involved in changes at the community scale. In the absence of straight departing or recovering clear dominance, trajectory is gradually directed towards a different ecological state from 2000 to 2020. The anatidae community mainly varied depending on the decline of two of the most numerous species *Branta bernicla* and *Mareca penelope*. Other influencing species are not consistent over time which resulted in a clear spring effect around the initial state. CTA results confirmed the conclusions of Sturbois and Ponsero (2019) and bring new insights concerning the way ecological variability could be expressed through trajectory properties of bird communities within a given site.

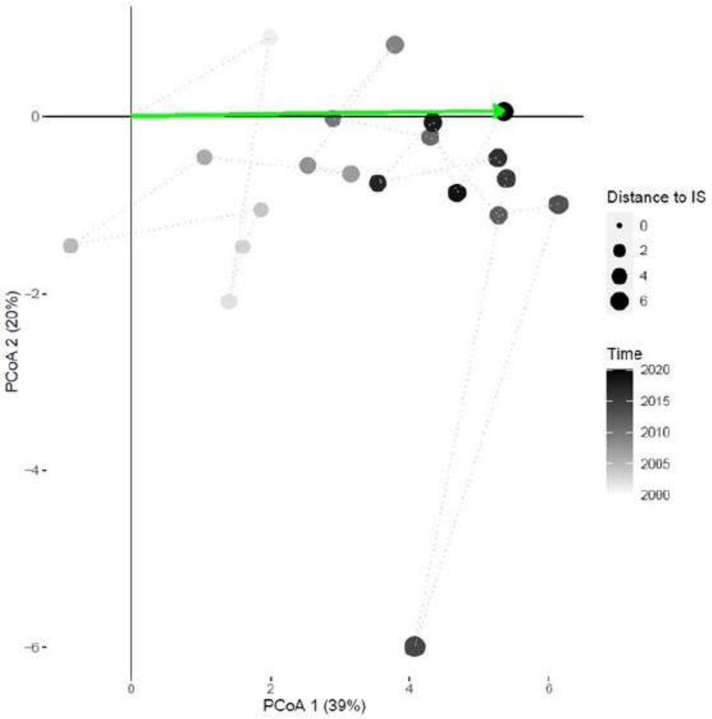


Figure 7: Anatidae community state relative to the initial state chart between 1999 and 2020. The origin of the chart represents the initial state characterized in 1999, points represent intermediate ecological states [size=length of each state to initial state, color= light grey (2000) to black (2020)] and lines represents segments between transitional state. The green arrow represents the net change between 2000 and 2020.

➲ *Trajectory map*: A map was used to represent site scale dynamics through the geometrical properties of trajectories in synthetic figures accounting for temporal variability at the sampling unit scale (Figure 8). In order to avoid multiple distance maps between every pair of surveys, I propose to use a single map to represent all at once for each site of a study area:

(1) net change between x_1 and $x_{n\text{-}survey}$;
(2) segment length (or subtrajectory length, Sb) $S_{i>1}$, and $S_{j>i}$;
(3) recovering or departing segment or subtrajectory lengths between x_i and $x_{n\text{-}surveys}$.

Net changes are represented through a circular symbol proportional to the length to vector x_1-$x_{j>i}$. On both sides, a bottom triangle symbol represents the x_1-$x_{i>1}$ vector and a top triangle the $x_{i>1}$-$x_{j>i}$ vector. For both triangles, the size is proportional to the length of respective vectors, while the orientation and color of the top triangle illustrate the direction (recovering or departing) of the second vector with respect to the initial or baseline state.

Spatio-temporal variability of benthic communities in the Rance basin (Brittany, France).

Context and methods - The spatio-temporal variability of benthic communities was studied in the Rance estuary (Brittany, France), a modified system whose main physical characteristics are controlled by the functioning of a tidal power station (Desroy and Retière, 2004). The construction of the facility began in 1963 and was completed in 1966. Before the construction of this infrastructure, the Rance was a ria with sectors differentiated by saline stratification whereas the system is now clearly separated into two main entities: the marine reservoir and the upstream estuary (brackish water). The construction step led to the formation of a hypohaline basin, inducing immediate strong mortality events for benthic macrofauna, and a period of instability after the tidal power station entered in functioning in 1966 (1967-1975). The control of the physical characteristics of the system has affected sediment dynamics, and deeply modified benthic habitats (Bonnot-Courtois, 1997; Bonnot-Courtois and Lafond, 1991; Retière, 1979).

Soft bottom benthic communities were sampled at 34 stations in 1976, 1995 and 2010 in the upstream estuary in order to analyse the ecological variability associated with the recovery process and sedimentary changes [Figure 8, (Desroy and Retière, 2004)]. A Hellinger transformation was performed on the overall data set prior to multivariate analysis (PCA) and coordinates of sites on the ordination diagram for the three surveys were used as inputs for CTA. A trajectory map was produced in order to synthetize trajectories of benthic communities on each site through the three surveys. After data aggregation depending on the station location (upstream vs down-stream), a second CTA analysis was performed in order to verify if local changes resulted in larger scale variations.

Results and discussion - The species richness dramatically decreased from 149 species in 1976 to 54 and 73 species in 1995 and 2010, respectively. 27 species were common to the three surveys. A high variability of faunal composition was observed since 14 species appeared and 70 disappeared between 1976 and 1995 vs 38 new species and 19 less between 1995 and 2010. At the scale of the overall monitoring period, 34 new species were observed between 1976 and 2010 and 71 species disappeared. According to the cumulative trajectory path length of all sites, the first period was characterized by a higher ecological variability 539.69 (15.87 ± 7.70) than the second 469.92 (13.82 ± 5.14). Considering trajectory path length at the station scale, seven stations (59, 66, 63, 67, 57, 61, 58) represented 32.48% (327.96) of the whole trajectory path and segment lengths were more important during the second period for 13 stations (31,71%). Two main spatial trajectory patterns were identified (Figure 8). A set of eight stations mainly located in the upstream part (south) of the study area were characterized by lower net (19.67 ± 3.84) and consecutive changes (9.07± 2.30). Inversely, higher changes characterized other stations mainly located in the downstream part (north), both at the scale of the overall study period (37.60 ± 13.98) and consecutive ones (16.41 ± 6.43). This increasing change along the upstream/downstream gradient is confirmed by significant correlations between latitude and net changes (0.40; p-value = 0.01944) and trajectory path lengths (0.45; p-value = 0.00685). RDT was positive for 12 sites and negative for 22, showing an overall departing from the initial state dynamics for 64.71% of sites, mainly located in the northern part of the study area (Figure 8). Lower NCR values indicate significant direction changes between 1976-1995 and 1995-2010 trajectory segments. It implies that changes are induced by different species groups between both periods. Differences in the magnitude of changes revealed at local scales areas also result in contrasted overall trends (Net change) at the larger scale of upstream (23.59) and downstream (49.77) communities.

The community described in 1976 was already undergoing a recovery process, which explains species losses and gains in the following surveys. According to the trajectory length of both periods and departing trajectories occurring in 64.71% of the stations, benthic communities are not yet stabilized in the study area. This seems particularly true for downstream stations, which suffered most changes. In this area, regular changes in environmental conditions according to the estuary functioning influenced by the power station would probably not lead to a stabilization of benthic communities except if some species characterized by high dynamics induce long term changes of sediment facies (e.g. invasive species such as *Crepidula fornicata* and *Ruditapes philippinarum).* Inversely, upstream stations are more stable probably due to environmental factors (influence of freshwater) which limit the variability of communities through a drastic selection of species. Future surveys will help verify these hypotheses.

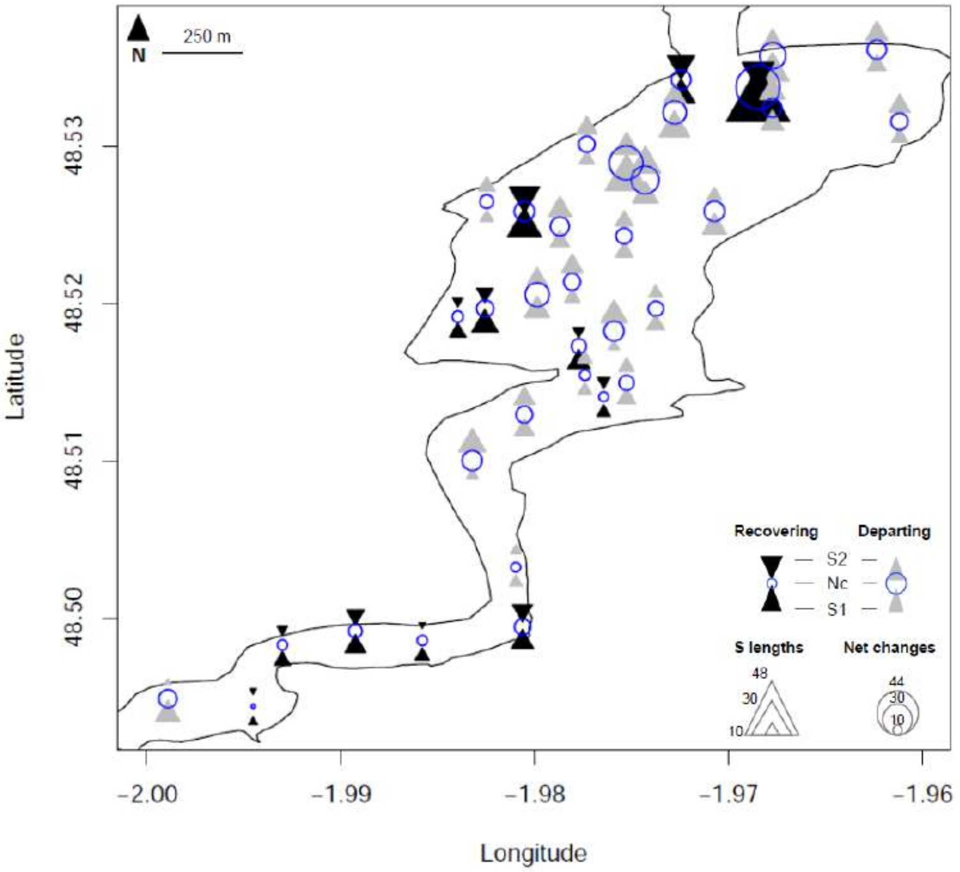


Figure 8: Benthic community trajectory map. Net changes (Nc) are represented with blue circles between 1976 and 2010. Bottom triangles represent S1 (1976 to 1995) and top ones S2 (1995 to 2010). The size of the symbols corresponds to lengths. For triangles, colors are used to distinguish recovering (black) from departing trajectories (grey).

➲ *Trajectory rose*: Trajectory Rose (TR) is proposed to represent the circular distribution of directions in the multivariate space Ω Figures 9 and 10), as it is traditionally done in meteorology to represent wind directions and speeds (Azorin-Molina et al., 2017; Cieszyńska and Stramska, 2018) or for current orientation (Dalbosco et al., 2020; Dufresne et al., 2014). The TR consists of a circular bar plot of angles ranging from 0° to 360°. The barplot structure of TR allows representing factors in different bar sections. The baseline state TR provides a synthetic visualisation of ecological trends at the scale of a study area according to directional changes (0-360°) of one vector with respect to the previous one for each consecutive triplet over time. Users can choose to represent distributions of ϴ, or ω, angles in order to analyse changes of direction of each triplet or the direction of each segment with respect to the previous or the first segment of the trajectory, respectively.

- *Distribution of Θ, ω values*

Angles Θ_i between segments x_i-$x_{j>i}$ and $x_{j>i}$-$x_{k>j}$ are defined between 0° and 180° when considering all multivariate dimensions, or can be reported in a 0-360° system if calculated from 2D coordinates. Angles ω_i between segments x_1-$x_{i>1}$ and $x_{i>1}$-$x_{j>i}$ are also reported in a 0-360° system when calculated on 2D coordinates. At this step of the procedure, the user must consider whether the variance explained by the two first components is sufficient to evaluate angles in a 0-360° system in an ecologically meaningful way.
A value of 0° indicates a straight *Departing* segment with no change of direction with respect to x_1-$x_{i>1}$ vector. The distribution of angles is represented in barplots whose size indicates the number of segments following a given direction: *Recovering* on the bottom part ($90° < \omega < 270°$) and *Departing* in both parts depending on the length of the second segment of each triplet. Lengths of vectors {x_j, x_k} are aggregated on the top of each bar section and colored according to distance, in order to underline if direction trends occur in short or long trajectories.

- *Distribution of α values*

α angles are calculated considering the second axis of the ordination diagram as the North (0°) and represented in a TR in order to illustrate distribution of segment direction in a 2D Euclidean space. It allows the characterization of the nature of change by comparing segment direction with respect to the interpretation of ordination axes. Variables names aiding the interpretation of directions can be indicated in the periphery of the TR

The trajectory rose concept has been tested for the representation of the:

(1) temporal sedimentary variability in a marine intertidal area (Angle α, Figure 9)
(2) response of boreal forests to insect outbreaks (Angle ω, Figure 10).

The temporal sedimentary variability was assessed in the southern intertidal part of the bay of Saint-Brieuc.

Context and methods - Grain size composition were studied at 42 sedimentary sites in the intertidal area of the bay of Saint-Brieuc in 1987 (Gros and Hamon, 1988), 2001 (Bonnot-Courtois and Dreau, 2002) and 2019 (**Article III**). At these dates, one sample of sediment was collected with a handcorer (5 cm diameter, depth of 5 cm) at each site and subsequently analysed for grain size distribution in the laboratory. Statistical analyses were performed with the package G2sd (Fournier et al., 2014). Sedimentary data from the three periods were combined in the same dataset subjected to CTA analysis. Two TR were then produced in order to illustrate the distribution of α angles for both periods with respect to sedimentary variables localised at the periphery of TR according to their position in the variable factor map (PCA). Finally, HR and Watson-William's tests were performed to test the homogeneity of angles distribution and the difference of segment direction between periods, respectively.

Results and discussion - The first two dimensions of the PCA explained 81.8% of the variance, which allowed the consideration of trajectory and segment properties with respect to these components. Trajectory path was lower for the period 1987-2001 (Total trajectory path: 72.17; mean: 1.72±1.55) than for the period 2001-2019 (99.67; 2.37±1.96) which indicated more sedimentary variability in the second period. However, the sedimentary dynamics (*i.e.* speed of changes) was quantitatively quite similar for the two periods (1987-2001:5.16 vs 2001-2019: 5.53). During the first period, 7 stations contributed to 46.38% of the trajectory path, whereas 12 stations were responsible for 59.20% of changes between 2001 and 2019. This reveals that few sites are characterized by a high sedimentary variability (length >3) while changes in most stations were more moderate. The TR qualitatively represents the pattern of the segments direction according to sedimentary variables (Figure 9). During the first period, segment direction mainly occurred in the bottom part of the rose (HR test: T=11.07, *p-value*=0.004) according to different sand variables from very fine to fine whereas for the segments of the second period it occurred in the top part of the rose (HR test: T=13.77, *p-value*=0.002) according to very fine sand, mud and coarse sediment variables (Watson test: T=0.896; p-value<0.001). Thirty years sedimentary changes in the intertidal part of the bay of Saint-Brieuc resulted in:

(1) an overall slight sloughing revealed by the increase in the contribution of very fine sediment classes over the study period;

(2) a high variability at few stations contrasting with moderate changes in the rest of the study area. This ecological application confirmed that angles and lengths are relevant trajectory properties to qualitatively and quantitatively describe trajectory patterns according to period or other factors such as habitat, management or pressure.

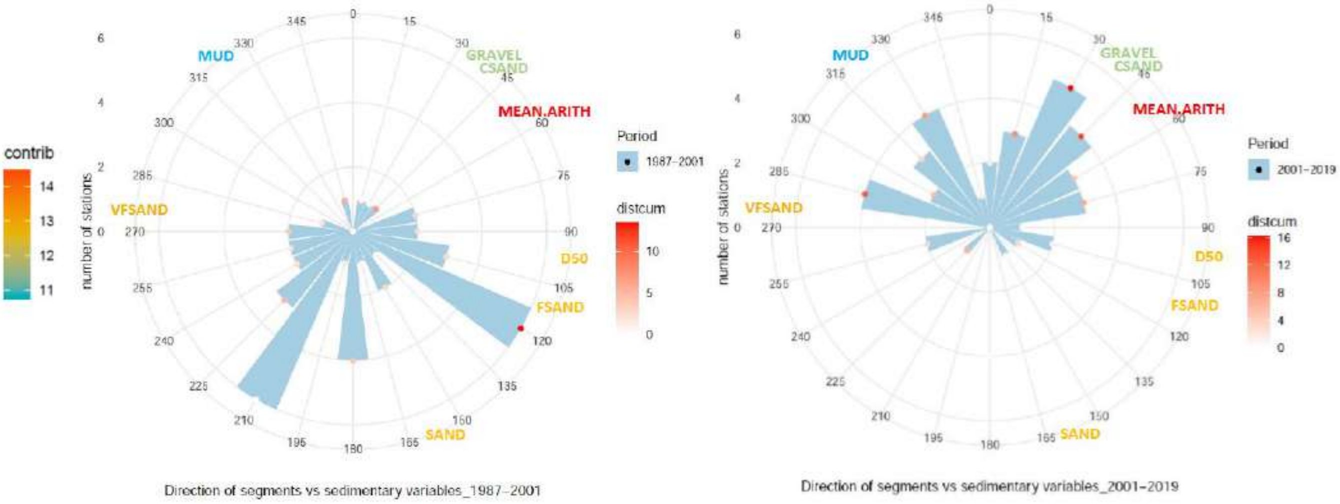
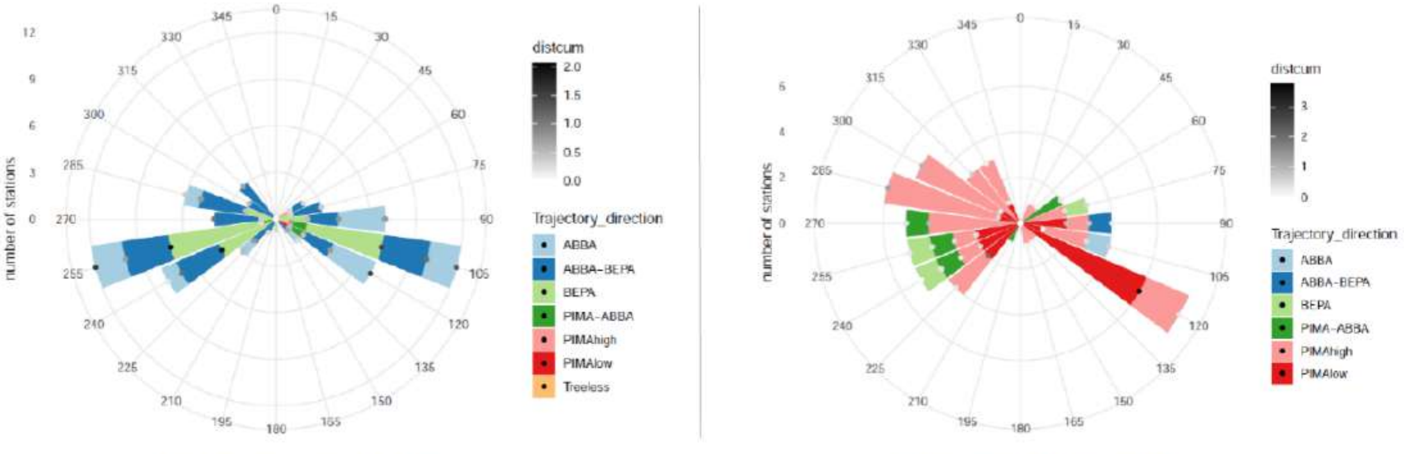


Figure 9: α trajectory rose for both periods (1987-2001 and 2001-2019) with respect to the two first components of the PCA (81.8% of the variance). Bars represent the number of stations concerned by each range (15°) of direction. Cumulative segment lengths are represented with point at the head of each bar and colored according to length values. Sedimentary variables occurred in the periphery of the TR faithfully to the PCA ordination diagram and are colored depending on their contribution to the two first components.

Response of boreal forests to insect outbreaks.

Context and methods - The response of boreal forests to insect outbreaks was analysed with trajectory metrics and representation. The spruce budworm (*Choristoneura fumiferana* Clem.) is considered among the most severe defoliating insects of boreal and sub-boreal forests of eastern North America (Blais, 1957). Every 30 to 40 years, its populations synchronously reaches outbreak levels over large spatial scales, generating dramatic ecological and economic impacts due to important mortality events in areas dominated by balsam fir (*Abies balsamea* L.) and spruce (*Picea* spp.). Whereas balsam fir usually presents higher levels of defoliation and mortality rates than spruce species of northern latitudes, a recent study (Sánchez-Pinillos et al., 2019b) found a higher resilience of forests dominated by balsam fir than by black spruce (*P. mariana* Mill.). On the contrary, black spruce forests proved to be highly resistant to the insect attack but collapsed under long and severe outbreaks. We used a subset of plots affected by spruce budworm outbreaks and selected by Sánchez-Pinillos et al. (2019b) from Quebec´s Forest Inventory (Ministère des Ressources Naturelles du Quebec, 2013) to assess forest responses to insect outbreaks with respect to individual pathways. In particular, we compared the dynamics of 74 mixed communities co-dominated by balsam fir and white birch (*Betula papyrifera* Marsh.) and 74 stands dominated by black spruce. Forest plots were characterised with species abundance and size classes for the most common species. CTA metrics were used to characterize forest responses to the perturbation and a TR of ω distribution to illustrate differential responses according to the type of forest.

Results and discussion - The changes in mixed fir-birch forests were reflected through longer trajectory paths (64.73) and lower net change (42.17) than the homologous in black spruce forests (47.70 and 59.95, respectively). However, both forests showed similar trajectory patterns, with longer distances between the pre-disturbance and disturbed states (sum $S_{1,\text{fir-birch}}$ = 37.95; sum $S_{1,\text{spruce}}$ = 39.12) than between the disturbed and post-disturbance states (sum $S_{2,\text{fir}}$ = 26.77; sum $S_{2,\text{spruce}}$ = 20.83). The TR of ω distribution showed a clear rupture in trajectory direction between disturbed and final state for both forest typologies. Many plots did not show changes in forest classification. It is important to note that dissimilarities between forest surveys were calculated by considering different size classes for the most common species in boreal forests (*P. mariana, P. glauca, A. balsamea,* and *B. papyrifera*). The TR analyses, therefore, illustrated the changes in forest structure resulting from the death of the most vulnerable trees. Thus, most black spruce forests remained with the same composition after the outbreak or changed toward forests with a lower basal area represented by a different forest typology (Figure 10-B, *PIMAhigh*). In the case of mixed forests of balsam fir and white birch (Figure 10-A, *ABBA-BEPA*), our results showed different successional stages including the dominance of white birch colonizing gaps, a transient stage of mixed fir-birch stands, and a last successional stage dominated by balsam fir.



A – Trajectories direction of stations – ABBA-BEPA

B – Trajectories direction of stations – PIMAhigh

Figure 10: ω trajectory roses for forest plot characterised as mixed forests of balsam fir and white birch (ABBA-BEPA, A) or dominated by black spruce (PIMAhigh, B) at the pre-disturbance state. Bars represent the number of segments concerned by each range (15°) of direction with coloured sections according to the type of forest defined at the final state: *Abies balsamea* (ABBA), *Betula papyrifera* (BEPA), *Picea mariana* (PIMA). Cumulative lengths of the second segments (disturbed to final state) of each triplet are represented with point at the head of each bar and colored according to lengths values (white to black). Direction 0° represents a straight departing in the same direction as the first segment of each triplet. Direction 180° represents the direction of the return to the initial state (first ecological state of each triplet).

2.3 | Stable Isotope Trajectory Analysis (Article II)

2.3.1 | Introduction

Stable isotope analysis has emerged as one of the most popular approaches to study the trophic ecology of organisms (Fry, 2008), fluxes of matter and energy within and between ecosystems (Peterson and Fry, 1987), and animal movements (Bouillon et al., 2011; Rubenstein and Hobson, 2019). The quantitative analysis of stable isotope data is based on a large variety of available analytical tools ranging from qualitative inferences using isotopic niche (Newsome et al., 2007) to complex Bayesian mixing models that can be used to characterize food-web structure and trophic pathways at multiple levels of biological organisation (Layman et al., 2012). Understanding and quantifying spatial and temporal changes is an overarching topic in stable isotope ecology but studies are, to date, largely qualitative and the development of quantitative approaches is needed.

The quantitative analysis of stable isotope dynamics in response to ecological and environmental changes, notably those induced by human activities, has been explored through the comparative analysis of temporal trajectories in a two-dimensional (usually $\delta^{13}C$ and $\delta^{15}N$) isotopic space (δ space). For instance, Schmidt et al. (2007) and Wantzen et al. (2002) quantified the direction and magnitude of temporal changes in food-web structure based on the geometric properties of δ space. Schmidt et al. (2007) used circular charts and statistics to represent and test direction shifts in the δ space. Turner et al. (2010) characterized attributes of path trajectories (size, direction and shape) over data sets containing more than two temporal samples to provide a quantitative description of how stable isotope compositions change in response to spatial and temporal gradients and tested their differences. Despite the fact that these works have provided substantial new perspectives notably for statistical and hypothesis testing, some limitations remain for the explicit quantitative description, analysis and representation of the magnitude and the nature of changes in stable isotope ecology.

In community ecology, several statistical frameworks have been proposed and used to test hypotheses on temporal dynamics (Buckley et al., 2021b; De Cáceres et al., 2019). The dynamics of ecological communities has been widely represented on ordination diagrams in which changes over time are represented by a set of vectors linking consecutive ecological states (Austin, 1977; Hudson and Bouwman, 2007; Legendre and Salvat, 2015; Matthews et al., 2013). The geometric properties of trajectories, defined in the space of an ordination diagram, are now considered as relevant parameters to quantify the dynamics of ecological systems. The potential of geometry-based methods was illustrated by De Cáceres et al. (2019) in the Community Trajectory Analysis (CTA) framework. Compared to previous approaches based on ordination diagrams, De Cáceres et al. (2019) considered community dynamics as trajectories in a chosen space of community resemblance, with no limit in the number of dimensions included. Trajectories are defined as objects composed of consecutive segments to be analysed and compared using metrics based on their geometry in the chosen space. CTA allows the calculation of distance- and direction-based metrics considering all components in multivariate spaces. Recently, Sturbois et al. (Article I) developed new CTA metrics and synthetic representation approaches, such as trajectory roses, and the inclusion of trajectory metrics in maps or ordination diagrams.

By analogy to community ecology, the term and the concept of trajectory have been sometimes used in stable isotope ecology to characterize dynamics and represent them in spaces of analysis [either δ space, p-space *sensu* Newsome et al. (2007), or spaces based on community-wide indices (e.g. Rigolet et al., 2015)]. The analysis and representation of stable isotope trajectories or contrasted patterns requires the use of quantitative geometric properties in 2D δ spaces often complemented by vectors in stable isotope scatter plots and/or circular representation (Agostinho et al., 2021; Black and Armbruster, 2021; Cucherousset et al., 2013; Schmidt et al., 2007). However, scientists are increasingly faced with multivariate datasets (i.e. >2 dimensions) in stable isotope ecology in response to the potential use of (1) other isotopes to complement $\delta^{13}C$ and $\delta^{15}N$ [e.g. $\delta^{34}S$ (Connolly et al., 2004), δD (Doucett et al., 2007), Δ199Hg (Besnard et al., 2021)] and (2) numerous structural and functional community wide metrics or indices (Cucherousset and Villéger, 2015; Layman et al., 2007). While the availability of long-term, large-scale, and high-resolution data is one of the most limiting factors to study temporal patterns in stable isotope ecology, the development of methods to analyse, synthesize, and ultimately represent the dynamics of ecological systems still remains an essential issue to complete current approaches by more quantitative and formal explicit frameworks.

This chapter section (**Article II)** aims to provide a quantitative framework for the analysis of stable isotope temporal dynamics at different levels of biological organisation, from individuals to ecosystems. In a new approach referred to hereafter as *Stable Isotope Trajectory Analysis (SITA)*, a definition of the trajectory concept applied in stable isotope ecology, and the adaptation of the CTA framework to stable isotope analysis and derived structural and functional trajectories are proposed. Potential applications in the analysis of stable isotope, structural and functional temporal and spatial patterns are illustrated using field, experimental or model-based ecological applications specially called in this thesis and including four main integration scales which are commonly addressed in stable isotope ecology:

(1) individual level;
(2) population level;
(3) structural and functional trajectories of entire food webs;
(4) modelling of stable isotope dynamics at high spatio-temporal resolutions.

Some examples are used to illustrate the interest of SITA and associated chart concepts. More details about the six ecological applications (Figure 11) are available in **article II.**

2.3.2 | Concepts, metrics & applications

Spaces supporting SITA

SITA requires the definition of Ω defined by the resemblance between pairs of observations, measured using a dissimilarity coefficient *d*. SITA analysis is based on the dissimilarity values contained in a distance matrix Δ=[*d*] (De Cáceres et al., 2019).

The trajectory concept in stable isotope ecology may be addressed in terms of stable isotope composition or food web structure and functioning involving similar attributes (*i.e.* trajectory metrics), but different data inputs and space of analysis (Figure 11).

➲ *Stable isotope Ω_δ space*: Ω_δ is defined with the stable isotope composition of different elements. Coordinates in this space of analysis corresponds to raw stable isotope data (δ). Despite $\delta^{13}C$ and $\delta^{15}N$ are the most commonly employed in a bidimensional context, other elements which are ecologically meaningful may also be considered for defining the Ω_δ space (*e.g.* hydrogen δD, sulfur δ^{34}S, or oxygen δ^{18}O). Coordinates in Ω_δ are used to compute the resemblance between ecological states using *d*, where we suggest to adopt the Euclidean distance, as it is commonly used in stable isotope ecology (Ben-David et al., 1997; Kline Jr. et al., 1993; Schmidt et al., 2007; Turner et al., 2010; Wantzen et al., 2002; Whitledge and Rabeni, 1997).

➲ *Structural and functional Ω_γ space*: Looking for general patterns in stable isotope ecology often required the use of community-wide metrics or any structural or functional indices based on raw stable isotope data (Cucherousset and Villéger, 2015; Layman et al., 2007; Rigolet et al., 2015). Ω_γ is defined with any indices derived from raw stable isotope data, used as ecological proxies, such as to characterize food web structure, and allow comparison within and among systems.

SITA metrics

SITA follows the CTA terminology and metrics defined by De Cáceres et al. (2019) and Sturbois et. al. (**Article I**) and detailed in the previous section. De Cáceres et al. (2019) also developed a geometrically-based approach to trajectory resemblance which includes the shape, size, direction and position of trajectories with respect to the resemblance between all observations (states) belonging to a same trajectory. The approach defines resemblance between pairs of segments or overall trajectories and allows the definition of trajectory clusters.

Representing trajectories in stable isotope ecology

➲ *Trajectory diagram*: Temporal dynamics in stable isotope ecology are sometimes represented in 1D or 2D δ space by segments or arrows between consecutive surveys (Agostinho et al., 2021; Guzzo et al., 2011). The trajectory diagram (TD) concept allows the customisation of ordination diagrams by adding notably SITA objects and metrics. Trajectory segments are represented by segments between surveys to form the trajectory path whose last segment is ended by an arrow. By doing so, the visualisation of distance- and direction-based metrics becomes more intuitive on diagrams. If one wants to go further in the representation of trajectory net changes, then:

(1) net changes may be represented at each transitional state by the data point size;

(2) the overall net change may be represented by a dotted line or arrow between the initial and last state of a time series. We recommend also the generalisation of density curves in the periphery of trajectory diagrams as it is sometime done to compare different food webs (Zapata-Hernández et al., 2021).

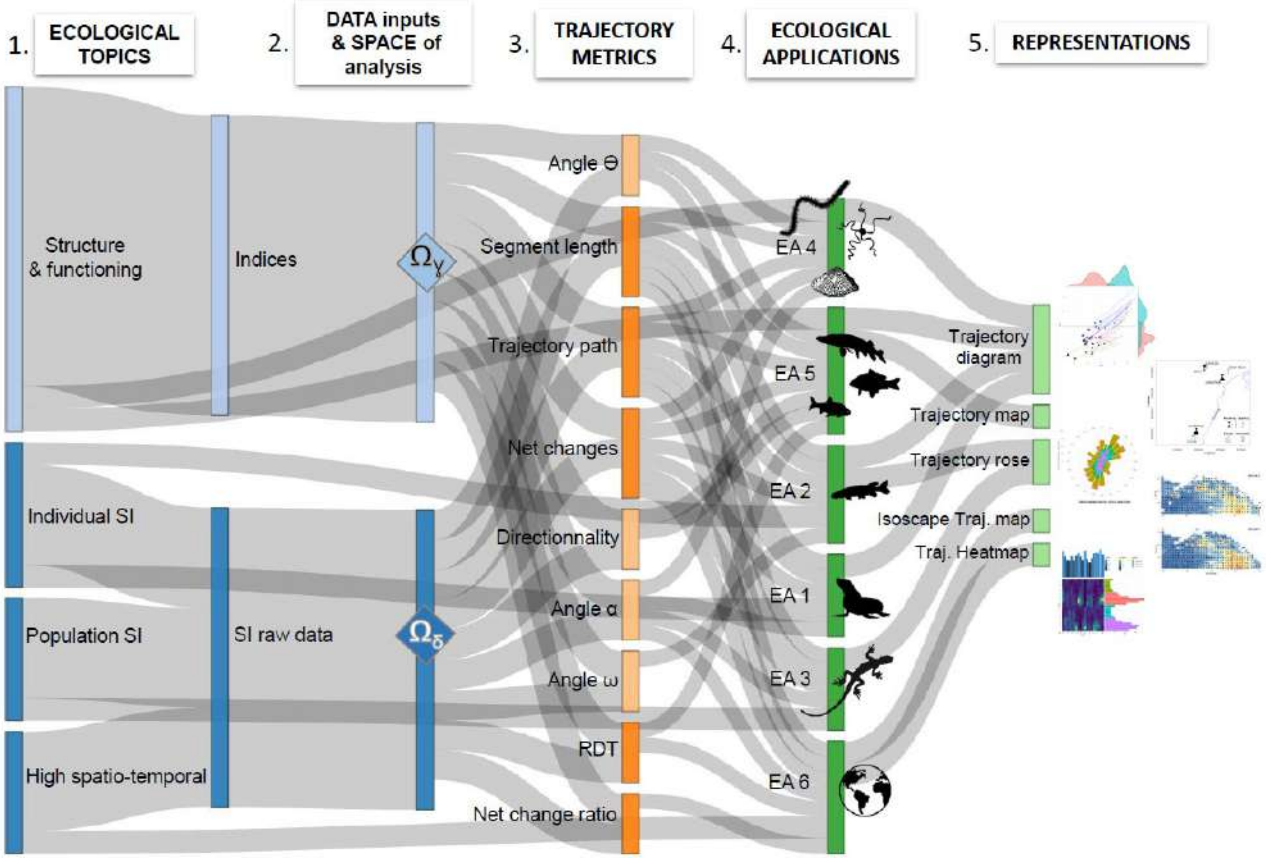


Figure 11 : Levels of analysis and ecological topics drive inputs data used to define the space of analysis supporting SITA analysis. While structural and functional analysis required community wide-metrics or indices to define Ω_γ, raw stable isotope data are used for the definition of Ω_δ that support SI trajectories at different levels from individual to population, or for ecological questions that involve high stable isotope spatio-temporal resolutions. The SITA adaptability allows the calculation of distance and directions based trajectory metrics in both, Ω_δ and Ω_γ, and their visualization in different figures devoted to the representation of dynamics. Six ecological applications were used to test and explore the potential of SITA: EA 1 - Spatial and temporal resource partitioning in two species and four populations of fur seals (Kernaléguen et al., 2012); EA 2 - Ontogenic stable isotope trajectories of juvenile fish in a capture-mark-recapture experiment (Cucherousset et al., 2013); EA 3 - Responses of Lizard sub-populations under contrasted experimental climatic conditions (Bestion et al. 2019a); EA 4 - Contrasted trajectories in pristine and impacted sandy beaches undergoing green tides events (Quillien et al., 2016); EA 5 - Trajectory of trophic structure in adult fish foodwebs of different lakes along the Garonne river (Zhao et al., 2019); EA 6 - Spatio-temporal variability of $\delta^{13}C$ and $\delta^{15}N$ modelled isoscapes in the Northeast Pacific (Espinasse et al., 2020).

Spatial and temporal resource partitioning in fur seal populations.

Context – Many generalist populations are composed of individual specialists and individual specializations are increasingly recognized as an important component of many ecological and evolutionary processes (Bolnick et al., 2003), making crucial testing the consistency of individual specialization.

Methods – $\delta^{13}C$ and $\delta^{15}N$ values of metabolically inert tissues reflect diet at the time of their growth, and continuously growing tissues can be used as time-recorders of individuals movements and dietary history. Fur seals [the Antarctic fur seal *Arctocephalus gazella* and subantarctic fur seal *A. tropicalis*] whisker stable isotope values yield unique long-term information on individual behaviour which integrates the spatial, trophic and temporal dimensions of the ecological niche (Cherel et al., 2009; Cherel and Hobson, 2007; Kernaléguen et al., 2012). The foraging strategies of these two species of sympatric fur seals were examined in the 2001/2002 winter at Crozet, Amsterdam and Kerguelen Islands (Southern Indian Ocean) by measuring the stable isotope compositions of serially sampled whiskers (see Kernaléguen et al., 2015, 2012 for stable isotope preparation and analyses). The method consists in the analysis of consecutive whisker sections (3 mm-long) starting from the proximal (facial) end, with the most recently synthesized tissue remaining under the skin. Only individuals (n = 47) with whiskers totalizing at least 30 sections were selected, and only those 30 sections were considered here, from t_1 (more recent values) to t_{30} (oldest values). SITA was performed to track individual specialization within and among four fur seal populations. Different distance-based metrics (segments lengths, trajectory path, net changes) were calculated in the 2D Ω_δ space ($\delta^{13}C/\delta^{15}N$) for each individual. Dissimilarities between individual trajectories were calculated [Directed Segment Path Dissimilarity (De Cáceres et al., 2019)], and used with the resulting symmetric matrix as input in a Hierarchical Cluster Analysis (Ward.D2 clustering Method), to define different groups of similar individual trajectories. Segment length, trajectory path length, and whisker $\delta^{13}C$ / $\delta^{15}N$ values were summarised to illustrate the trophic variability for each trajectory cluster.

Results - SITA revealed contrasted stable isotope dynamics among species, sexes, and individuals. Hierarchical cluster analysis identified six main trajectory clusters, characterised by differences in SITA metrics and whisker $\delta^{13}C$ / $\delta^{15}N$ values (Figure 12). Clusters 1, 3, and 4 were exclusively composed of trajectories corresponding to males, from the Antarctic fur seal only (clusters 1 and 4) or from both species (cluster 3). These clusters were characterized by the highest values in distance-based metrics, revealing wider foraging strategies. Cluster 1 and 4 were characterized by lower $\delta^{13}C$ values contrasting with cluster 3. Cluster 2, characterized by a lower isotopic variability, grouped all of the 15 female Antarctic fur seal from Crozet and Kerguelen and included also 1 male Antarctic fur seal and three female subantarctic fur seal. Individuals of cluster 5 (5 females and 1 male subantarctic fur seal from Crozet) exhibited the lowest isotopic variability. Cluster 6 was exclusively composed of females subantarctic fur seal from Amsterdam revealing a clear trophic segregation of females breeding on this island.

Different foraging strategies characterized by some overlaps, and partly influenced by breeding sites were revealed for male Antarctic fur seal (distributed in four trajectory clusters) and female subantarctic fur seal (3 clusters). Each individual exhibited a more or less well defined trophic cycle whose amplitude and period depended on trajectory clusters.

Discussion – The estimated $\delta^{13}C$ values of the Polar Front and of the Subtropical Front for fur seal whiskers are approximatively -19 and -16 ‰, respectively (Cherel et al. 2009). Accordingly, Kernaléguen et al. (2015, 2012) showed:

(1) a spatial foraging gradient from southern cold waters to northern and warmer areas for, in order, male Antarctic fur seal, female Antarctic fur seal and male and female subantarctic fur seal;
(2) males benthic feeding strategy near breeding places;
(3) $\delta^{13}C$ and $\delta^{15}N$ oscillation patterns in most whiskers.

Trajectory analysis results are congruent with those conclusions, but this approach goes beyond showing that individual feeding strategies transcend pre-established categories such as species, genders and breeding places, which was not obvious from the initial analysis at the population level. This application confirms that SITA metrics and representations are relevant to track the shape and the magnitude of stable isotope trajectories in δ space at different scales from individual to population, particularly to reveal subtle relevant functional patterns in spatio-temporal resource partitioning.

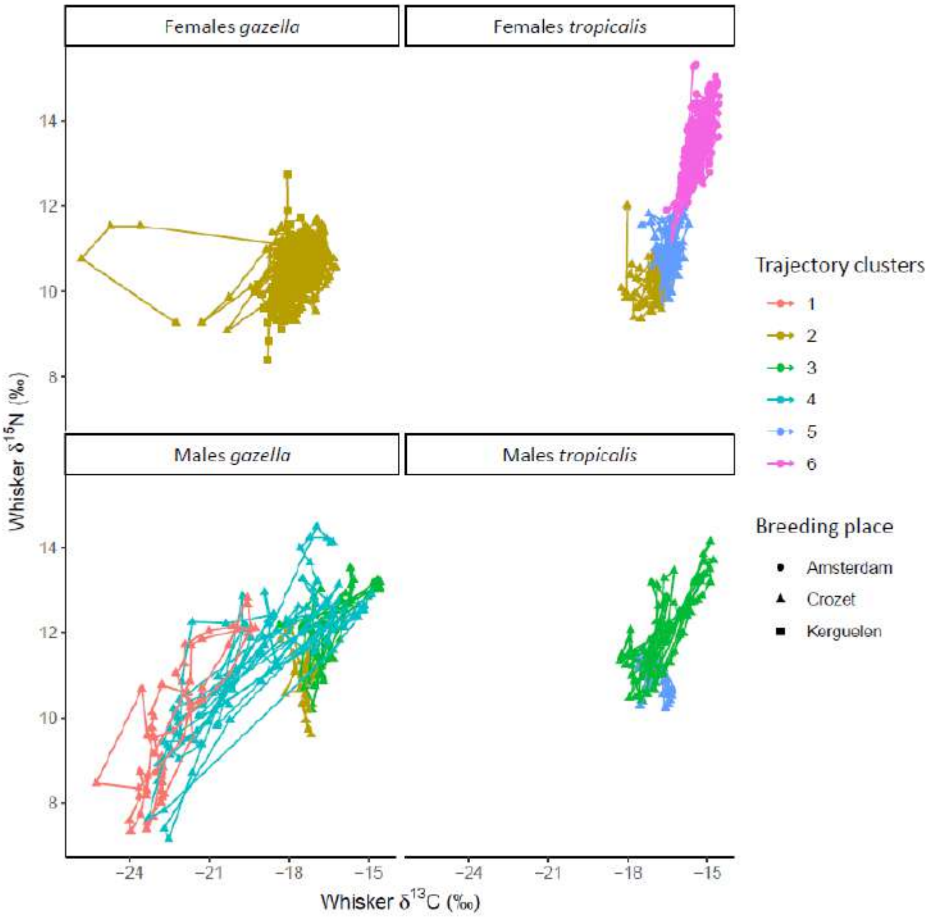


Figure 12: Individual trophic trajectories for males and females of *A. gazella* and *A. tropicalis*. Arrows connects all whiskers section stable isotope values from t_1 to t_{30} (i.e. most recent to oldest stable isotope values). Colours corresponds to trajectory clusters and shape to breeding sites. Data from Kernaléguen et al. (2012).

Contrasted trajectories in pristine and impacted sandy beaches undergoing green tide events.

Context - Excess nutrient inputs is one of the most important human-induced pressures in freshwater and marine water bodies. The assessment of the consequences of the resulting eutrophication on ecosystems functioning is necessary to identify and describe disturbance patterns, especially in comparison with unaffected habitats.

Methods - Quillien et al. (2016) studied changes in sandy-beach (SB) food web structure and functioning in response to *Ulva spp*. proliferation during green tide events (GT). Field work was conducted seasonally in the bay of Douarnenez (Brittany, France) in May, July, September and November 2012 at two SB: one impacted by GT and the other one under pristine conditions (No_GT). Sampling and laboratory steps performed for community and stable isotope analyses are described in Quillien et al. (2016). At the food web level, functional diversity indices (Villéger et al., 2008) were calculated in the stable isotope space as proposed by Cucherousset and Villéger (2015) and Rigolet et al. (2015): Isotopic functional richness (IFRic), evenness (IFEve) and divergence (IDFiv). Mean distance to nearest neighbour (MNN) and centroid (MDC) were also calculated. Patterns of biomass were assessed by weighting stable isotope values of every species prior to indices calculations. A principal component analysis, followed by SITA was performed on trophic indices (Ω_{γ}) to analyse changes in food webs properties at pristine and impacted SB over time. Distance (segment length, net changes) and direction based metrics (DIR, angles Θ) were calculated.

Results - The pristine SB was characterised by a lower structural and functional temporal variability (Trajectory path = 6.09, Mean segment length = 2.33 ± 0.48) than impacted SB (16.13, 5.38 ± 1.46) (Figure 13). Low DIR indicates non-straightforward trajectories for both sites (No_GT= 0.45 vs GT= 0.33). Considering the first two Ω_{γ} dimensions, responsible for 92% of the total variance, the first trajectory segments (*i.e.* between May an July) were quite similar in direction for both sites (Angle α: No_GT= 89.06° *vs* GT= 69.07°) but different in magnitude (S1 length: No_GT= 2.29 *vs* GT= 5.43), thus highlighting similar trends of index values, excepted for IFDiv (Figure 13). For GT SB, S1 and S2 was followed by a directional rupture in Ω_{γ} (Θ_1=107.00°; Θ_2=133.14°) implying contrasted functional and structural shifts. At No_GT SB, S2 followed a more straightforward path, while S3 was characterised by an important direction change (Θ_1=34.03°; Θ_2=138.90°). At the scale of the overall study period, structural and functional variability was higher in SB harbouring GT (NC=4.74) than in pristine SB (NC=3.30). Between May and November, pristine SB was characterized by positive shifts in IFRic, and MDC and MNN and negative shifts in IFEve and IFDiv. At GT SB, IFDiv and IFRic were characterized by moderate increase while MNN, IFEve and MDC decreased. At the scale of each trajectory segment, No_GT SB was mainly characterised by shifts in IFRic values whereas GT SB was typified by highest magnitudes of changes and contrasted shifts. Specifically, the decrease in MDC and MNN values occurring between July and September started to recover in November.

Discussion – Results are congruent with conclusions of Quillien et al. (2016) who showed a simplification of food web structure and functioning in sandy beach where green tide occurred. The interest of SITA consists in the consideration of both sites through their own dynamics exhibited at different levels. Specifically, SITA analysis pointed out:

(1) low differences and variability of food web centroids at both beaches;
(2) contrasted structural and functional trajectories depicting the initiation of two food web cyclic dynamics, which differ in nature and magnitude.

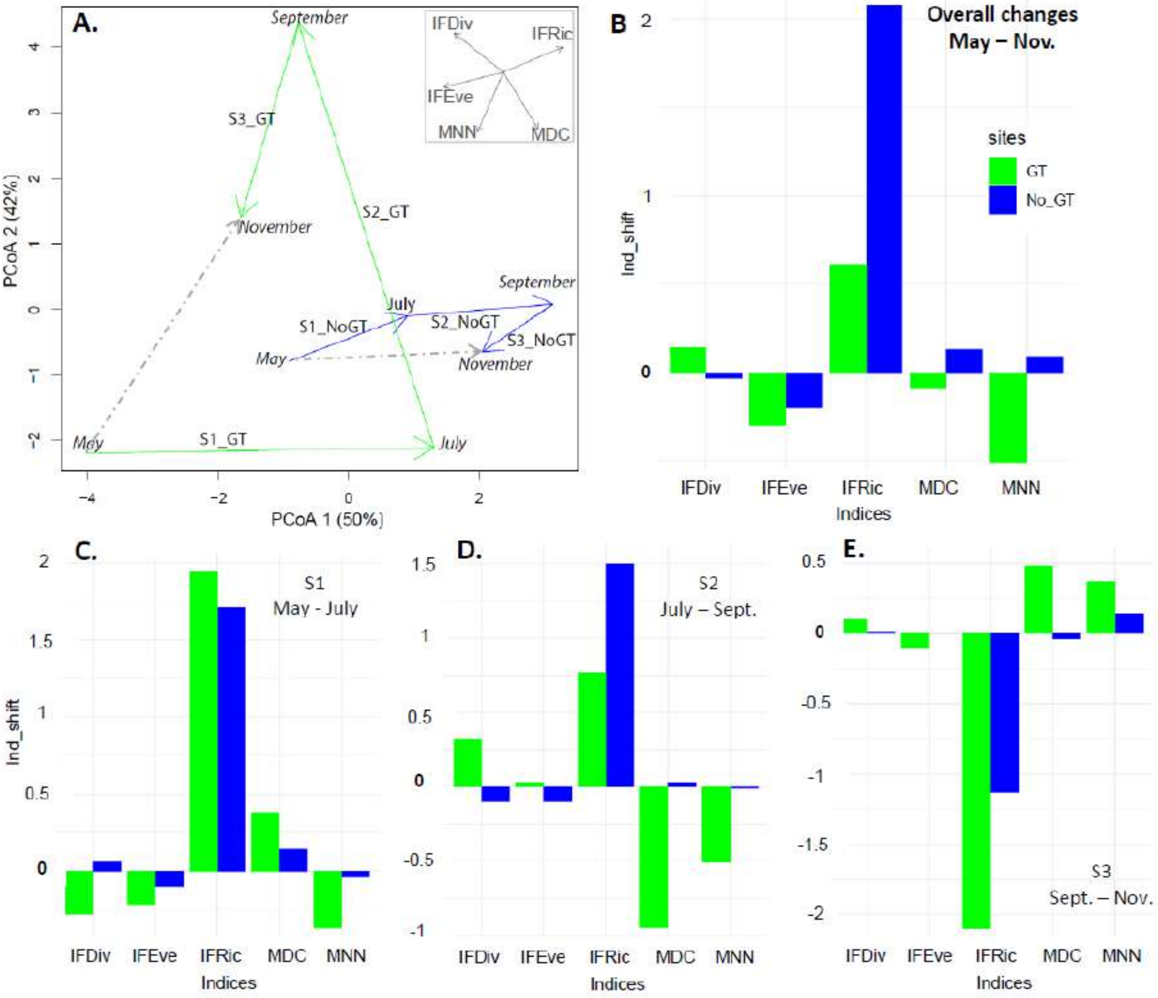


Figure 13: Structural and functional trajectories at impacted (green) and pristine (blue) beaches. A. Trajectory diagram in Ω_χ space. Only two dimensions are shown, representing 92% of the total variance. Solid lines ending with an arrow represent segment lengths and dotted arrows net changes. B. to E. Bar plots represent shift in value of five structural and functional indices: isotopic functional richness (IFRic), evenness (IFEve), divergence (IDFiv), and mean distance to nearest neighbour (MNN) and centroid (MDC). Bar plots panels show changes in indices values between May and November (B.) and for all pairs of consecutives periods (C.: May to July, D.: July to September, E. September to November). Data from Quillien et al. (2016).

Trophic dynamics of lake fish communities in response to biological invasion.

Context – Community assembly can strongly impact the dynamics of biological diversity and the functioning of ecosystems (Bannar-Martin et al., 2018). Environmental changes strongly affect the way species interact and how community assemble and it is therefore important to assess how the trophic structure of communities will respond to these changes.

Methods – This question was investigated by quantifying the temporal dynamics in the trophic structure of fish communities in a network of gravel pit lakes displaying varying levels of biological invasions (Zhao et al., 2019). Fish were sampled in 2014, 2016 and 2018 using a standardised protocol (gill netting and electrofishing) in six gravel pit lakes located along the Garonne river (Alp et al., 2016; Evangelista et al., 2017; Zhao et al., 2019). Fish were identified at the species level, counted, measured, and fin clips were collected for $\delta^{13}C$ and $\delta^{15}N$ analysis. The overall data set (all lakes and sampling year pooled) included 19 species. Five species were present in more than 75% of all communities (18 lakes*years): two non-native species, namely pumpkinseed (*Lepomis gibbosus)* and black bullhead (*Ameiurus melas*) and three native species, namely roach *(Rutilus rutilus), perch (Perca fluviatilis)* and rudd *(Scardinius erythrophthalmus,*). Rarer species such as *Oncorhynchus mykiss, Gymnocephalus cernua, Anguilla anguilla* and others were sampled only one year in one lake. Across all sites and all years, the most abundant species included two invasive species (mosquitofish *Gambusia affinis* (22.98 % ± 18.35) and black bullhead (17.46 % ± 16.37) followed by the native roach (15.72 % ± 14.55). The variability of frequency and relative abundance among lakes and years illustrated the strong community dynamics occurring in lakes. A trajectory analysis was performed to determine if changes in community composition were associated to changes in the stable isotope structure of communities over time. Four stable isotope structure indices [namely isotopic richness, $\delta^{13}C$ range, $\delta^{15}N$ range, isotopic evenness following Cucherousset and Villéger, 2015 and Layman et al., 2007)] were calculated using abundance data and used in SITA analysis for Ω_{γ}. Distance (Segment length, Net change, Trajectory Path, NCR, RDT) and direction based (Angle Θ, Directionality) were calculated and represented in a trajectory diagram.

Results – SITA highlighted a high level of variability between lakes. Lakes Lamartine (Trajectory path : 6.70), Lavernose (4.95) and Bidot (4.45) were characterised by a recovering pattern (Figure 14 A and B.) between 2016 and 2018, as indicated by high Angles Θ (146.05°, 164.09°, 172.41°), low DIR (0.19, 0.09, 0.04) and moderate NCR (0.35, 0.48, 0.31) values, respectively. The efficiency of recovering pattern contributed to low Net changes (2.37, 2.37, 1.38). At the opposite, lakes Pouvil (TP: 4.54), Birazel (3.94) and Bois-Vieux (2.90) were characterized by different trajectory patterns characterised by lower Angles Θ (63.25°, 16.22°, 100.99°), and higher DIR (0.65, 0.91, 0.44) and NCR (0.88, 0.99, 0.66) values. Differences were also observed in the nature of the structural trajectories among lakes (Figure 14 A. & B.). Specifically, the structural trajectory of lake Bidot was mainly characterised by a decrease of $\delta^{13}C$ range, contrasting with lake Birazel trajectories that were mainly characterised by a strong increase in $\delta^{13}C$ range and isotopic richness, and a moderate increase in $\delta^{15}N$ range and isotopic Evenness. We also found that the structural trajectories of lake Pouvil were primarily characterised by a strong increase in $\delta^{15}N$ range and isotopic richness and a decrease in Evenness.

Discussion – SITA approach provided a global and quantitative analysis to compare the magnitude and nature of structural changes over time and across multiple lakes with different invasion levels. Coupling distance and direction based metrics underlined recovering and departing trajectories characterised by contrasting changes in isotopic indices. In some lakes exhibiting departing trajectories, direction-based metrics underlined persistent changes though strong linear trajectories, while potential cyclic dynamics were suggested for recovering lakes over the study period. The trajectory map constitutes a synthesis of distance based metrics and an efficient way to compare the structural food web variability of all lakes (Article II). The SITA approach could therefore help understanding the patterns of trophic structure variability in disturbed ecosystems.

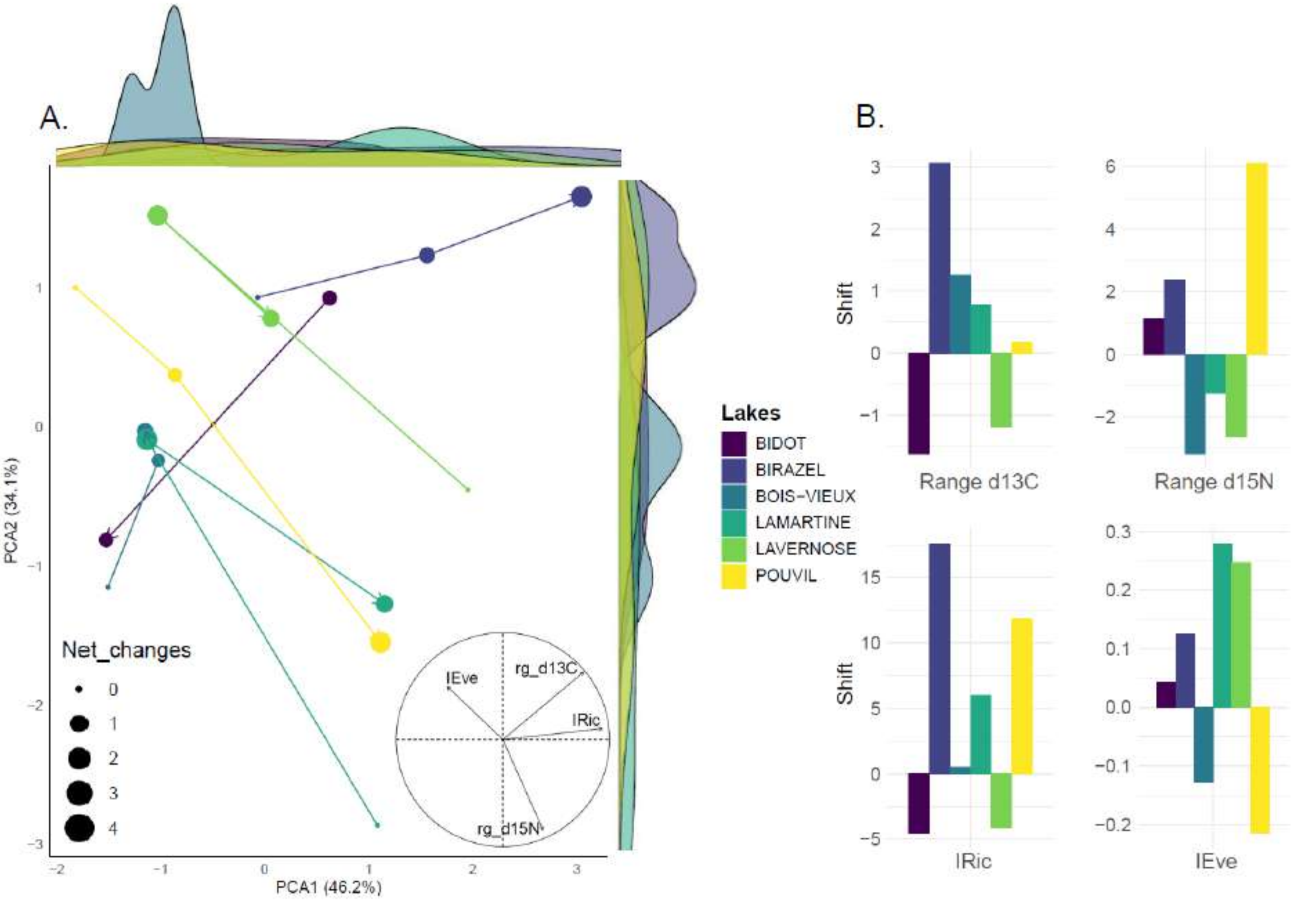


Figure 14: Structural trajectories of fish communities in six gravel pit lakes. A. Trajectory diagram in Ω_{γ} space. Only two dimensions are displayed, representing 80.3% of the total variance. Bar plots represent shift in value of four structural indices: isotopic functional richness (IFRic), evenness (IFEve), $\delta^{13}C$ and $\delta^{15}N$ ranges. B. Bar plots panels decline changes in indices values. Data from Zhao et al., (2019).

➲ *Trajectory rose* : Schmidt et al. (2007) first introduced the use of direction and distance in their arrow diagrams. Building on this approach, and on the trajectory rose (TR) diagrams (Article I), stable isotope dynamics are represented in a circular way. The TR diagram consists of a circular bar plot of angles ranging from 0° to 360°. The barplot structure of TR allows representing factors in different bar sections. Depending on the aim of the analysis, users can choose to represent the distribution of ϴ, ω or α angles. To illustrate the trajectory rose concept, I used a dataset refering to the trophic consequences of experimental warming on lizards (Bestion et al., 2019a).

Trophic consequences of experimental warming on lizards.

Context – Climate change is an important facet of ongoing environmental changes induced by human activities. While there is an increasing knowledge of how species will respond to climate changes in term of distribution, our ability to understand and predict changes in biotic interactions, such as predator-prey dynamics, is limited.

Methods - Bestion et al. (2019a) experimentally quantified the consequences of a 2°C warming on the trophic niche of a generalist lizard predator (*Zootoca vivipara*). Climate was manipulated in 10 × 10 m enclosures with similar natural vegetation and invertebrate communities, and a wide variety of thermal micro-habitats [(dense vegetation, rocks and logs, ponds), see Bestion et al. (2019a) for more details]. In June 2013, individuals juveniles and adult *Z. vivipara* from both sexes were allocated at similar density to ten enclosures: five enclosures with a 'present-day climate' and five enclosures with a 'warm climate', i.e. 2°C warmer on average. There was no difference in $\delta^{13}C$ and $\delta^{15}N$ values between treatments at the beginning of the experiment. In mid-September 2013, surviving lizards were recaptured and a tail tip was collected for stable isotope analyses. Because stable isotope values of trophic resources varied among enclosures, a baseline correction ($\delta^{13}C_{cor}$ and $\delta^{15}N_{cor}$) was performed to allow between treatment comparisons (Bestion et al., 2019a, 2019b). Enclosures from the two treatments were paired in five blocks (A to E used as replications), and use to characterize, respectively, the initial (present-day climate) and final (warmer climate) states of a one-segment trajectory for five paired lizard populations in response to warming. Because the analysis focused particularly on shifts rather than absolute stable isotope values, we favoured the representation of net change and angle α, calculated in Ω_δ, in TR.

Results – Some differences in the magnitude of trajectories were observed among pairs of enclosures (Figure 15). Block C was characterized by the highest net change (1.63 ± 0.19) for all individuals (adults and juveniles of both sexes), while shifts in stable isotope values in response to warming were more limited in other blocks (A: 0.36 ± 0.15; B: 0.39 ± 0.36; D: 0.55 ± 0.44; E: 0.47 ± 0.21 ‰). Some differences were also observed within paired enclosures where net changes were contrasted between individuals. For instance, in block D, adult males displayed the highest response (1.12) while juvenile females displayed the lowest response (0.12). Differences were also observed in the direction of the trajectories (Figure 15). In block C, all individuals display similar directional changes (10.23 ± 3.88°) with trajectories mainly implying increase in $\delta^{15}N_{cor}$ values and limited $\delta^{13}C_{cor}$ shifts. The other blocks displayed more variable responses to warming. For example, individuals from block A exhibited different directions in Ω_δ revealing different patterns of stable isotope changes.

Discussion – Using conventional statistical analyses, Bestion et al. (2019a) concluded that lizards from warmer conditions had higher $\delta^{15}N_{cor}$ values while non-significant changes in $\delta^{13}C_{cor}$ values were observed. By pairing enclosures for trajectory analysis, SITA results were in accordance with these findings but they also highlighted the existence, in some cases, of other responses to warming, with approximately 25% of all individuals (life stage, sex and blocks) displayed slight decreases in $\delta^{13}C_{cor}$ and $\delta^{15}N_{cor}$ values. These findings may reveal some additional context-dependency in the response to warming observed at the individual level.

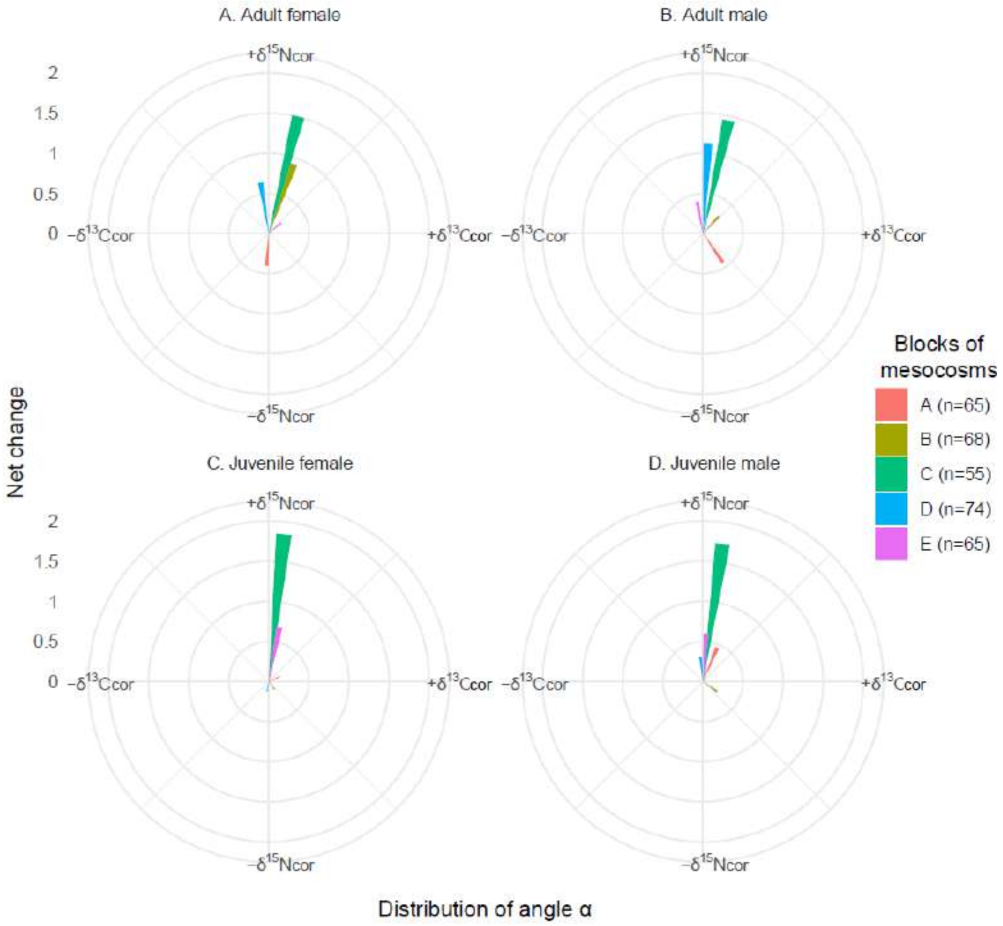


Figure 15: Angle α trajectory roses for each lizard life stage/sex categories within each block of enclosures (warming between present day and warm treatments). Angles α were calculated in 2D Ω_δ space ($\delta^{13}C_{cor}$ and $\delta^{15}N_{cor}$). Bars size represent the net change for each enclosure block (colors) and each life stage/sex (A.: adult females; B.: adult males; C.: juvenile females; D.: juvenile males). Data from Bestion et al. (2019).

➲ *Trajectory map*: Trajectory metrics are used as trajectory map input for the representation of temporal patterns in sampling units on geographic coordinates (Article I). This chart concept also demonstrates its ability to represent the trophic structure dynamics of lake fish communities in response to biological invasion (Zhao et al., 2019) according to represent site scale dynamics in Ω_γ for six lakes along the Garonne river (see Article II for further details).

➲ *Isoscape trajectory map:* The spatial distribution of isotopes in the environment can be predicted, using models of isotope-fractionating processes and data describing environmental conditions (from remote sensing for instance), and represented though isotopic landscape, called isoscapes (Bowen, 2010; West et al., 2008). Despite isoscapes provide a large scale overview of the variations of stable isotope composition, this tool is currently limited for the synthetic analysis of stable isotope dynamics. The trajectory map concept was adapted for isoscape datasets characterised by high spatial resolutions and a minimum of two temporal surveys or modelling. This particular concept of trajectory map is inspired by wind/current map where the magnitude and the direction of wind/current are represented though multiple vector covering large areas. In the isoscape trajectory map (ITM), direction of arrows represent angles α in a 2D Ω_δ space (e.g. $\delta^{13}C/\delta^{15}N$), and size illustrates trajectory length. The representation of trajectory length is improved by a color raster following a length values interpolation.

The ITM provides a relevant visual synthesis of the spatio-temporal dynamics, which is complementary to isoscapes. I have used this new tool to represent the spatio-temporal variability of δ^{13}C and δ^{15}N of phytoplankton modelled isoscapes in the Northeast Pacific [Figure 16, Espinasse et al. (2020)].

➲ *Trajectory heat-map:*

Stable isotope datasets characterised by high temporal resolutions may require special representations as they can potentially saturate trajectory diagrams or trajectory roses. I have proposed the concept of trajectory heat-map (TH) to represent long-term stable isotope dynamics. The heat-map is a two-dimensional representation of data in which the matching intensity of time and a chosen trajectory metrics is represented by cells colours. The TH allows the representation of the distribution of distance and direction based trajectory metrics. Angles ϴ, ω or α can be represented in a matrix of fixed cell size whose colours vary depending of the number of a given direction range occurring in a given period. As in the TR, we advise the use of any direction range (e.g. 15°) to provide a synthetic representation. TH can be easily completed by peripheric bar plots in order to represent trajectory lengths involved in each direction range and period. In the 2D Ω_δ space, angle α illustrate for example different stable isotope trajectory patterns according to respective increase and/or decrease of the two stable isotope value. A trajectory heat-map was used to represent the long-term variability of δ^{13}C and δ^{15}N modelled isoscapes in the Northeast Pacific from 1998 to 2017 [Figure 17, Espinasse et al. (2020)].

Spatio-temporal variability of δ^{13}C and δ^{15}N modelled isoscapes in the Northeast Pacific.

Context – Isoscapes are increasingly used to assess the relative trophic position of higher trophic levels, to provide information on the relative productivity of different regions, as well as to track the migration of animals.

Methods - Espinasse et al. (2020) tested the application of isoscapes modelled from satellite data to the description of secondary production in the Northeast pacific. Few key parameters (sea surface temperature, sea level anomaly, and chlorophyll-a) were used as inputs on a general additive model. The output model fits in a 0.25° x 0.25° spatial grid covering the region spanning from 46 to 62°N and from 195 to 235°E and supporting δ^{13}C and δ^{15}N isoscapes from 1998 to 2017 (Espinasse, 2020). We subset δ^{13}C and δ^{15}N values of a 1° x 1° spatial grid from the original modelled dataset. Isoscapes modelled for 2013, 2015 and 2017 were selected as they were characterised by high stable isotope dynamics and consequently constitutes relevant inputs to test our ITM concept. Modelled stable isotope values for which one of the parameter was missing were excluded. Mapping trajectory metrics requires stations to be synchronously surveyed. Consequently, stations for which one date within each pair of dates (2013-2015 and 2015-2017) was missing for were also excluded. The subset of stations supporting SITA analysis finally included 489 and 488 stations for the periods 2013-2015 and 2015-2017, respectively. Segment lengths (2013-2015 and 2015-2017), and angles α were calculated in the modelled 2D Ω_δ space (δ^{13}C/ δ^{15}N) for all stations and periods and used as input in a modelled ITM. RDT and overall NCR were also calculated to qualify departing or recovering patterns between 2015 and 2017 with respect to the δ^{13}C and δ^{15}N values modelled in 2013. Additionally, a long-term SITA analysis was performed from 1998 to 2017 using directions and net changes calculated for all pairs of dates (1998-1999,…,2016-2017) as input for a TH.

Results – Modelled ITM revealed contrasted dynamics between 2013-2015 and 2015-2017 (Figure 16). While differences in the nature of changes (i.e. direction) were highlighted in the ITM, the overall magnitudes of the dynamics were similar (total segment length = 638.90 between 2013 and 2015 vs 620.41 between 2015 and 2017). Few areas concentrated an important part of the overall dynamics especially in the southeast part and, to a lesser extent, in the northern part of the modelled area. The ITMs suggest an overall recovering pattern between 2015 and 2017 with respect to the model defined in 2013, which is confirmed by a RDT<0 for 76% of stations and a low overall mean of NCR values (0.21).

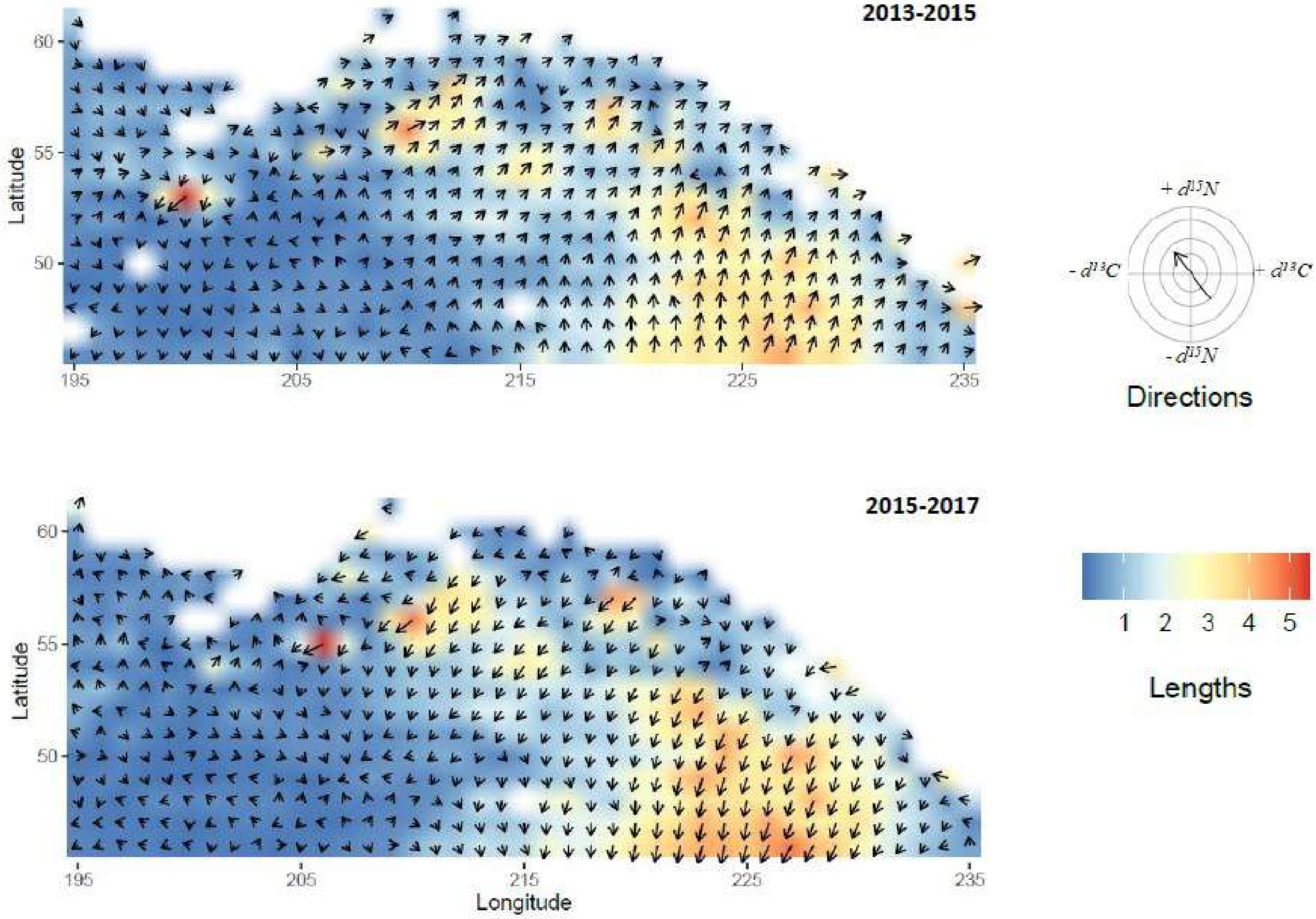


Figure 16: Isoscape trajectory maps in the Northeast Pacific for the periods 2013-2015 and 2015-2017. SITA metrics were mapped to illustrate stable isotope spatio-temporal dynamics. Direction of arrows (angle α) illustrate direction in the modelled 2D Ω_δ space according to increase and/or decrease in $\delta^{13}C$ and $\delta^{15}N$ values (0-90°: + $\delta^{13}C$ and + $\delta^{15}N$; 90-180°: + $\delta^{13}C$ and - $\delta^{15}N$; 180-270°: - $\delta^{13}C$ and - $\delta^{15}N$; 270-360°: - $\delta^{13}C$ and + $\delta^{15}N$). Length of arrows and colored background rasters illustrate modelled trajectory segment length at each station. Data from Espinasse et al. (2020).

The TH (Figure 17) revealed that angles α ranging from 0 ° to 90° and 180° to 270° were the most frequent from 1998 to 2017. While stable isotope trajectories characterized by increases in $\delta^{13}C$ and $\delta^{15}N$ values alternated with decreasing patterns in both isotope values and exhibited the major part of the overall changes, some fine scales patterns were also revealed at the beginning of the modelled period.

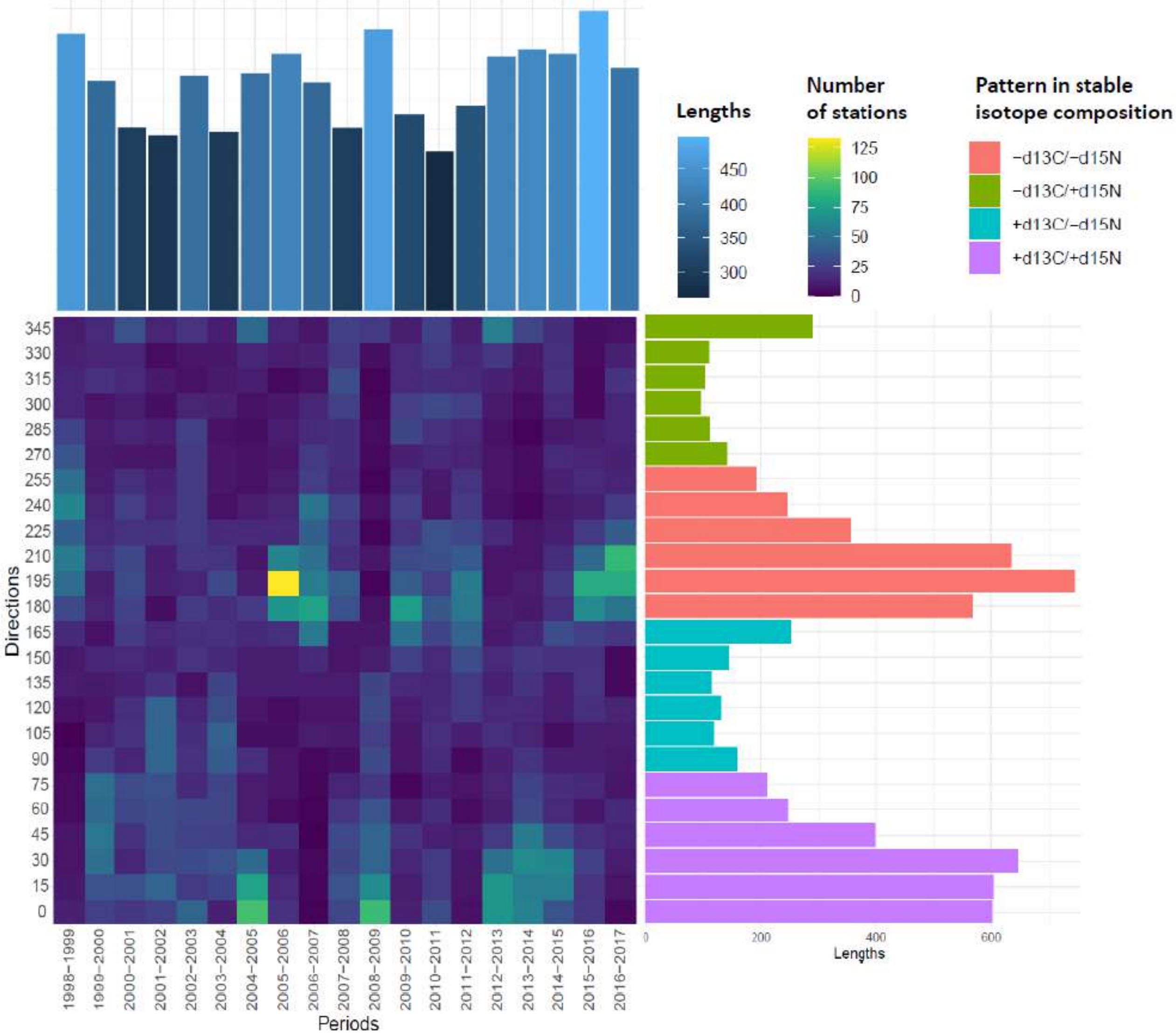


Figure 17: Trajectory heatmap. *Heatmap panel:* Angles α in the modelled 2D Ω_δ space exhibited by all stations within all pairs of dates (1998-1999,…,2016-2017) are represented by range of direction (15°) according to period. Color gradient from dark blue to yellow indicate the number of stations exhibited by a given range of direction within a given period. *X barplot:* Sum of segment lengths across stations and times, exhibiting the chosen angle. The blue gradient indicates the net change magnitude. *Y barplot*: Overall net changes according to range of directions (angle α). Bars are colored according to increase and/or decrease in δ13C and δ15N values (Pink: 0-90°: + δ^{13}C and + δ^{15}N ; Blue: 90-180°: + δ^{13}C and - δ^{15}N; Red: 180-270°: - δ^{13}C and - δ^{15}N; Green: 270-360°: - δ^{13}C and + δ^{15}N). Data from Espinasse et al. (2020).

Discussion - The ITM provides a relevant visual synthesis of (1) spatio-temporal dynamics complementary to (2) modelled isoscapes. (1) ITM, including trajectories of two stable isotopes, highlight areas of high variability associated to eddies which enhance local production in the open ocean (Espinasse et al., 2020). It also allows to easily identify areas where stable isotope compositions are stable over time, which is useful for animal tracking studies (Trueman and St John Glew, 2019). (2) Modelled isoscapes also illustrate this pattern beyond the decrease in δ^{13}C and δ^{15}N values from the coast to offshore (Espinasse et al., 2020). One solution to identify this second pattern in the ITM may consist in the addition of trajectory clusters (color of vectors) from a trajectory similarity analysis. In such case, users should be careful about figure readability. The main advantage of this concept of trajectory map lies in its ability to synthesize spatio-temporal dynamics from four isoscapes, which is a major challenge when dealing with massive amounts of spatialized data.

The TH provides an effective synthesis of high temporal resolution stable isotope dynamics for a 20 years period, highlighting cyclic patterns of enrichment and depletion in ^{13}C and ^{15}N isotopes. Coupled with quantitative SITA metrics, ITM and TH appear as promising tools for isoscapes space-time analyses. These innovative figure concepts allow illustrating differences in the magnitude and nature of spatio-temporal stable isotope dynamics, and they can be easily coupled with statistics to track accurately for significant patterns in high resolutions data sets.

2.4 | Software availability

In 2019, De Cáceres et al. proposed the community trajectory analysis framework and functions for the calculation of associated metrics. These functions were available in the package 'vegclust'. In 2021, new functions were added in the github repositories and 'vegclust' following the extension of the Community Trajectory Analysis framework with new metrics and figure concepts (Article I). I used this tool for taxonomic trajectory, as well as functional dynamics for the exploration of trajectory analysis beyond sites*species matrix (Articles III and IV). In article II, I went further in the adaptation of CTA, bridging a gap identified in the consideration of dynamics in stable isotope ecology.

All these recent development claimed for a new package specifically devoted to Ecological Trajectory Analysis to allow taxonomic, functional or stable isotope trajectory analyses within a same tool though complementary spaces of analysis (Ω).

The package 'ecotraj' [De Cáceres (2019), Sturbois et. al. (Article I)] assists ecologists in the analysis of temporal changes of ecosystems, defined as trajectories on a chosen multivariate space, by providing a set of trajectory metrics and visual representations. It includes functions to perform trajectory plots and to calculate a set of distance and direction-based metrics (lengths, directionality, angles…) as well as metrics to relate pairs of trajectories (dissimilarity and convergence). Currently, Ecological Trajectory Analysis (CTA and SITA) can be performed using the 'ecotraj' functions available on CRAN and GitHub repositories. Some vignettes have been added in the documentation of the package to facilitate the use and the customization of the trajectory chart concepts.

2.5 | Discussion

The ETA framework (CTA and SITA) represents a valuable approach to assess ecological dynamics based on the geometric analysis of trajectories defined in a multidimensional space of community resemblance. In this thesis, I went further in the definition of geometric properties of trajectories by complementing the available metrics and proposing synthetic methods of applied representation that facilitate the interpretation of ecosystem dynamics over time. For that, new tools (function options, new functions, vignettes and R codes for chart conception) were gathered with the original CTA functions into the package 'ecotraj' [De Cáceres (2019), Sturbois et. al. (Article I)]. ETA metrics provide a valuable toolbox for trained ecologists (aware of multivariate applications and limitations), to analyses ecological variability and trajectories with respect to a baseline state. The different case studies highlighted the complementarity and the ability of figure concepts to illustrate spatio-temporal trends in different fields in ecology.

The CTA extension (Article I) and the SITA development (Article II) showed the importance to plot trajectory metrics in specifically designed figure concepts adapted for the representation of dynamics. All metrics and representation concepts can be adapted for both ETA frameworks. Similarly, the initiation of the δ_γ-space in the SITA framework must beneficiate to CTA for the analysis of structural and functional community properties. The entire figure concepts proposed for ETA are far from being exhaustive and I invite potential future users to innovate in the representation of trajectory metrics and in the customisation of charts.

Ecologists are increasingly using sophisticated methods for dealing with measured data (Fry, 2013). While it is always tempting to favour approaches that provide quantitative analysis, it is important to keep in mind the biological meaning of associated assumptions, and their inherent simplifications (Layman et al., 2012). If the ETA frameworks and the associated metrics and representations constitute potential management and decision-making assistance tools, users interested in sharing them with stakeholders or managers must keep in mind that interpretation must be done carefully with a hand of experienced multivariate analysis and good knowledges in the given domain of ecology.

Multivariate ecological methods are descriptive by nature which results in common limitations, which are shared with the ETA framework. Ordination spaces are specifically constructed for each given data set. Therefore, any data transformation on raw data or sampling decision is likely to affect trajectories, and subsequently, all metrics to be calculated. In SITA, this effect should be tested before any overall transformations of raw data such as scaling and/or baseline correction of stable isotope values, or any biomass or abundance weighing prior to indices calculation. Such overall transformations includes changes in sampling design and/or suppression of rare species in a community data set. Furthermore, when choosing a dissimilarity coefficient, users should check the coefficient properties, to determine whether it is suitable for the objectives of the study (Legendre and De Cáceres, 2013) and implications in ETA performing. Similarly, ETA may be complemented with additional analyses to statistically test for other aspects of changes or to provide statistical backgrounds (Buckley et al., 2021a).

ETA analysis also shares numerous limitations inherent to the given domains of ecology. For instance, SITA shares some limitations inherent to stable isotope properties and analysis (Fry, 2008; Garvey and Whiles, 2017). The dynamics of basal source stable isotope composition influences the stable isotope compositions of consumers (Matthews and Mazumder, 2004) and potentially the metrics used to describe the variability, and the food web structure and functioning. However, SITA offers the possibility to explore both sources and consumers dynamics (Articles II and V). Additionally, many other factors are known to influence food assimilation and finally the isotopic composition of consumers such as fractionation variability or the type of tissue analysed (Fry, 2008). In complex ecosystems characterised by similar stable isotope composition of basal sources and in underdetermined cases where multiple outcomes are feasible from isotope tracer measurements, different feeding pathways may lead to similar positions in δ space (Fry, 2013; Layman et al., 2007). Just like stable isotopes are irrelevant to unravel trophic fluxes in those situations, the SITA framework makes no exception, and complementary approaches will be required. In contrast, SITA will be more relevant when differences in stable isotope values of basal sources induce contrasted position of consumers. When performed at the population level, mean stable isotope values are used as input in SITA analysis, which has the drawback of hiding the stable isotope composition variability at intra-specific levels (Bearhop et al., 2006; Matthews and Mazumder, 2004).

CHAPTER III

Benthic assemblages variability in the bay of Saint-Brieuc

CHAPTER III | Benthic assemblages dynamics and food web variability in the bay of Saint-Brieuc

3.1| Introduction

The English Channel. The English Channel is a transit zone between the Atlantic Ocean to the west and the North Sea water masses. It forms a shallow arm of sea between England to the north and France to the south (Figure 18). The English Channel is commonly subdivided in three major basins (Holme, 1966):

(1) the eastern Channel, between the Pas-de-Calais in the east and a line from Cap d'Antifer to Beachy head in the west;

(2) the central Channel, delimited in the east by a line connecting Cap d'Antifer and Beachy Head, and in the west by a line connecting Cap de la Hague and Portland;

(3) the western Channel. The western part can be subdivided into four main areas: the English bays, the Normand-Breton Gulf, the Armorican Channel and the northwestern Channel.

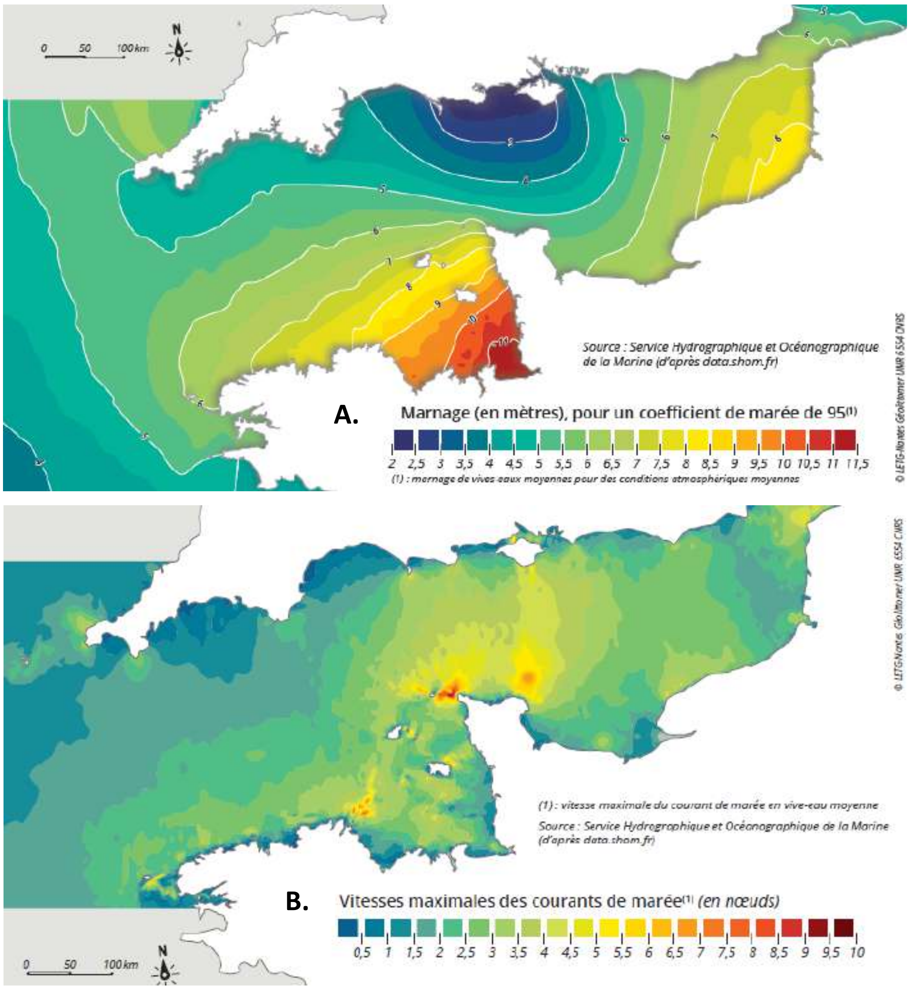


Figure 18: A- Dissymmetry and tidal range values in the English Channel, from Le Mao et al. (2019). B- Maximum tidal current speed in the English channel, from Le Mao et al. (2019). ©LETG-Nantes Géolittomer UMR 6554 CNRS. https://archimer.ifremer.fr/doc/00612/72370/71329.pdf

The English Channel is characterised by an exceptional tidal regime (Figure 18 A), with a tidal range reaching 15.5 m in the bay of Mont-Saint-Michel. The instantaneous currents are intense (Figure 18 B), favouring a strong mixing of the water column (Pingree and Maddock, 1977; Salomon and Breton, 1993). Depth exceeds 100 metres very locally in the western part (173.5 m in the Fosse des Casquets) and globally decreases to the east. As an epicontinental sea, the English Channel is subjected to strong anthropic pressures.

The Normand-Breton Gulf. The Normand-Breton Gulf covers a total area of around 14000 km², including a coastline of around 450 km along the Cotentin peninsula to the east and the coast of Brittany to the south. It is bounded on its maritime side by a line joining the Cap de la Hague to the island of Bréhat (Figure 19). The bathymetry is low and does not exceed 60 m in depth. The Gulf is punctuated by multiple topographical irregularities including numerous islands (Guernsey, Jersey, Sark, Alderney, Chausey islands) and rocky areas (Minquiers, Ecréhoux, Roches Douvres). These structures profoundly influence the circulation and direction of the important tidal currents encountered in the Gulf.

The residual circulation in the Gulf is strongly marked by the presence of cyclonic or anticyclonic eddies (Figure 20) located around the Channel Islands or near the main capes (Salomon and Breton, 1991). The main cyclonic eddies are located around the islands of Guernsey and Jersey and around the Minquiers rocky outcrops. The anticyclonic structures are located in the north and west of Jersey, in the north of the Bay of Saint-Brieuc and at the Bay of Mont-Saint-Michel entrance. These eddy structures are generally very stable and not very sensitive to meteorological effects (Pingree and Maddock, 1977; Salomon and Breton, 1993).

The different coastal morphologies influences the diversity of landscape and ecosystems, between sandy and rocky foreshores, exposed and sheltered areas, strong or weak hydrological regimes, large rocky complexes and large bays fed by small rivers, archipelagos and some large flushing rocky reefs. The distribution of sediments within the Normand-Breton Gulf is highly dependent on the hydrodynamic conditions. Although, overall, the intensity of residual currents decreases along a gradient from the open sea to the coast, the spatial distribution of sediments is highly heterogeneous, leading to the topographical complexity of the sea bed. This sedimentary "mosaic" reveals a strong dominance of coarse sediments (*i.e.* pebbles, gravels and gravelly sands) at the scale of the Gulf. Only a coastal fringe is characterised by the presence of a sediment mainly composed of medium to coarse sands, fine sands and muds (Figure 21).

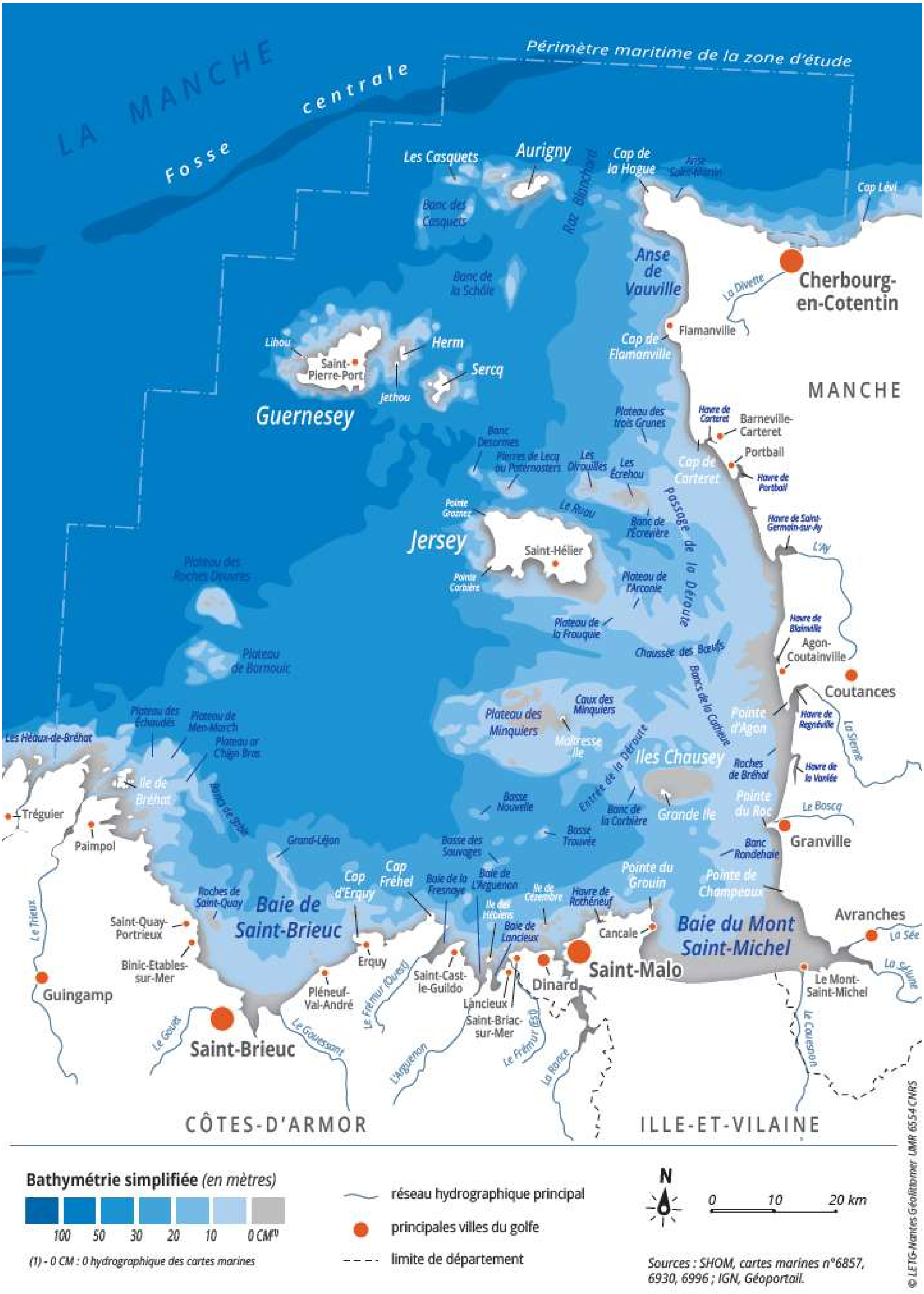
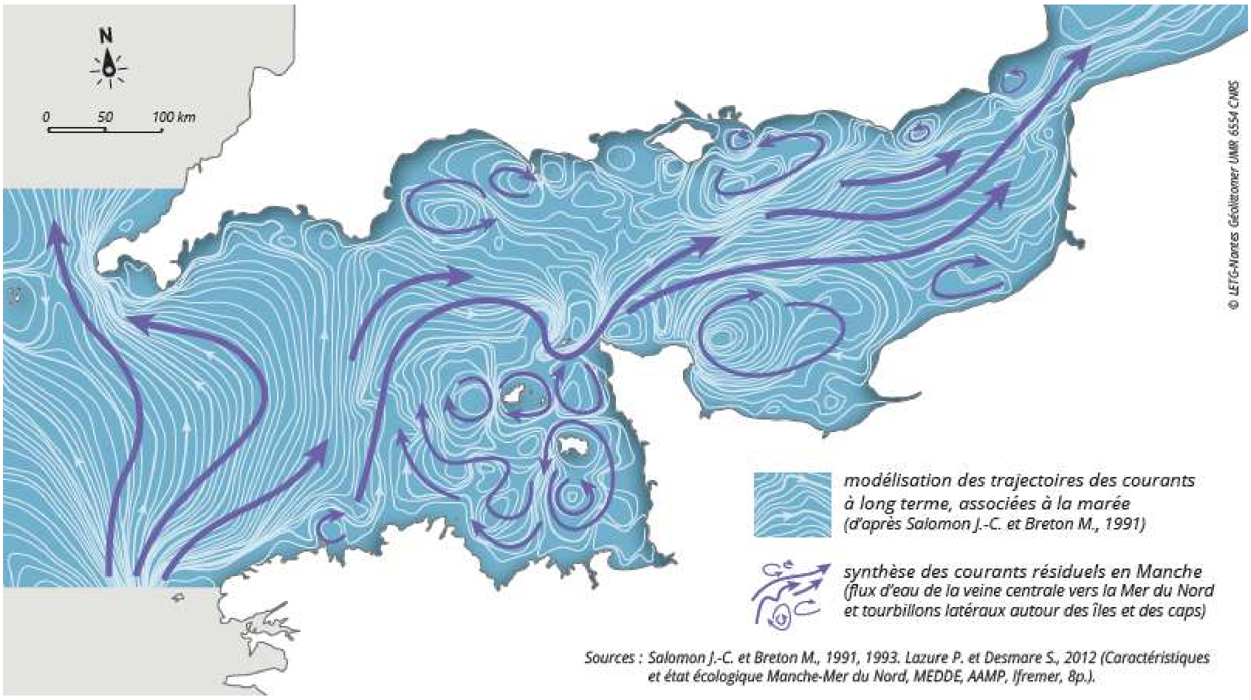


Figure 19: Bathymetry and toponymie of the English Channel, from Le Mao et al. (2019). ©LETG-Nantes Géolittomer UMR 6554 CNRS. https://archimer.ifremer.fr/doc/00612/72370/71329.pdf



Sources : Salomon J.-C. et Breton M., 1991, 1993. Lazure P. et Desmare S., 2012 (Caractéristiques et état écologique Manche-Mer du Nord, MEDDE, AAMP, Ifremer, 8p.).

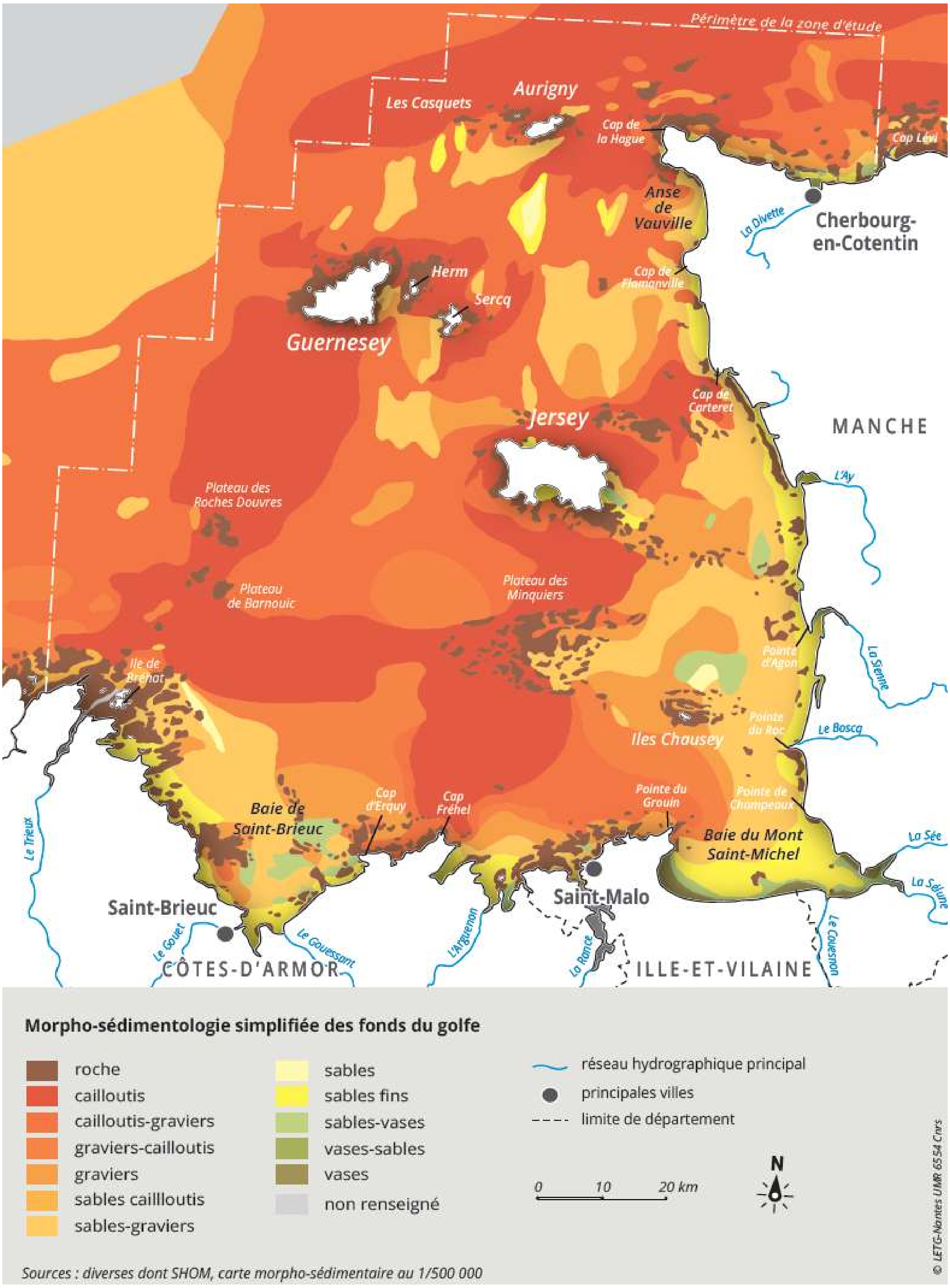
Figure 20: Resilient tidal current in the English Channel, from Le Mao et al. (2019). ©LETG-Nantes Géolittomer UMR 6554 CNRS. https://archimer.ifremer.fr/doc/00612/72370/71329.pdf

Surface waters temperatures vary according to a north-west south-east offshore-inshoregradient, which reverses seasonally. In winter, the coldest waters, lower than 7°C (Le Mao et al., 2019), are observed in shallow bays (*e.g.* Mont-Saint-Michel, Saint-Brieuc). While temperatures remain below 10°C in the south of Jersey, temperatures of up to 11.5°C can be recorded in the northern part of the gulf. Conversely, in summer, the warmest temperatures are recorded near the end of the Normandy-Breton Gulf (i.e. up to 24°C in the Bay of Saint-Brieuc), while mean temperatures in the north of the Gulf do not exceed 18°C.

The great topographical variability that characterises the Normand-Breton Gulf and the marked climatic gradients influence the diversity of the benthic fauna of this zone (Holme, 1966; Retiere, 1979). More details are presented in the 'Atlas de la faune marine invertébrée du golfe Normano-Breton' (Le Mao et al., 2019) from which figures 18 to 21 of this subsection where collected.

The Bay of Saint-Brieuc. Located in the south-west of the Normand-Breton Gulf, the bay of Saint-Brieuc is bounded to the west by the Bréhat archipelago and to the east by the Cap Fréhel (Figure 19). The eastern coast includes some major rocky promontories (Cap d'Erquy and Fréhel). On the west, the cliffs that dominate the bay are among the highest on the coasts of Brittany, reaching more than 100 m at Plouha.

The bay covers an area of about 800 km^2 up to the 30 m isobath, located more than 30 kilometres from the southernmost parts of the bay. Bottoms are characterised by a regular slope of around 0.1%. The morphology of the sea bed is punctuated by multiple reliefs which can reach 20 m height (rocky shoals such as the rocks of Saint-Quay, the Plateau des Jaunes, the Grand Léjon and the Grand Pourrier, or sandy banks such as the Horaine (Augris and Hamon, 1996).



Sources : diverses dont SHOM, carte morpho-sédimentaire au 1/500 000

Figure 21: Simplified morpho-sedimentary facies in the English Channel, from Le Mao et al. (2019). ©LETG-Nantes Géolittomer UMR 6554 CNRS. https://archimer.ifremer.fr/doc/00612/72370/71329.pdf

The study area. The study area encompasses about 15 000 ha of shallow soft-bottom sediments located in the southern of the bay of Saint-Brieuc (Figure 22).

Intertidal flat

The intertidal area covers 2900 ha, influenced by a semi-diurnal megatidal regime, generating strong tide currents (between 0.3 and 0.5 m/s). The intertidal flat is divided in two coves (Yffiniac and Morieux) mainly dominated by fine to medium sands. The upper shore is dominated by salt marshes (125 ha) characterised by a current dynamic of extension and a good conservation status (Sturbois and Bioret, 2019). A bathymetric inshore-offshore gradient leads to difference in mean daily submersion time among intertidal habitats: salt marsh (2h07 per 24h), upper shore muddy sands (4h59), fine sands (12h21) and lower shore medium sands (20h35). Tidal range varies between 4 m at neap tides and nearly 13 m during spring tide. Freshwater inputs in the bay come from three main rivers (Gouët, Urne, Gouessant). Channels divagation is particularly dynamic, increasing in the lower levels of the shore. The upper part of the flat (1140 ha) is included in the National Nature Reserve of the bay of Saint-Brieuc, created in 1998 to protect wader populations.

The intertidal area is characterised by past and current anthropogenic activities (including horse riding, hiking, sports, hunting, professional and recreational fishing, mussel farming, extraction and deposition of sediments…) which make the bay of Saint-Brieuc a complex eco-socio-system (Ponsero et al., 2019a). According to their localisation and respective characteristics, these anthropogenic activities have influenced, and still do, intertidal marine habitats.

Main past activities:

Silt exploitation - The exploitation of silt and mud provided the raw materials for a brickworks set up to the north of the Langueux shores [Figures 22-3 and 23 (station 3)]. In 1870's, the production reached 30 tons per day. This activity declined after the Second World War and stopped in 1950s.

Marl extraction - The exploitation of marl for agricultural purposes has been developed since the 12th century. At the beginning of the 20th century the volume extracted was about 1000m^3/year^{-1}. The extraction was subject to authorisation. With the creation of the Nature Reserve in 1998, the extractions took place in three sectors of the Yffiniac cove located along the coasts of Hillion, Langueux and Saint-Brieuc. From 2000, extraction was limited to Langueux. Marl extraction ended in 2004. Over the last 18 years of operation, the annual amount removed was approximately 950 m3 of sediment per year for a total of 17000 m3.

Salt industry - The salt industry in the Bay of Saint-Brieuc originates from the 11th century. In 1084, Geoffroy, Count of Penthièvre, owned saltworks in the bottom of the Yffiniac cove. These saltworks were located on the shores of Langueux, Hillion, Yffiniac. In 1832, at the highlights of the activity, there were 53 saltworks (49 of them located in Langueux), which represented a ploughing surface of 79.5 ha from which some of the sediment was then removed. The impacts on the benthic fauna and the potential for colonisation by vegetation were significant. The tidal marshes and grasslands were exploited and used for grazing by cattle, sheep, geese and pigs. In 1852, the activity had already declined, and had practically disappeared in 1862. It had stopped at the end of the 19th century (Sturbois and Bioret, 2019).

Salt marsh grazing - Grazing on the salt mash is an ancient activity in the Yffiniac cove. It was linked to an agricultural system of small family farms, based on mixed farming and livestock. The generalization of the use of salt marsh as pasture took place during the 19th century, in response to the scarcity of cultivable lands. Grazing of herd of few cows and sheeps started in the salt marsh. These practices continued until the early 1950s on

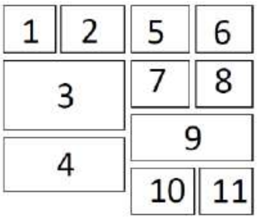


Figure 22: 1: Muddy areas in the Yffiniac cove (©LGO-UBS). 2-3: Areas characterized by high sedimentary dynamics (©LGO-UBS). 4: Lower part of the intertidal area characterised by the divagation of tidal channels and fishing activities (©A. STURBOIS). 5-6: The intertital area is an important foraging zone for birds including Sanderlings, Knots and Barnacles geese (©A. STURBOIS). 7-8: The salt marsh is characterised by a current dynamic of extension and a good conservation status (©A. STURBOIS). 9: Mussel farming covers more than 300 ha in the lower part of the intertidal area (©A. STURBOIS). 10-11: Recurrent green tides events lead to high surfaces of stranding *Ulva spp.* (©LGO-UBS)

the marsh on the right bank of the Urne. Until 2005, only one farmer maintained a grazing activity on an area 18 ha. The area was grazed by cattle between March and October, and this activity ended in 2005. Sheep grazing was envisaged but the negative opinions of the Scientific Council of the Nature reserve and the stakeholders committee, validated by a prefectural decision, led to an unfavorable outcome.

Main current activities:

Cockle fishing - The cockle fishing ground is subject to a traditional fishery since several decades. In the 1930s, Lambert (1943) evaluates that the quantity of cockles harvested per day was about 3 tons, which were shipped from Saint-Brieuc and sent to various points in France and England. This activity is now regulated by a prefectoral decree. Cockle fishing still represents an economic issue in the Bay of Saint-Brieuc. Its fishing is regulated (days, hours, places) and controlled by the Direction Mer et Littoral and the Departmental Fisheries Committee. A total of 25 professionals fish cockles since the 2000s, while they were up to a hundred in the 1990s. Recreational fishers harvest between 10 and 13 tons a year. Recreational fishers also target additional species such as scallop (*Pecten maximus*) and the lugworm *Arenicola marina.*

Mussel farming - Mussel farming in the Bay of Saint-Brieuc started in the 1960s when the pioneer basin of the Bay of Aiguillon became saturated and the mussel farmers from Charente looked for new sites. After few experimentations in 1960, mussel farming was developed in the bay in 1964, by granting 68 km of bouchots in the cove of Morieux to Charente mussel farmers and to some local fishermen and farmers (680 lines of 100 m with a maximum of 200 stakes per line). The length of the bouchots was increased to 81.9 km in 1971. It is currently 88.9 km. The concessions cover about 320ha (277 ha in 1987 to 386 ha in 2001 and 312 ha in 2019). Morieux Bay is the second largest mussel farming area in Northern Brittany and the fourth largest in France, with an annual production of around 4000 tons (10% of French mussel production), provided by 18 companies.

Sediment deposition - Located in the Gouët estuary, the port of Le Légué is situated on the border of the communes of Plérin and Saint-Brieuc. The first developments on the Légué port originates from the second half of the 18th century, with the construction of the first quays. They continued in the 19th century with the extension of the quays and the installation of the lock. From 1938 to 1973, maritime traffic increased steadily, reaching a total of 525000 tons in 1972, before decreasing. It seems to be holding at around 300000 tons per year (366000 tons in 2014). Fishing is declining while yachting is developing. The transport of sediment (sand and maerl) represents 25% of the total volume transited. In 1982, an economic study concluded that the port was insufficiently equipped to withstand the competition of modern ports, due to the reduced surface area of the platforms and the entry constraints linked to the tide. Modernisation and extension of the facilities started in 1986. The port was extended over the flat in an area of 158ha, characterised by a community dominated by *Macomangulus tenuis*. This extension was carried out in three phases: (1) the creation of a vast riprap in 1985, which accommodated (2) the port infrastructures over an area of 17.5 hectares; (3) the creation of a perpendicular breakwater in 2000. A new project includes the construction of a fourth quay by filling in 7.6 ha of mudflat to "ensure the maintenance and development of maritime transport" facilitating the reception of ships of more than 3000 tons. Maintaining the capacity to receive ships required the dredging of sediments and their deposit on the foreshore from 2004 to 2020. The authorities are currently studying new projects for a restarting of sediment deposit on the flat, while the fourth quay scenario became uncertain.

Subtidal area

The subtidal area encloses 11700 ha of shallow soft-bottom sediments. It borders the National nature reserve of the bay of Saint-Brieuc and partially belongs to the Natura 2000 "Baie de Saint-Brieuc-Est" site (FR5300066). This label does not prevent the area from being subjected to various anthropogenic pressures. On the western part, mussels are farmed on ropes, around stations 81, 99 and 100 (see section 3.2.2.1). The seabed is also exposed to a long-term scallop dredging activities as the bay of Saint-Brieuc is characterised by the highest fishing pressure in Brittany. Regulation changes have led, since 2006-2007, to the concentration of dredging at the beginning of the fishing season, in the very coastal area where the non-indigenous slipper limpet *Crepidula fornicata* is present.

Adjacent to the study area, the "Pays de Saint-Brieuc" counted 225795 inhabitants in 2019 and farmland occupies more than 60% of the territory's surface. These two characteristics are major drivers of water quality in the catchment. The bay suffers from eutrophication resulting in macroalgae proliferation and cyclic green tides episodes (Charlier et al., 2007; Gravier, 2012), which may notably impact fishes nursery grounds (Le Luherne et al., 2017, 2016).

A need of knowledge updating. The detection of future potential changes in species distribution and assemblages compositions, which can be helpful for monitoring and conservation issues (Desroy et al., 2002; Schückel et al., 2013; Veiga et al., 2017) requires the establishment of baseline knowledge. On the French coast of the English Channel, scientific studies have largely focused on benthic communities of the main coastal bays and estuaries [*e.g.* Rance estuary, (Desroy and Retière, 2004), bay of Seine (Bacouillard et al., 2020; Dauvin and Desroy, 2005; Desroy et al., 2007) or bay of Mont-Saint-Michel (Trigui, 2009)]. In the bay of Saint-Brieuc (Western English Channel), the first benthic surveys were carried out in 1987 in the framework of the Euphorbe program ("Eutrophisation et phénomènes d'origine benthique"). These studies led to the bio-sedimentary mapping of the intertidal and shallow subtidal benthic communities in the southern part (Gros & Hamon, 1988). Subtidal benthic communities were not revisited since this date, while intertidal ones have been re-investigated in 2001 (Bonnot-Courtois and Dreau, 2002; Le Mao et al., 2002).

In the intertidal area, the national nature reserve of the bay of Saint-Brieuc established in 1998 has favoured the development of studies which notably include benthic communities. The close link between waders and benthic resources has been highlighted (Ponsero et al., 2011; Sturbois et al., 2015; Ponsero et al., 2016) and supports the importance for managers to study and conserve benthic habitats. However, managers still question the trophic functioning and notably the potential influence of salt marsh vegetations and *Ulva spp.* bloom in supporting benthic food webs.

The objectives of this study were consequently to:

(1) analyse long-term ecological changes through taxonomic and functional trajectories of benthic assemblages (intertidal and subtidal) using protocols and historical baselines of previous studies and specify conservation status;

(2) characterise spatio-temporal patterns of the benthic food web.

These objectives are essential to provide up-to-date knowledge to policy makers and managers in order to optimize the management of this coastal area.

3.2 | Taxonomic and functional trajectories of benthic assemblages

3.2.1 | Intertidal area (Article III)

3.1.1.1 | Material and methods

Field sampling

Macrofauna was sampled during winter (March) in 1987, 2001 and 2019 at 42 stations, following the sampling grid (Figure 23) and the protocol defined in 1987 by Gros and Hamon (2021). At each site, four replicates were collected for macrobenthos analysis using a 1/32m² hand corer (diameter: 20 cm), at a depth of 25 cm. The core content was gently sieved on site through 1-mm square mesh sieve. Retained material was preserved for analysis in 5% buffered formaldehyde. Density per m² of *Arenicola marina,* species difficult to sample with a handcorer, was estimated visually by counting worm casts at each station within 10 quadrats of 1 m². A visual description of the sediment type was recorded and two samples of sediment were collected from additional cores (diameter 5 cm, depth 5 cm) and subsequently analysed for grain size distribution, and water and organic matter contents. All replicates were collected at the four corners of a 1m² square, using GPS position-fixing (GPS Etrex Garmin).

Laboratory analysis

Macrofauna was identified to the lowest possible level (usually species level), counted, and abundances were expressed as densities per 1 m^2. Taxa were named following the World Register of Marine Species. For grain size analysis, sediment was desalted with freshwater during 48 h before being dried at 60°C for 48 h, sieved through AFNOR standard sieves (from 40 to 25000 µm), and weighed. Water and organic matter contents were respectively determined after drying (60°C for 48 h) and combustion of sediment at 550 °C for 4 h (Hedges and Stern, 1984; Salonen, 1979).

Traits collection

The functional dataset was composed of six traits divided in 23 modalities. Chosen traits characterized the morphology (body size, flexibility and fragility) and behavioural traits [feeding behaviour, living habit and tolerance (*i.e.* ecological group), (Degen and Faulwetter, 2019)]. This set of traits is related to the vulnerability of species to mechanical disturbances (associated to recreational and professional fishing activity and the circulation of vehicles) and organic enrichment (tolerance). They were chosen to reveal functional changes in the community, in relation to the main pressures identified in the study area. Information was extracted from primary literature on specific taxa, expert knowledge and three publicly available databases. Scores were attributed to species according to their affinity to each category of traits, using a fuzzy coding from 0 (no affinity) to 3 [high affinity (Chevene et al., 1994)]. Community-weighted trait values (CWMs) were calculated to characterize the functional structure.

Data analysis

Data collected in 1987, 2001 and 2019 were analysed to track taxonomic and functional changes. The analysis of sediments and α-diversity was followed by a spatial taxonomic clustering and taxonomic and functional trajectory analysis.

Nine sedimentary parameters were selected to describe sediment characteristics: water content (H_20), organic matter content (OMC), arithmetic mean, median (d50), gravel (>2 mm), coarse sand (1 mm to 250 µm), fine sand (250 to 125 µm), very fine

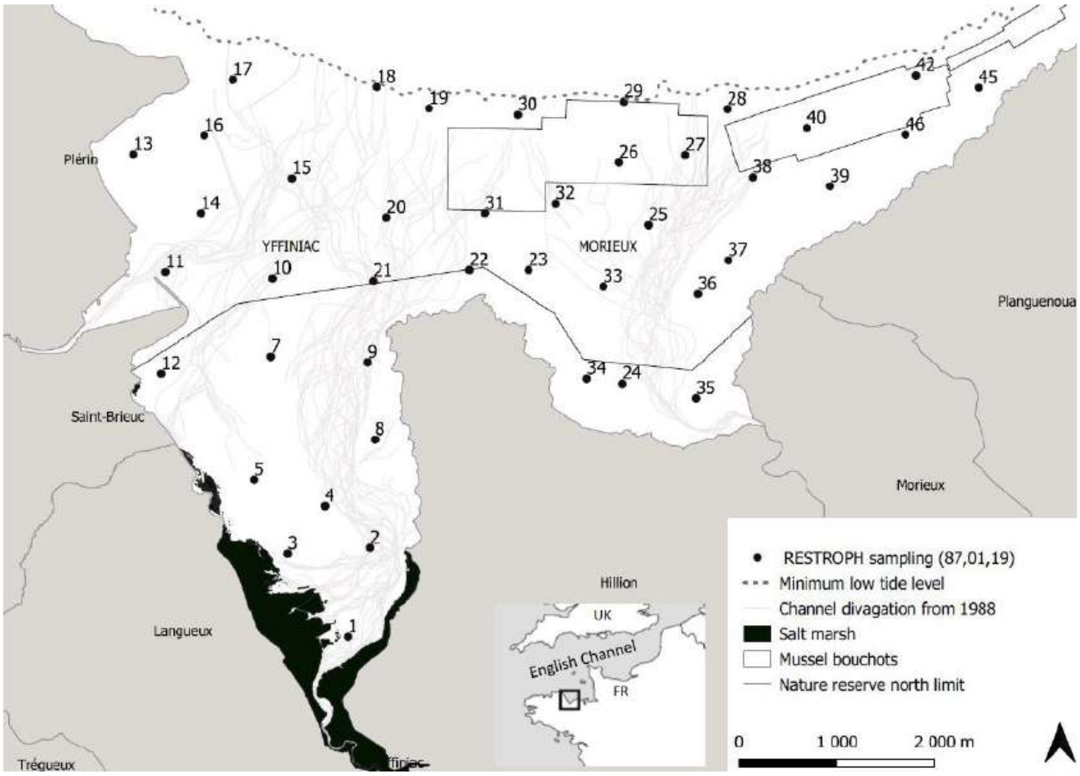


Figure 23: Location of the study area and sampling strategy. Black dots corresponds to the 42 stations of the ResTroph research program sampled in 1987, 2001 and 2019. The North limit of the Nature reserve is indicated by a black line and mussel bouchots by polygons.

sand (125 to 63 µm), and mud (<63 µm) contents.

Taxonomic α-diversity

In order to assess the different components of α-diversity, the mean number of individuals per m² (N), taxa richness (S), Shannon-Weaver index (H'), Simpson index (D) and Pielou's species evenness (J) were calculated for each station prior to any transformations of the dataset.

Spatial taxonomic clustering

Hierarchical Cluster Analysis (HCA) was performed to distinguish benthic assemblages (*i.e.* site groups) at each campaign by using the Hellinger distance between each pair of samples (Legendre and Gallagher, 2001) and by applying the Ward's clustering method. The indicator value method (Indval) was performed to characterize assemblages (Dufrene and Legendre, 1997).

Detecting trajectory patterns

PCAs were performed on Hellinger transformed data and followed by Community Trajectory Analysis (CTA). CTA is based on the geometrical properties of ecological trajectories (De Cáceres et al., 2019a). The original framework and its new extension (Article I) were used to study and represent temporal changes at the station scale taking into account all the dimensions of the multivariate analysis through trajectories of surveys in the multivariate space. A set of distance-based metrics were calculated. Segment-length represents, for a station, the distance between two consecutive surveys. S1 informs about changes between 1987 and 2001, and S2 between 2001 and 2019. The trajectory path represents the sum of segment length (S1+S2). Net changes were calculated to analyse trajectories between 1987 and 2019, considering the 1987 data set as an initial state (*i.e.* the first ecological state of the time series). Net changes informs about the overall change occurring during the study. The net change ratio represents the ratio between the net changes and the trajectory path. It informs about the straightness of recovering and or departing processes with respect to the initial state. Recovering and departing consecutive trajectory segments (RDT) were identified by subtracting Net change n-1 to Net change n (Article I). Dissimilarities between ecological trajectories (1987-2001-2019) were calculated to test their resemblance (De Cáceres et al., 2019a) to underline potential spatial pattern with HCAs. Indicator value method (Dufrene and Legendre, 1997) was performed on taxonomic trajectory clusters to test differences between 1987, 2001 and 2019. The relative contribution of all categories of functional traits between 1987, 2001 and 2019 were compared for each functional trajectory clusters and at the scale of the whole study area.

3.1.1.2 | Results

The sampling area was dominated by fine sediment at the three sampling dates. Sand was the most represented grain size class over the last three decades: 97.0% ± 1.9, 98.5% ± 4.1 and 95.6% ± 5.6. Mud and gravel were less represented and respectively ranged between 1.2% ± 4.0 to 3% ± 5.5, and 0.3% ± 0.8 to 1.4% ± 5.0. Overall, surficial sediment of the study area can be summarized as fine sands organised along a *continuum* from fine to very fine sands characterised by local variations in mud or gravel contributions.

The number of taxa reported in the intertidal flat was variable across the sampling period (Table II). In comparison to 1987, 11 taxa disappeared and 14 taxa appeared in 2001 and 14 taxa disappeared and 46 taxa appeared in 2019. 36 taxa were common to the three datasets and represented 95.5% ± 2.9 of the total abundance. Polychaetes, crustaceans, and molluscs were dominant. The number of taxa of these three dominant groups increased over the study period.

Table II: General description of macrofauna (N: number of taxa).

	1987	2001	2019	All years
Total Richness	50	53	85	133
Mean Richness	10.4 (sd=3.21)	10.8 (sd=5.23)	16.8 (sd=6.69)	
N Annelids	26	23	32	54
N Crustaceans	13	19	35	45
N Echinoderms	1	2	1	2
N Molluscs	9	9	15	24
N Nemertines	0	0	1	1
N Platyhelminthes	0	0	1	1
N Sipuncles	1	0	0	1
N Constant taxa	7	4	12	
N Common taxa	5	13	12	
N Occasionnal taxa	13	11	11	
N Rare taxa	25	25	50	
Total abundance	34222	95991	50639	
Mean abundance	815 (sd=1617)	2286 (sd=4496)	1206 (sd=1530)	
Shannon (H)	1.62(sd=0.46)	1.46 (sd=0.76)	1.98 (sd=0.70)	
Simpson (D)	0.70(sd=0.153)	0.61 (sd=0.29)	0.74 (sd=0.21)	
Pielou (J)	0.70(sd=0.153)	0.65 (sd=0.29)	0.71 (sd=0.21)	

In 1987, macrofauna was dominated by molluscs excepted in the low shore, where annelids were the most numerous group. In 2019, distribution between taxonomic groups was less contrasted, especially in the low shore, mostly due to an increase in mollusc abundances. Abundance of crustaceans also increased in most of the study area and a clear extension of the echinoderms distribution was observed in the western part of the study area, mostly due to the ophiuroid *Acrocnida spatulispina*.

Hierarchical classification

The Hierarchical Cluster Analysis separated four clusters in 1987 and 2001 and five clusters in 2019 (Figure 24). Mainly influenced by bathymetry, the distribution and structuration of assemblages was stable from the upper to the lower flat, despite the south-westward extension of assemblage IV, and the apparition of a new assemblage in 2019.

Assemblage I, located in muddy sands on the upper part of the flat, was characterized by *Pygospio elegans* in 1987, and *Peringia ulvae* in 2001 and 2019 (first rank indval). *P. ulvae* was dominant in 1987 and 2019, whereas *Corophium arenarium* was the most abundant species in 2001.

Assemblage II, associated to very fine to fine sand of the upper mid-flat, was characterized by *Macomangulus tenuis* in 1987 and 2019 and *Urothoe poseidonis* in 2019. *M. tenuis remained* the most abundant species over the study period.

Assemblage III, associated to very fine to fine sand of the lower mid-flat, was characterized by *U. poseidonis in 1987* and *Acrocnida spatulispina* in 2001, and 2019. This assemblage was dominated by *M. tenuis* in 1987, *U. poseidonis* in 2001, and *A. spatulispina* in 2019.

Assemblage IV, associated to sands mainly located near low water marks, was characterised by *Scoloplos armiger* in 1987, *Donax vittatus* in 2001, and *Magelona mirabilis* in 2019. It was dominated by *Polycirrus medusa* in 1987 and *D. vittatus* in 2001 and 2019.

A **new assemblage** was identified in 2019, in the upper part of the shore, on bare sands associated to major sand intakes. *Eurydice affinis* characterized this assemblage and *Bathyporeia pilosa* was the most abundant species.

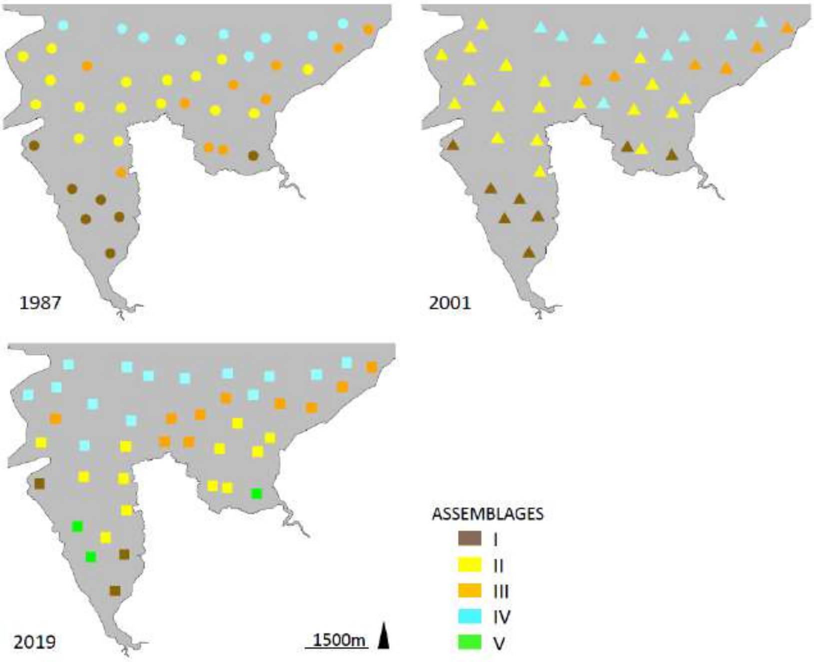


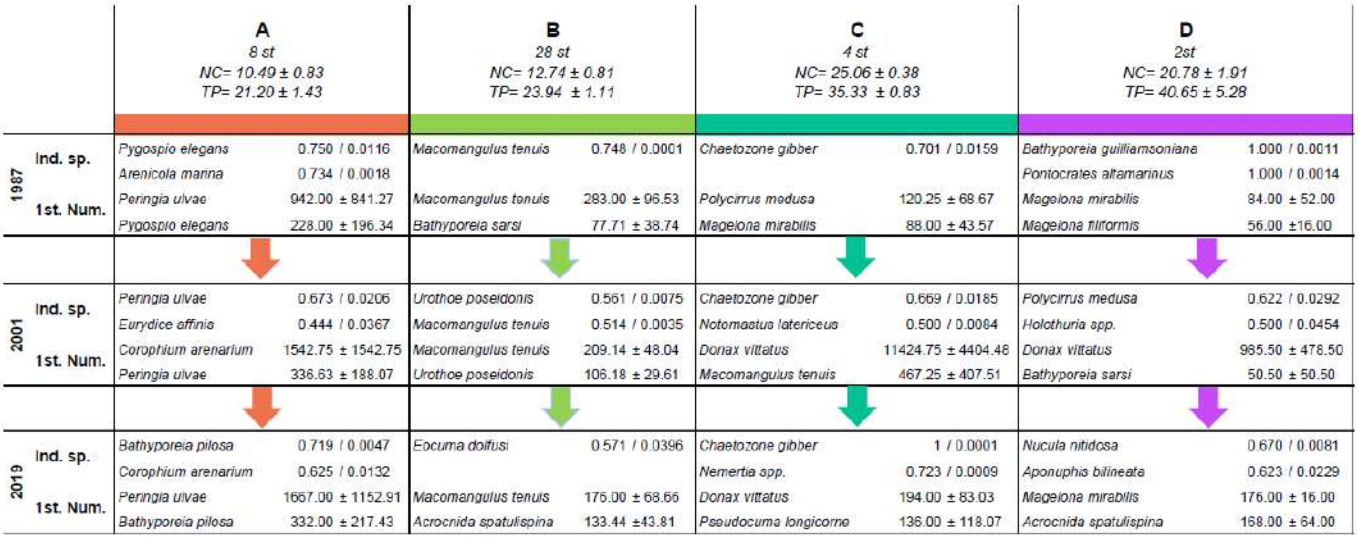
Figure 24: Spatial distribution of benthic assemblages identified with Hierarchical Cluster Analysis performed on 42 stations in 1987, 2001 and 2019.

Taxonomic trajectories

The first period was characterized by less change (total S1 lengths = 453.05, mean= 10.79 ± 3.46) than the second [total S2 lengths= 582.34, mean= 13.87 ± 5.56 (Figure 25, A)]. The highest net changes occurred in the low shore where eight stations concentrated 31% of changes (179.24). A positive correlation (0.529, p<0.001) was found between net change and latitude. RDT was positive for 31 stations (71.43%) and negative for 11 stations, showing an overall departure dynamics from the initial taxonomic state. Total net change (582.34) represented only 56 % of the total trajectory path (1035.39). This low net change ratio (53.14% ± 0.12) indicated significant direction changes (*i.e.* driving species groups) in the multivariate space between 1987-2001 and 2001-2019 for departing trajectories, and included recovering ones. The HCA performed on CTA of trajectory similarities separated four main clusters of taxonomic trajectories (Figure 25, B and C).

The **taxonomic trajectory cluster A** was composed of eight stations from the sheltered part of the bay, and describing the evolution from an assemblage characterized *P. elegans* in 1987 and *B. pilosa* in 2019 and dominated by *P. ulvae* in 1987 and 2019 and *C. arenarium* in 2001 (Table III). **Cluster B**, the most common group (28 stations), was characterised by *M. tenuis* in 1987, *U. poseidonis* in 2001 and *E. dolfusi* in 2019. *M. tenuis* remained the most numerous species over time. Cluster C (NC=25.06 ± 0.38; TP=35.33 ± 0.83) and D (NC=20.78 ± 1.91; TP=40.65 ± 5.28) were characterised by longer net changes and trajectory path compared to cluster A (NC=10.49 ± 0.83; TP=21.20 ± 1.43) and B (NC=12.74 ± 0.81; TP=23.94 ± 1.11), but represented a limited number of trajectories (14 % of stations). **Cluster C** grouped four stations located in the north-west, characterized by *C. gibber* at the three campaigns and dominated by *P. medusa* in 1987 and *D. vittatus* in 2001 and 2019. **Cluster D,** which regrouped only two stations located in the eastern low shore, was characterised by *Bathyporeia guilliamsoniana* in 1987, *P. medusa* in 2001 and *Nucula nitodosa* in 2019. *Magelona mirabilis* was the most numerous species in 1987 and 2019 and *D. vittatus* remained dominant in 2001.

Table III: Characteristics of ecological states of trajectory clusters in 1987, 2001 and 2019. Taxonomic trajectory are coloured according to trajectory clusters and described with distance-based metrics mean ± se (NC: net change, TP: Trajectory path). Distribution of species used to describe taxonomic trajectory clusters (Ind.sp.: Indicative species, 1st. Num.: two first numerous species) are detailed in Supplementary material, Appendix D.



		A *8 st* *NC= 10.49 ± 0.83* *TP= 21.20 ± 1.43*		**B** *28 st* *NC= 12.74 ± 0.81* *TP= 23.94 ± 1.11*		**C** *4 st* *NC= 25.06 ± 0.38* *TP= 35.33 ± 0.83*		**D** *2st* *NC= 20.78 ± 1.91* *TP= 40.65 ± 5.28*	
1987	**Ind. sp.**	*Pygospio elegans*	0.750 / 0.0116	*Macomangulus tenuis*	0.748 / 0.0001	*Chaetozone gibber*	0.701 / 0.0159	*Bathyporeia guilliamsoniana*	1.000 / 0.0011
		Arenicola marina	0.734 / 0.0018					*Pontocrates altamarinus*	1.000 / 0.0014
	1st. Num.	*Peringia ulvae*	942.00 ± 841.27	*Macomangulus tenuis*	283.00 ± 96.53	*Polycirrus medusa*	120.25 ± 68.67	*Magelona mirabilis*	84.00 ± 52.00
		Pygospio elegans	228.00 ± 196.34	*Bathyporeia sarsi*	77.71 ± 38.74	*Magelona mirabilis*	88.00 ± 43.57	*Magelona filiformis*	56.00 ±16.00
		↓		↓		↓		↓	
2001	**Ind. sp.**	*Peringia ulvae*	0.673 / 0.0206	*Urothoe poseidonis*	0.561 / 0.0075	*Chaetozone gibber*	0.669 / 0.0185	*Polycirrus medusa*	0.622 / 0.0292
		Eurydice affinis	0.444 / 0.0367	*Macomangulus tenuis*	0.514 / 0.0035	*Notomastus latericeus*	0.500 / 0.0084	*Holothuria spp.*	0.500 / 0.0454
	1st. Num.	*Corophium arenarium*	1542.75 ± 1542.75	*Macomangulus tenuis*	209.14 ± 48.04	*Donax vittatus*	11424.75 ± 4404.48	*Donax vittatus*	985.50 ± 478.50
		Peringia ulvae	336.63 ± 188.07	*Urothoe poseidonis*	106.18 ± 29.61	*Macomangulus tenuis*	467.25 ± 407.51	*Bathyporeia sarsi*	50.50 ± 50.50
		↓		↓		↓		↓	
2019	**Ind. sp.**	*Bathyporeia pilosa*	0.719 / 0.0047	*Eocuma dolfusi*	0.571 / 0.0396	*Chaetozone gibber*	1 / 0.0001	*Nucula nitidosa*	0.670 / 0.0081
		Corophium arenarium	0.625 / 0.0132			*Nemertia spp.*	0.723 / 0.0009	*Aponuphis bilineata*	0.623 / 0.0229
	1st. Num.	*Peringia ulvae*	1667.00 ± 1152.91	*Macomangulus tenuis*	176.00 ± 68.66	*Donax vittatus*	194.00 ± 83.03	*Magelona mirabilis*	176.00 ± 16.00
		Bathyporeia pilosa	332.00 ± 217.43	*Acrocnida spatulispina*	133.44 ±43.81	*Pseudocuma longicorne*	136.00 ± 118.07	*Acrocnida spatulispina*	168.00 ± 64.00

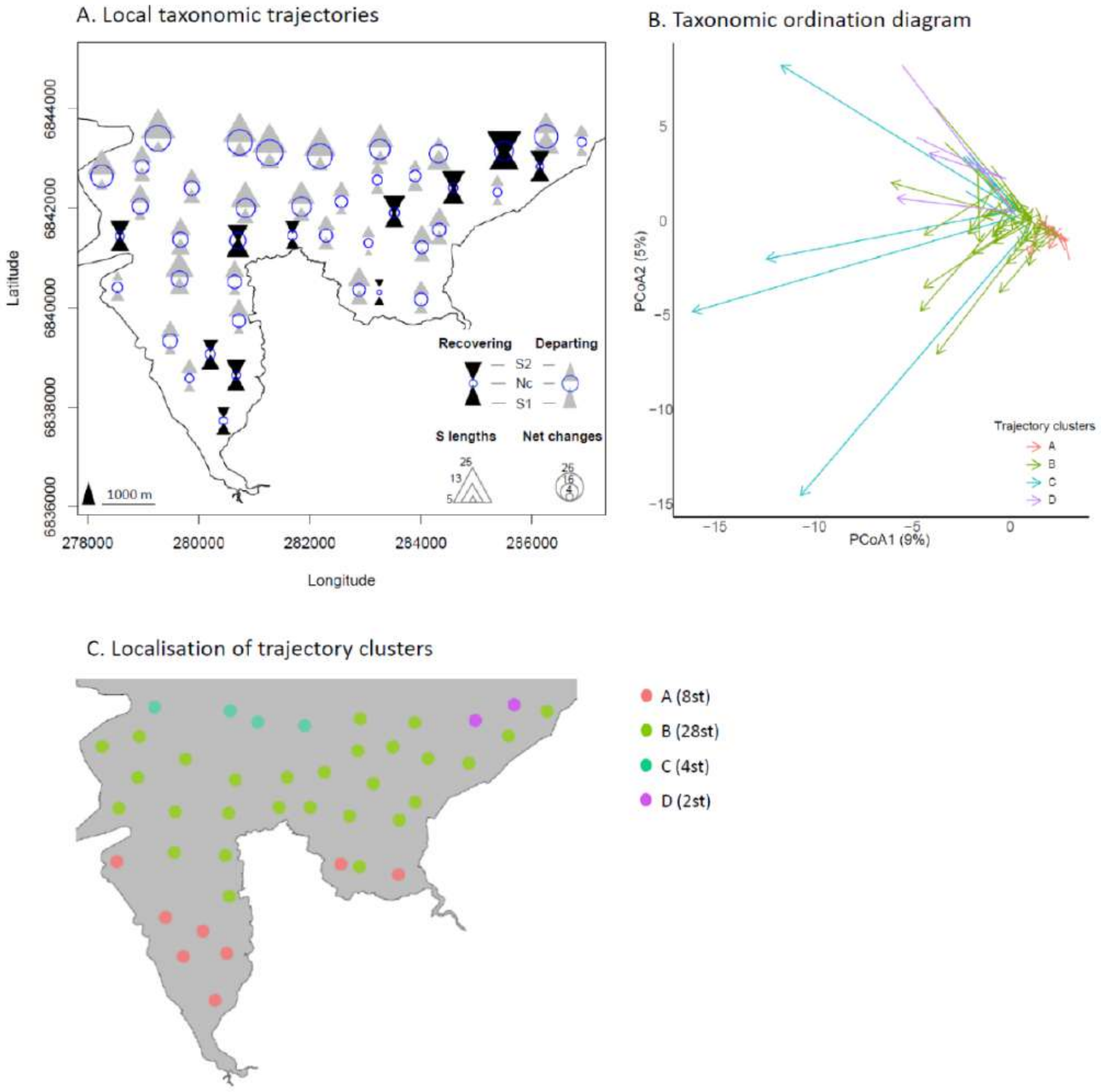
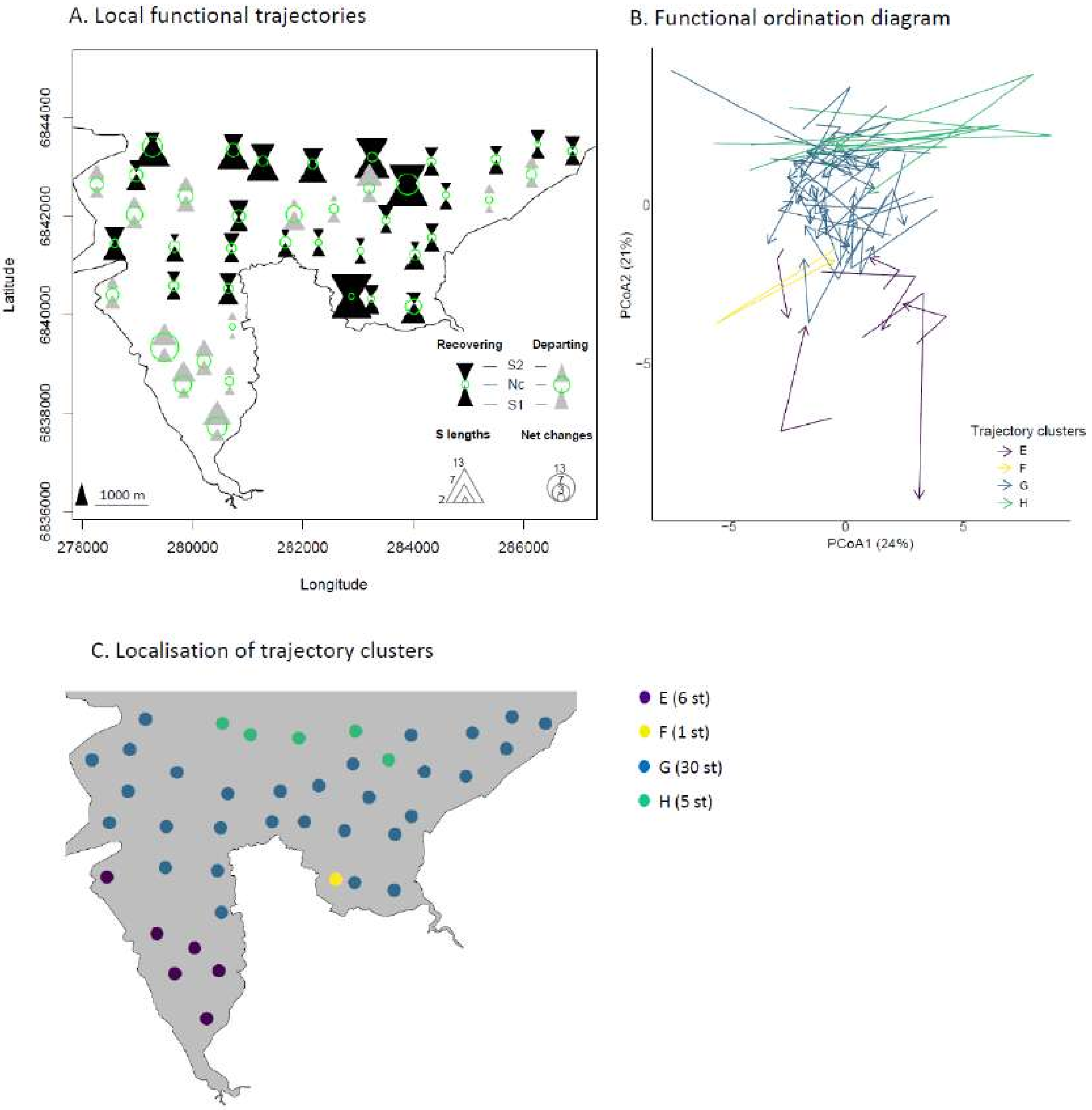


Figure 25: Taxonomic trajectories. A: Trajectory map. Distance-based metrics are represented with circular and triangle symbols. Net changes are represented with blue circles between 1987 and 2019. Bottom triangles represent the trajectory segment S1 (1987 to 2001) and top ones S2 (2001 to 2019). The size of symbols corresponds to lengths. For triangles, colors are used to distinguish recovering (black) from departing trajectories (grey). B: Trajectory ordination diagram. The three ecological states of each station were connected with arrows in order to represent the whole trajectory path. Each trajectory path was coloured according to taxonomic trajectory clusters defined with Hierarchical Cluster Analysis based on CTA trajectory similarity analysis. Even though trajectory distance-based metrics and dissimilarity were calculated considering all of the dimensions of the PCA, here the first two dimensions represent only 14% of the total variation, therefore potentially hiding some patterns. C: Localisation of trajectory clusters within the study area.

Functional trajectories

Functional trajectory paths were, for all sites, similar for both periods, revealing similar level of functional variability between 1987 and 2001 (254.55, 6.06 ± 2.88) and 2001 and 2019 (223.41, 5.32 ± 2.61). A set of seven stations concentrated 30 % (143.67) of the overall trajectory path, illustrating a high functional variability in these areas over the last 30 years. RDT revealed recovering trajectories for 25 stations (60 %), evenly distributed in the study area (Figure 26, A). The low net change ratio (46.78% ± 0.11) was influenced by recovering trajectories. The HCA performed on CTA of trajectory similarities separated four main clusters according to the shape of functional trajectories (Figure 26, B and C).



A. Local functional trajectories

B. Functional ordination diagram

C. Localisation of trajectory clusters

Figure 26: Functional trajectories. A: Maps of local trajectories. Distance based metrics are represented with circular and triangle symbols. Net changes are represented with green circles between 1987 and 2019. Bottom triangles represent the trajectory segment S1 (1987 to 2001) and top ones S2 (2001 to 2019). Size of symbols corresponds to lengths. For triangles, colors are used to distinguish recovering (black) from departing trajectories (grey). B: Trajectory ordination diagram. The three ecological state of each station were connected with arrows in order to represent the whole trajectory path. Each trajectory path was coloured according to functional trajectory clusters defined with Hierarchical Cluster Analysis based on CTA trajectory similarity analysis. C: Localisation of trajectory clusters within the study area.

The **functional trajectory cluster E** grouped six stations located in sheltered and upper parts of the shore and characterised by the highest net changes (7.50 ± 1.27) and moderate trajectory path (10.80 ± 1.09). Cluster E trajectories were mainly defined by an increase in the contribution of very sensitive, free living and small species (Figure 27).

Cluster F, which concerned only one station, was characterised by the highest trajectory path (27.29) but one of the smallest net change (2.63) in relation with an effective recovering trajectory between 1987-2001 and 2001-2019.

Cluster G was the most common pattern of functional trajectories (30 stations) characterized by moderate net changes (4.66 ± 0.28) and trajectory path (9.53 ± 0.48). This cluster was characterised by moderate functional changes, except for an increase in the contribution of flexible and small size species.

Cluster H grouped five stations of the low shore characterised by high trajectory path (19.97 ± 1.72) and moderate net changes (5.71 ± 0.94), in relation with recovering trajectories occurring at this sites. The main functional shift in cluster H concerned a positive shift of suspension-feeders, free living, medium fragile, and rigid species, notably attributable to strong variation of *D. vittatus* observed at these stations. Despite some local functional shift depending on functional trajectory clusters, and some slight significant shifts for some categories of traits, the overall functional properties remained stable over time at the site scale (Figure 28).

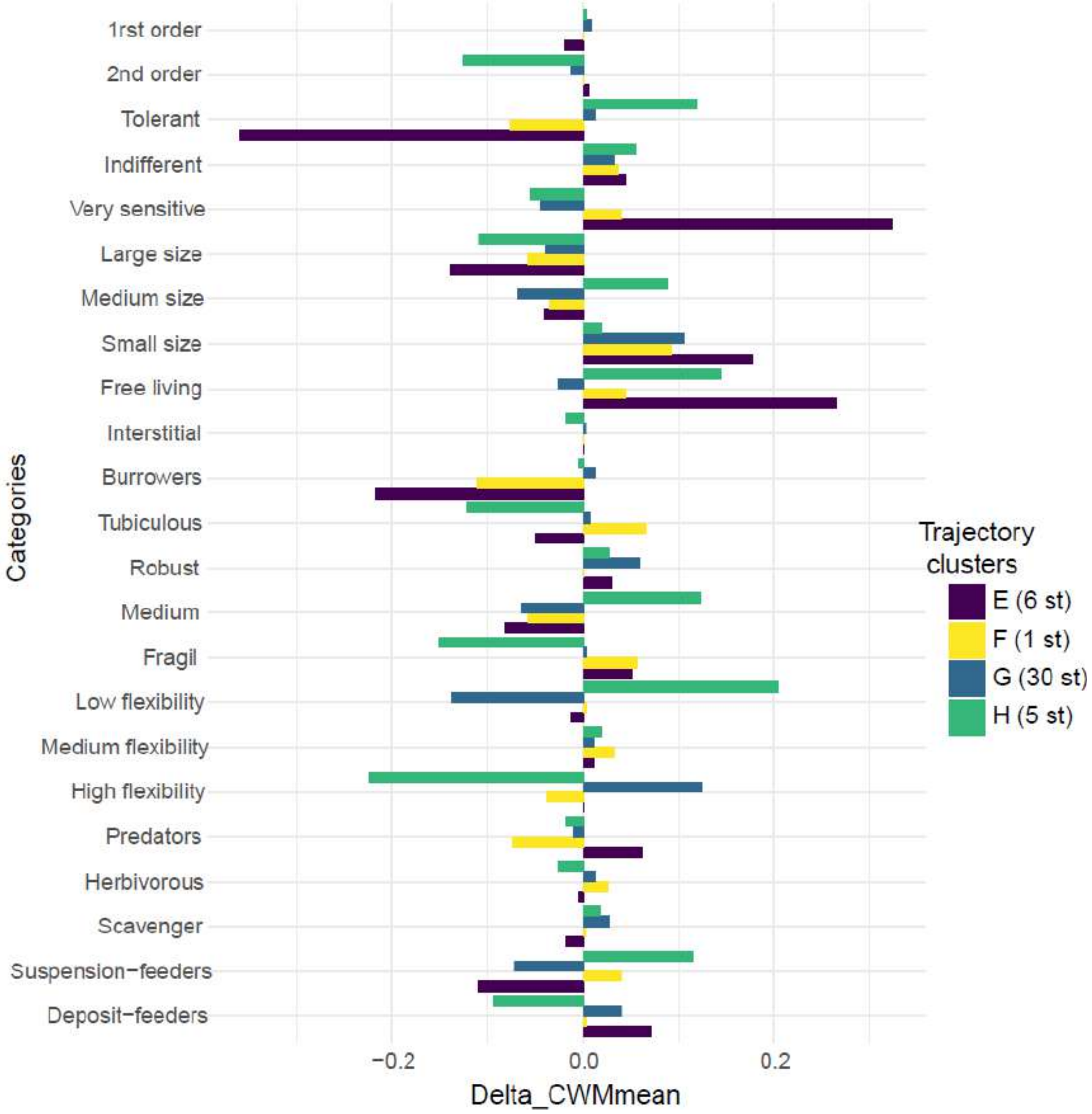


Figure 27: Barplots of Community-weighted trait values (CWM) values shift for each categories of traits (mean 2019 – mean 1987). Bars are coloured according to functional trajectory clusters.

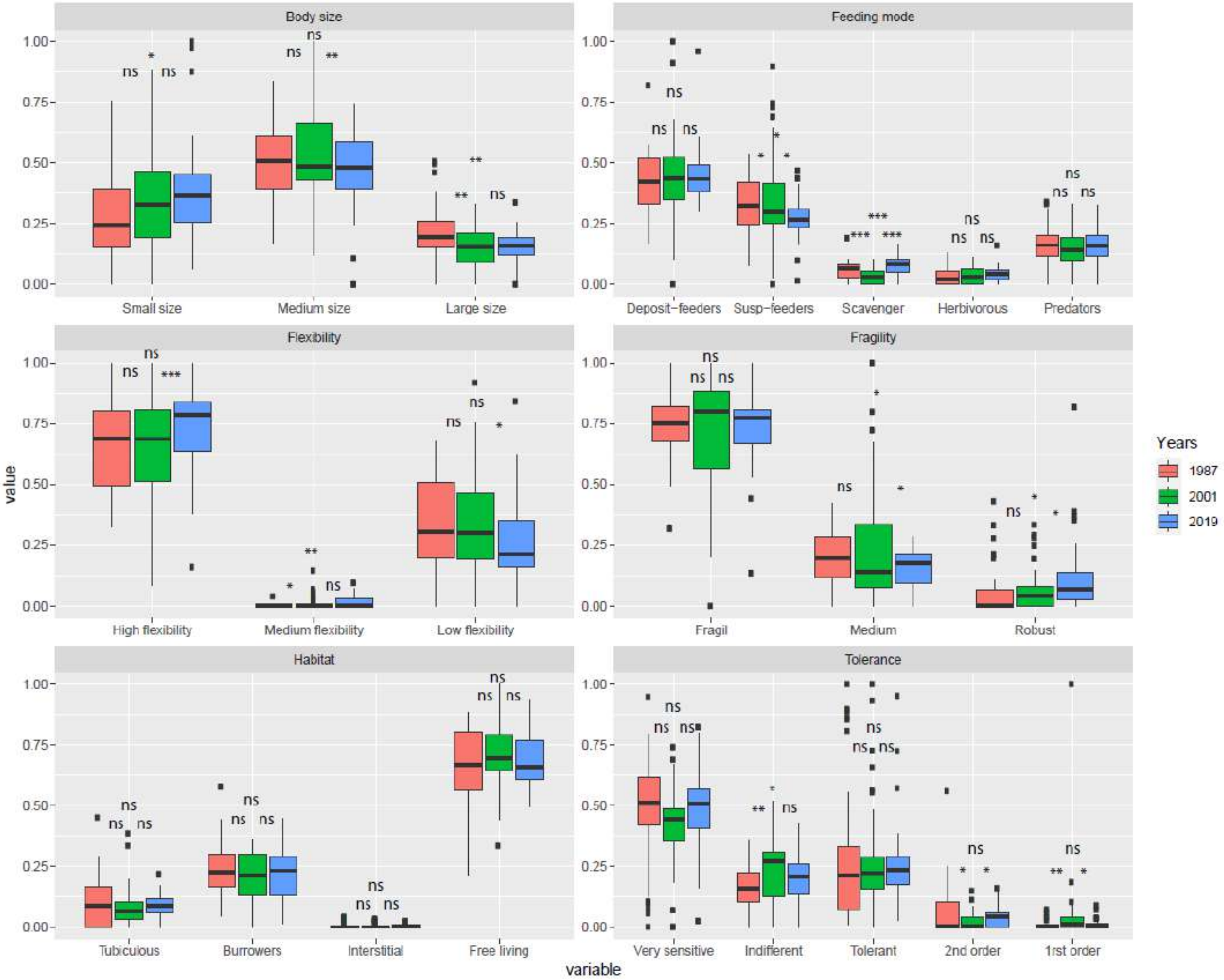


Figure 28: Box plots of Community-weighted trait values (CWM) traits values in levels of respective categories according to year (1987: red; 2001: green; 2019: blue). Box plot indicates the median (line in the box), the first and third quartiles (hinges) and extreme data points (black points). Significance of Student permutation paired tests are indicated for each category traits (ns: non-significant; *: pval<0.05; **: pval<0.01; *** pval:<0.001).

3.1.1.3 | Discussion

Local ecological dynamics influence benthic assemblages

A consortium of 36 species common to the three sampling periods represents 95.5% of the total abundance. Such a pattern reveals a strong stability in the pool of species influencing community abundance and composition. Some gains and losses of occasional and rare species influenced variations of the relative contribution of taxonomic group to overall richness. Changes in assemblages mainly involved some of the prevalent species, suggesting a strong impact of fluctuating population dynamics rather than species replacement in the community.

Many species were involved in the definition of assemblages and taxonomic trajectory clusters, but the contribution of some of them was constant over time, notably *P.ulvae, L. balthica, U. poseidonis, C. edule, M. tenuis, C. gibber* and *M. mirabilis*. At the scale of stations, despite an overall departing taxonomic trend, we observed mainly recovering functional trajectories.

Two main mechanisms are involved in the long-term variability of benthic assemblages: the dynamics of structuring species and the existence of strong local variability.

1. *Dynamics of structuring species.* Coupled with random gain or losses of species (Legendre, 2019), the dynamics of structuring species results in moderate specific taxonomic changes in the multivariate structure of assemblages. However, several species can induce strong trends, such as *D. vittatus* [whose abundance varied from 13.4 ± 15.0 ind.m² (20 stations) in 1987 to 3107.0 ± 6347.0 ind.m² (16 stations) in 2001 and 72.8 ± 101.0 ind.m² (19 stations) in 2019] or *A. spatulispina* and *Kurtiella bidentata* [whose occurrence and abundance increased over time]. In assemblage I, the decline in *L. balthica* population is potentially attributable to climate change (seawater temperature increase) as suggested by different works in European regions (Beukema et al., 2009; Genelt-Yanovskiy et al., 2017; Jansen et al., 2007; Ong et al., 2017; Philippart et al., 2003; Van Colen et al., 2018). The bay of Saint-Brieuc being located in the southern part of *L. balthica*'s distribution, populations are likely to be affected by climate warming.

2. *Sediment and hydrodynamics.* The strong local variability is able to induce changes in assemblage definition, according to the initial state defined in 1987. The identification of a new assemblage in 2019, in relation to sedimentary variations (Figure 22-2 and -3), and the re-affectation of some stations to different assemblages illustrate such spatial changes. The distribution of *A. spatulispina* and *K. bidentata* in particular significantly extended their distribution in the sampling area over time.

At some stations, local taxonomic variability was of higher magnitude than the within-assemblage dispersion observed in 1987, which resulted in changes in their affectation in assemblage over time.

At the opposite, others trajectories buffered local functional changes in some stations at the assemblage scale, especially in the lower part of the shore. Considered separately, stations were characterized by different functional trajectories, and the concentration of local recovering trajectories in these assemblages contributed to explain the overall functional persistence. Macrobenthic communities are often associated to a mosaic of micro-habitats where natural disturbance events result in the creation of patches characterized by different recovering stages (Defeo et al., 2009; Ellis et al., 2000).

According to Grimm and Wissel (1997), persistence is defined as a stability property of ecological systems which nevertheless integrate moderate temporal variations. It differs of the concept of constancy, which describes unchanged systems. Despite changes observed at the scale of assemblages coupled with fluctuating population dynamics of structuring species, we assume an overall persistence of the whole benthic community in the bay of Saint-Brieuc. Such assumptions are in accordance with Bacouillard et al. (2020), who suggest that local turnover can be very high, especially in response of hydrologic and sedimentary dynamics (Desroy et al., 2007), without adversely affecting the long-term persistence of the community.

Low shore concentrates taxonomic changes

The CTA approach revealed that the taxonomic variability increased following a bathymetric gradient. In the upper flat, sheltered conditions, strong influence of salinity variations and emersion time limit the number of species and the variability due to species gains. Inversely, species richness increasing towards the lower flat contributes to the magnitude of change in low levels. As observed in 2019 for *Aponuphis bilineata* and *Nucula nitidosa*, the local presence of subtidal species on the intertidal flat constitutes a source of variation.

The northwestern part of the bay, characterised by professional and recreational fishing activities known to impact benthic communities (Boldina et al., 2014; Mosbahi et al., 2016), concentrated the highest net changes. Hydrodynamics associated to tidal range is particularly strong in our study area and recognized as a dominant factor shaping the variability of coastal systems (Monbet, 1992; Wildish, 1977; Wildish and Kristmanson, 1979). This factor is responsible for surficial sediment distribution and, consequently, for the dynamics of macrofaunal communities as demonstrated by Fujii (2007) in the Humber estuary (UK), Compton et al. (2013) in the Wadden sea, or Veiga et al. (2017) on the North Portuguese coast. The influence of intertidal channels divagation (within a 1420 ha area since 1988; Figures 22-4 and 23) must also be considered as a driver of sediments resuspension and habitat resetting, particularly important in the low western shore. In the eastern part, low net changes associated with high trajectory path and recovering trajectories could be explained by sand banks displacement from north to south (Figure 22-2). Departing trajectories may be associated to the sandbank crossing on the area and recovering trajectories, to the restauration of initial conditions after its passage. Such impact of sediment transport has already been highlighted in different coastal areas in New Zealand (Thrush et al., 2003), France (Gouleau et al., 2000) or experimentally in the UK (Whomersley et al., 2010). In this way, we expect any anthropogenic activity potentially modifying sedimentary parameters (bio-deposition, sediment deposition, beach nourishment, dredging…) to, in turn, modify intensely the composition, structure and functioning of soft bottom assemblages as suggested by Veiga et al. (2017).

Whomersley et al. (2010) suggested that benthic communities frequently disturbed by sediment movements or other natural environmental conditions would show greater resilience against further physical disturbance. Such resilient responses to disturbance, due to the selection of adapted species, depend on the history of prior disturbance and on the inherent ecological plasticity exhibited by species (Davic, 2003). In our study, 36 prevalent species contribute to the persistence of the community over time. Most of these species are adapted to living in mobile sediments (McLachlan and Brown, 2006) and facing erosion and sedimentation. They could then persist because of their tolerance to the selective environmental conditions as suggested by Callaway (2016). In the bay of Saint-Brieuc, the strong sedimentary and hydrologic dynamics are the driving factor of the persistence of the system.

In many coastal ecosystems, multiple disturbance sources, both natural and anthropogenic, are often confounded (Whomersley et al., 2010), which makes difficult to define their respective contribution (Harris, 2012). Our study confirms the complexity to disentangle factors of changes in dynamic areas, where strong natural variability results in regular community resets (Defeo and McLachlan, 2013), which may overshadow anthropogenic impact. In the bay of Saint-Brieuc, which is characterised by severe natural pressures, further studies coupling experimental and high frequency field samplings should help to understand the respective role of hydrodynamics and anthropogenic activities in resetting benthic communities. Studies should concern shear stress measurement in area concerned and not by the circulation of mussel farming vehicles or analysis of the benthic macrofauna variability coupled with different gradients of fishing activities and/or local environmental dynamics.

Functional properties of the community persist over time

The CTA revealed contrasted taxonomic and functional trajectory patterns (*i.e.* net changes, departing and recovering trajectory). Clare et al. (2015) showed that density compensation by redundant taxa buffers ecological functioning changes, but that functional stability is subjected to aperiodic disruption due to substitutions of dissimilar taxa or uncompensated population fluctuations. Accordingly, high trajectory paths observed in the low shore reflected an important functional variability, but recovering trajectories notably influenced by *D. vittatus* fluctuating population dynamics led to low net changes. Functional properties persisted over time at the scale of the whole community. The low sensitivity of traits such as body size, flexibility, fragility to genus and, in a lesser extent, species changes also contribute to limit the influence of taxonomic variability on the functional stability. Lower influence of traits relative to feeding behaviour finally suggested no major changes at the scale of intertidal sedimentary habitats, in accordance with Sturbois et al. (Article 1) who showed that high sedimentary variability was limited to few sites.

When choosing the set of traits in relation to main pressures, we hypothesised that fishing activities in the lower flat may influence benthic assemblages over time according to changes in relative values of body size, flexibility, fragility. Since 1994, 67 tons of *Cerastoderma edule* have been harvested on average per year with high interannual variability in tonnage (min: 0 ton, max: 378 tons) and number of fishers involved (min: 0 ton, max: 140 tons). The 1995-2000 period (254 tons have been harvested in average per year by 117 fishers) contrasts with the 2000-2016 period which is characterized by a smaller fishing effort (11 tons per year, 15 fishers). Recreational fishing has been studied by social survey and estimated (Anger, 2010). The number of fishing sessions (1 recreational fisher, 1 day), extrapolated per year, reaches 4439 sessions in 2012 for 12.9 tons and 3727 sessions in 2013 for 10.8 tons. Low net changes in the lower part of the shore for the widespread functional trajectory cluster G and the influence of *D. vittatus* in the functional trajectory of cluster H does not support such a functional response to human pressures.

A similar interest was devoted to the tolerance of species to organic matter enrichment according to the eutrophication process, mainly due to green tides. No major change was observed at the scale of the whole study area in the contribution to the ecological groups. In accordance, changes were moderate in the different functional clusters except in cluster E characterized by an important positive shift in the contribution of very sensitive species. Despite a slow long-term water quality improvement trend and a progressive decrease of green tides associated to local water development and management plan, these events still strongly affect the study area. Quillien et al. (2015a) discussed the potential influence of *Ulva sp.* mats on abundance peak of *D. vittatus* (by improving recruitments and affecting negatively predators of larvae), which could explain high densities, reaching 21 487 ind.m² in 2001 and 14 685 ind.m² in 2011 observed in the bay of Saint-Brieuc. Quillien et al. (2015b) also highlighted large-scale effects of green tides on macrotidal sandy beaches in Brittany, showing notably that the echinoderm *A. spatulispina* and the mollusc *K. bidentata* were stimulated in soft bottom sediments impacted by green tides, contrary to the crustaceans *B. elegans* and *Cumopsis spp*., which were negatively affected. In our study, the abundance and occurrence of these four taxa increased over the study period, revealing a more complex gradient of sensitivity to green tides, local anoxia and/or nutrient enrichment and the implication of other driving factors. As suggested by Bolam et al. (2000), Everett (1994), and Raffaelli et al. (1999), generalisations on the effect of algae mat are not straightforward. In our study area, we believe that the association between important green-tides and nutrient uptake buffers the influence of nutrient enrichment on macrofauna.

3.2.2 | Subtidal area (Article IV)

3.2.2.1 | Material and methods

Field sampling

Benthic macrofauna was sampled at 38 stations during winter (March) in 1987 and 2019 (ResTroph research programme) following the grid (Figure 29) and the protocol defined in 1987 by Gros & Hamon (1988). During both surveys, five replicates were collected at each station with a small Hamon grab (1/8m²) for macrobenthos analyses. The grab contents were gently sieved on board either through:

(1) a 2 mm circular mesh sieve (1 replicate) to describe benthic assemblages;

(2) a 5 mm circular mesh sieve (4 replicates) to specifically analyse bivalve populations.

The retained material was preserved for analysis in 5% buffered formaldehyde. Only the replicate sieved on a 2 mm mesh was used for the long-term comparison of the benthic community. Two samples of sediment were collected in one additional grab using a handcorer, and subsequently analysed for grain size distribution and organic matter content respectively. All replicates were collected at a maximal distance of 50 m from each station, using DGPS position-fixing.

To complete the ecological status monitoring, data collected at one station (R) in the framework of the Water Framework Directive were considered to assess the year-to-year variability of taxonomic and functional diversity. Station R was sampled yearly (nine replicates, following national recommendation of the REBENT benthic network as part of the WFD) in March from 2005 to 2019, with a Smith McIntyre grab (0.1 m²), and sieved on 1 mm circular mesh sieve.

Data and laboratory analysis

Analyses performed on the subtidal data sets were similar from those performed on the intertidal data sets (see section 3.1.1.2 and article III for more details). Briefly, data collected in 1987 and 2019 were analysed to track taxonomic and functional changes. Analysis of sediments and α-diversity were followed by spatial and temporal taxonomic clustering and taxonomic and functional trajectory analyses.

3.2.2.2| Results

Changes in sediment composition

On the whole area, sediments were dominated by sands in 1987 (74.3% ± 12.8, mean +/- sd) and 2019 (78.7% ± 12.3). Fine sands (125-250 µm) were the most represented sedimentary class in both years (42.3% ± 17.9 in 1987; 46.6% ± 18.0 in 2019). Mud content significantly decreased in 79 % of stations (-11.1% ± 6.9; min= -0.8%; max= -31.1%, p-value < 0.001). In contrast, 21% of stations were characterized by an increase in mud content (+11.5% ± 17.6) especially at stations 101 (+52.5%), 81 (+16.2%), and 100 (+13.6%). Gravel accounted for 8.4% ± 10.6 in 1987 and 10.2% ± 6.9 in 2019. Mean particle size (356.5 µm ± 258.9 vs 421.5 µm ± 192.5) slightly and significantly increased (p-value < 0.001) over the study period.

At station R, sediment properties varied inter-annually: after a first period of high inter-annual variability between 2005 and 2014, sediment granulometry was less variable from 2015 onward.

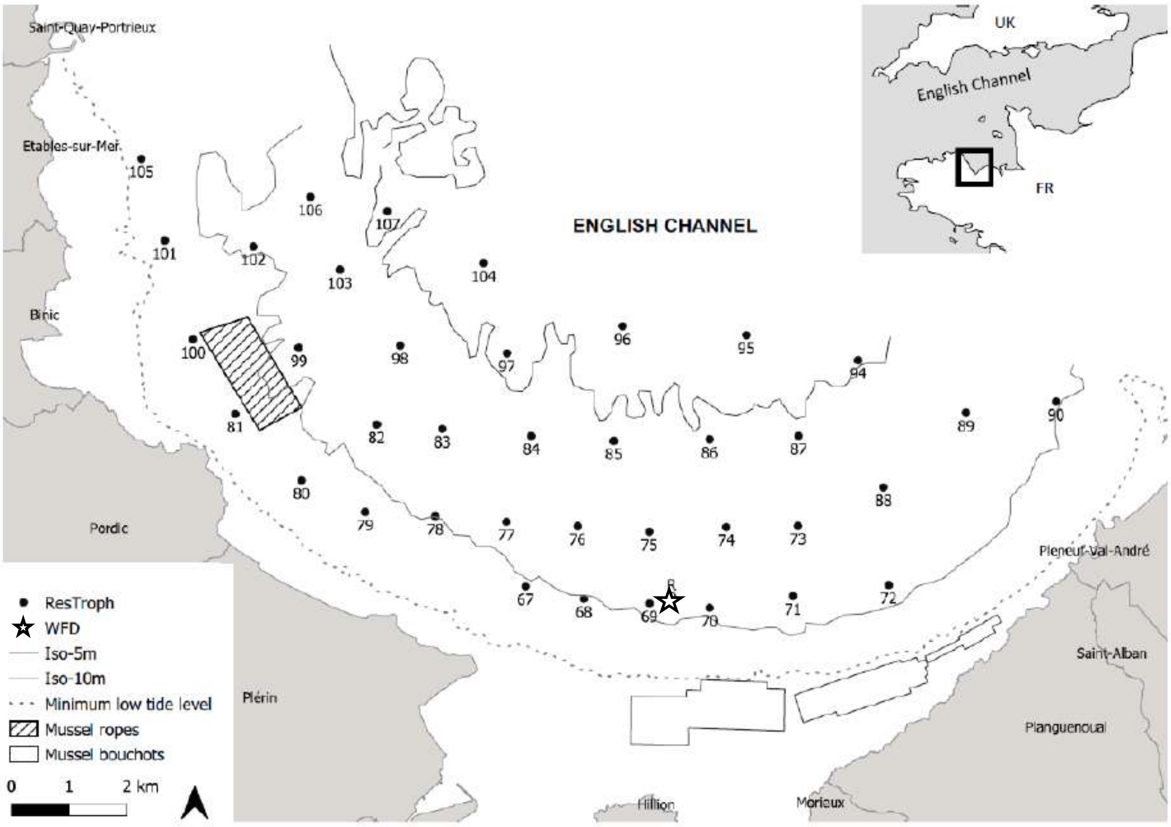
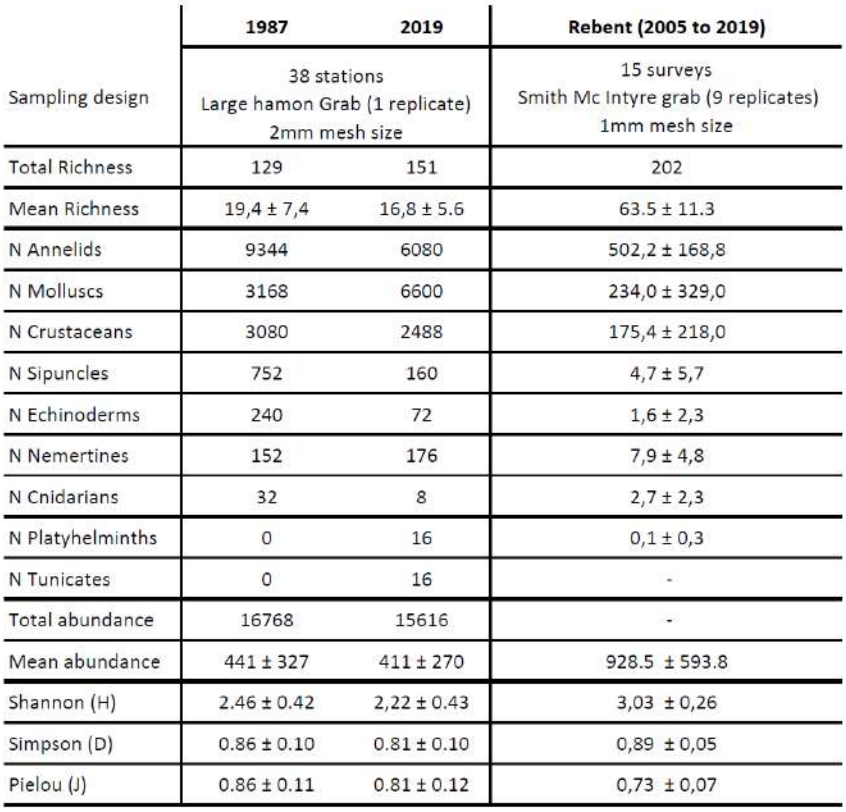


Figure 29: Location of the study area and sampling strategy. Black dots correspond to the 38 stations of the ResTroph research program sampled in 1987 and 2019 and the white one (station R) to the Water Framework Directive (WFD) monitoring program conducted from 2005 to 2019. Water depth is represented by dotted (0 m) and continuous lines (5 and 10 m) and mussel culture on bouchots and ropes by polygons.

General description of fauna

On the whole area, 208 taxa were collected in 1987 and 2019 (Table IV) on the 2 mm mesh size sieve (with 72 taxa common to both datasets). A total of 57 taxa were lost whereas 79 were gained between the two dates. Macrofauna was dominated by annelids, molluscs and crustaceans. In 1987, annelids were the most numerous taxonomic group (9344 ind., 55.7%) ahead of molluscs (3168 ind., 18.9%) and crustaceans (3080 ind., 18.4%). Molluscs were the most numerous group in 2019 (6600 ind., 42.3%) ahead of annelids (6080 ind., 38.9%) and crustaceans (2448 ind., 15.7%). Sipunculids, echinoderms, platyhelminths and nemerteans contributed less than 5% of the total species richness and abundance. H', D, J and mean Richness all slightly decreased over time while total richness increased.

Table IV: General description of the benthic macrofauna according to sampling campaigns. N: number of individual per m².



	1987	2019	Rebent (2005 to 2019)
Sampling design	38 stations Large hamon Grab (1 replicate) 2mm mesh size		15 surveys Smith Mc Intyre grab (9 replicates) 1mm mesh size
Total Richness	129	151	202
Mean Richness	19,4 ± 7,4	16,8 ± 5.6	63.5 ± 11.3
N Annelids	9344	6080	502,2 ± 168,8
N Molluscs	3168	6600	234,0 ± 329,0
N Crustaceans	3080	2488	175,4 ± 218,0
N Sipuncles	752	160	4,7 ± 5,7
N Echinoderms	240	72	1,6 ± 2,3
N Nemertines	152	176	7,9 ± 4,8
N Cnidarians	32	8	2,7 ± 2,3
N Platyhelminths	0	16	0,1 ± 0,3
N Tunicates	0	16	-
Total abundance	16768	15616	-
Mean abundance	441 ± 327	411 ± 270	928.5 ± 593.8
Shannon (H)	2.46 ± 0.42	2,22 ± 0.43	3,03 ± 0,26
Simpson (D)	0.86 ± 0.10	0.81 ± 0.10	0,89 ± 0,05
Pielou (J)	0.86 ± 0.11	0.81 ± 0.12	0,73 ± 0,07

At station R, a total of 202 taxa were reported over 15 years. Richness (63.5 ± 11.3) and abundance (928.5 ind.m^{-2} ± 593.8) increased over the study period. Annelids, molluscs and crustaceans dominated the community (Appendix E). *Chaetozone gibber* (133.07 ind.m^{-2} ± 94.1), *Varicorbula gibba* (95.9 ind.m^{-2} ± 187.3), *Aponuphis bilineata* (60.1 ind.m^{-2} ± 34.4), *Abra alba* (44.7 ind.m^{-2} ± 92.8), *Ampelisca sarsi* (44.0 ind.m^{-2} ± 128.1), *Notomastus latericeus* (25.7 ind.m^{-2} ± 26.1), and *Ampelisca brevicornis* (24.9 ind.m^{-2} ± 31.0) were dominant over the period studied. Some of them exhibited strong temporal variations, especially in the second part of the time series between 2012 and 2019 (Figure 30).

Fauna dynamics

Changes were observed in the contribution of the main taxonomic groups to the total local abundance between 1987 and 2019 (Figure 31, A and B): the contribution of molluscs increased in most stations, especially in the southern part of the study area. This change, also visible in the fauna of the station R occurred around 2015 (Figure 31, C). Before 2015, the abundance of each taxonomic group at station R was similar to the abundances measured in 1987 at the southern stations of the bay of Saint-Brieuc (stations 62 to 72).

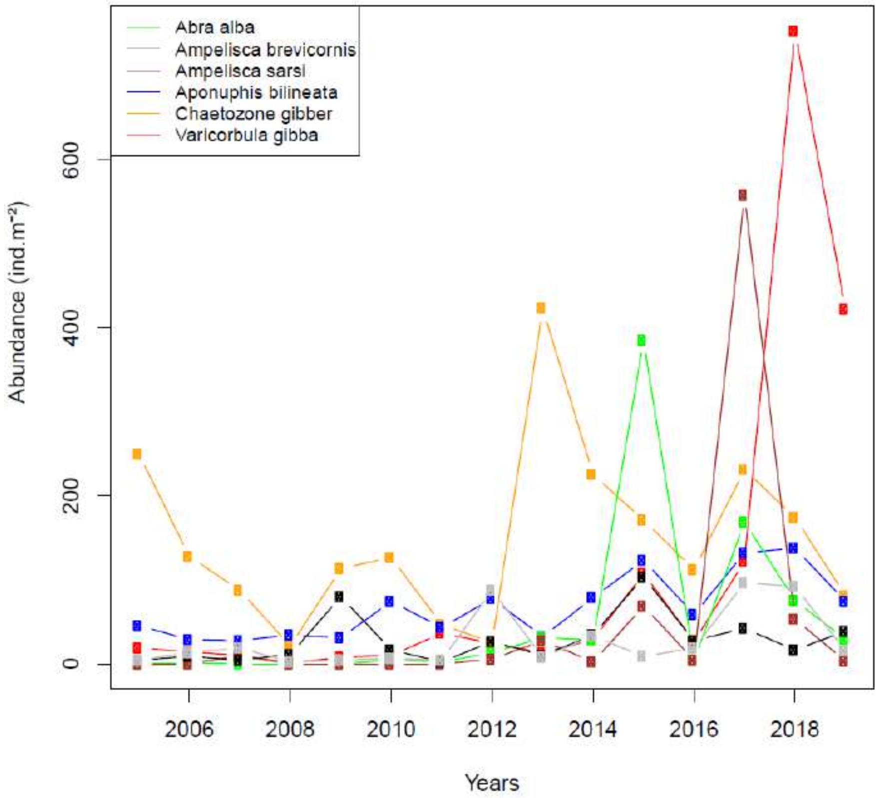


Figure 30: Abundance (ind.m^{-2}) of dominant species sampled at station R.

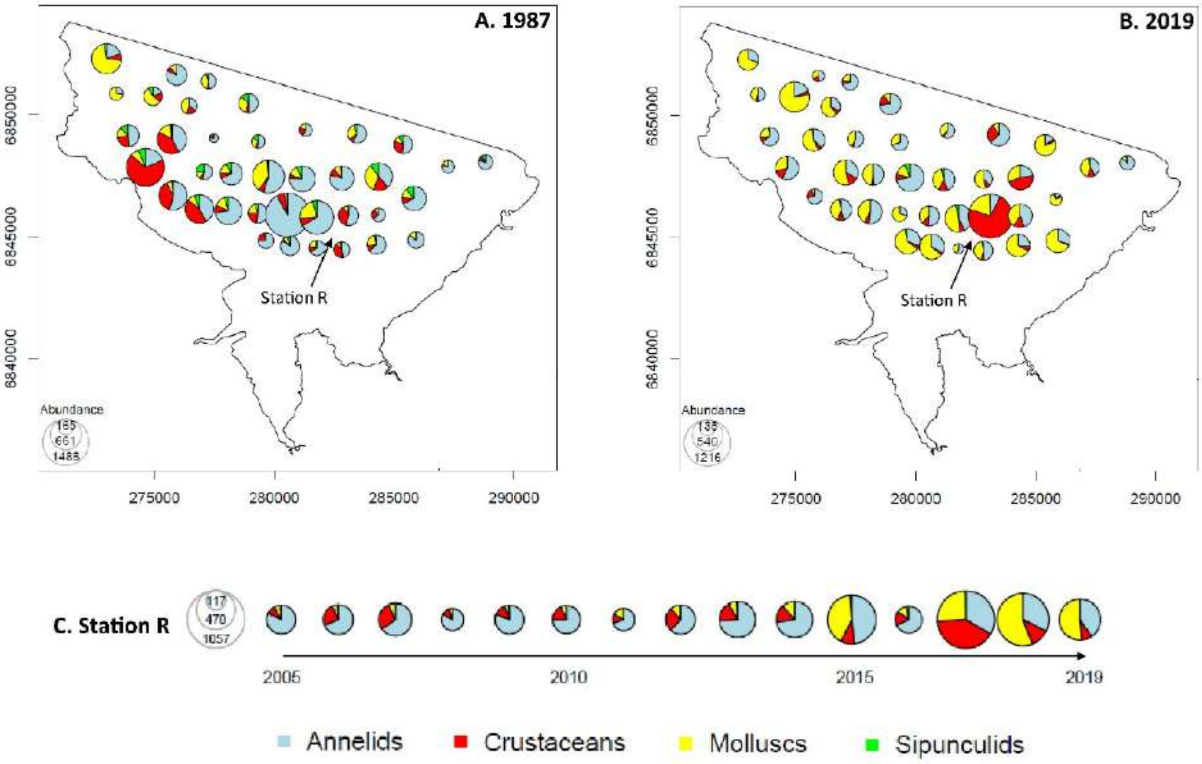


Figure 31: Distribution maps of main taxonomic groups. Colours represent the following groups: Annelids (blue), Crustaceans (red), Molluscs (yellow) and Sipunculids (green). Pie sections correspond to the relative abundance of each taxonomic group and size to total abundance. A and B represent 1987 and 2019 ResTroph surveys and C represents surveys conducted from 2005 to 2019 at station R.

Hierarchical classification

Spatial taxonomic clustering in 1987 and 2019. For both campaigns, HCAs separated the stations into four main clusters (*i.e.* benthic assemblages) (Figure 31). Indicator values (p-value< 0.05) and the two most abundant species were used to characterise each cluster.

In 1987, the following assemblages were distinguished:

(1) The southern **assemblage I-87**, characterized by *C. gibber* and *Sigalion mathildae*. These species occurred in shallower fine sands (Table I). *C. gibber* and *A. bilineata* were the most abundant species.

(2) The **assemblage II-87**, mainly located in western muddy-sands. It was characterized by *A. brevicornis* and *V. gibba* and dominated by *A. brevicornis* and *Euclymene oerstedii*.

(3) The **assemblage III-87**, mainly located in the central part of the study area, which occurred in muddy heterogeneous sediment. It was characterized by *Ampharete* spp. and dominated by *Ampharete* spp. and *Crepidula fornicata*.

(4) The **assemblage IV-87,** located in the north of the study area. It was characterized by *Nototropis vedlomensis* and *N. latericeus,* and dominated by *N. latericeus* and *Nucula hanleyi*.

In 2019, were identified:

(1) The **southern assemblage (I-19),** was the most widespread assemblage (19 stations). It occurred in fine to muddy sands located between the southern and the central part of the study area and was characterized by *V. gibba* and *Phyllodoce groenlandica* and dominated by *V. gibba* and *A. tenuicornis*.

(2) The **assemblage II-19**, occurring at nine stations mainly located in the northern-central part. It was characterized by *Nephtys hombergii* and dominated by *N. latericeus* and *V. gibba*.

(3) The **assemblage III-19** (six stations), identified in muddy heterogeneous sediments in the north and central parts. It was typified by *C. fornicata* and *P. maximus* and dominated by *C. fornicata* and *N. latericeus*.

(4) The **assemblage IV-19,** characterized and dominated by *Timoclea ovata* and *N. hanleyi* and limited to four north-western stations.

Species diversity was variable among assemblages. In 2019, the lowest H' values were observed in assemblages I-19 and IV-19. Temporal changes in the distribution of assemblages were concentrated in the southern part of the bay (Figure 32). The overall diversity (H', D, J) decreased in the shallower parts, as a consequence of the increase of *V. gibba*. Shallower bottoms were more homogeneous as showed by the assemblage I-19 distribution, which represent 50% of the stations in 2019.

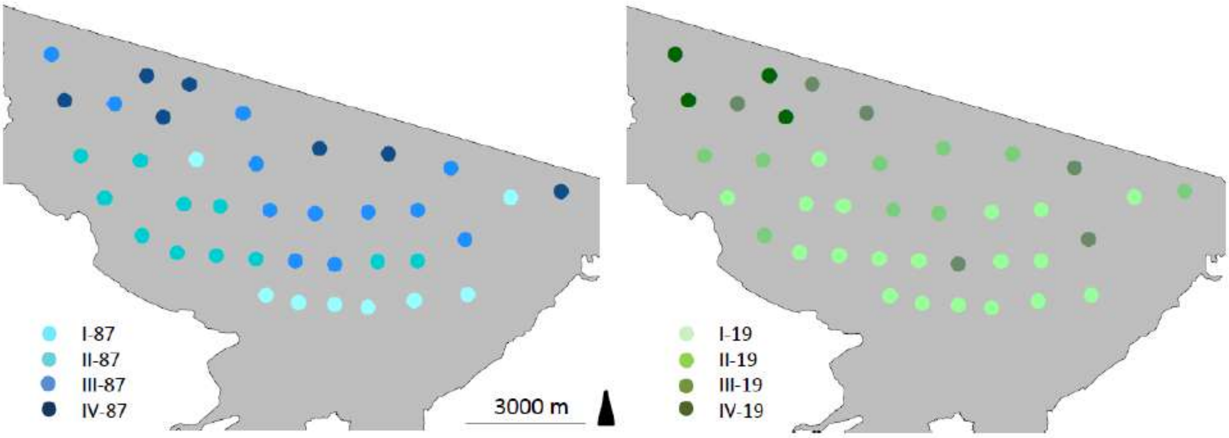


Figure 32: Spatial distribution of benthic assemblages identified with Hierarchical Cluster Analysis of the ResTroph data set (38 stations) in 1987 and 2019.

Temporal taxonomic clustering from 2005 to 2019. The HCA performed on the station R dataset separated three clusters:

(1) Cluster I, composed of seven years (2005, 2009, 2011-14, 2016), and characterized by *Caulleriella alata and Edwardsia claparedii.*

(2) Cluster II (4 years: 2006-08, 2010), characterized by *Cirratulidae* spp. and *Tritia varicosa*.

(3) Cluster III, composed of four of the most recent surveys (2015, 2017, 2018, 2019). It was typified by the molluscs *Calyptraea chinensis* and *Spisula elliptica*.

C. gibber, *A. bilineata* and *Ampelisca* spp. remained in the top five highest-ranking species in terms of abundance over the entire study period, but *V. gibba* and *A. alba* became dominant during last years of the series. Taxonomic diversity indices were quite stable between clusters except richness and abundance, which increased in the most recent observations.

Species changes in bivalve populations

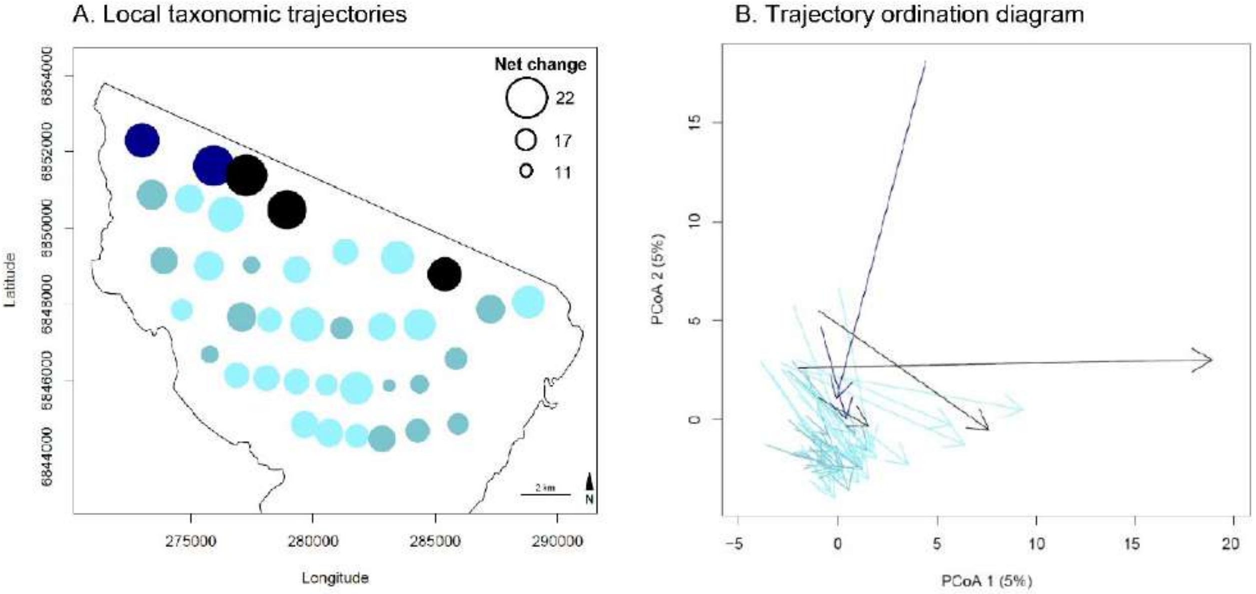
The abundance and distribution of the main bivalve species changed over time. Significant increases in abundance were detected for *Varicorbula gibba, Anomia ephippium, Bosemprella incarnata, Moerella donacina, Nucula hanleyi, Nucula nitidosa, Timoclea ovata* and *Pecten maximus*. Inversely, *Polititapes rhomboides* and, to a lesser extent, *Fabulina fabula* decreased significantly over time.

Taxonomic trajectories

Long-term comparison. All sampling stations were characterised by taxonomic changes over time (Figure 33, A & B). The mean net change (± sd) calculated on the 38 stations was variable spatially (15.5 ± 2.23), ranging from 11.4 (station 74) to 21.5 (station 104). The HCA performed on CTA analysis of trajectory similarities separated four clusters according to the shape of taxonomic trajectories (Figure 33, A, B & C).

Cluster A was composed of 20 stations describing the evolution from an assemblage dominated by *Ampharete* spp. and *A. brevicornis* in 1987 to an assemblage dominated by *V. gibba* and *C. fornicata* in 2019. Cluster B grouped 13 stations characterized by *A. bilineata* in 1987 and *V. gibba* in 2019. A shift between the dominant species *A. brevicornis* and *A. bilineata* (1987) to *V. gibba* and *A. tenuicornis* (2019) was observed. Mean net changes (± se) were slightly lower in cluster B (16.59 ± 1.09) than in cluster A (20.35 ± 0.66). The two other clusters characterized a limited number of specific trajectories exhibiting longer trajectory path in the northern part of the study area (stations 105 and 106 and 107, 104 and 94). Most stations encountered similar changes in the multivariate space, as indicated by the similar trajectory directions. Direction and trajectory length supported most of the cluster separation. The convergence of most trajectories, especially from clusters A and B, which grouped 87 % of trajectories, illustrate a homogenization over time with respect to the ecological state described in 1987.

Inter-annual dynamics. A first period from 2005 to 2014 was characterized by lower net changes than measured at the end of the time series, indicating an overall stability as underlined by consecutive departing and recovering patterns. This period was followed by a recent period of higher variability in composition and characterized by higher net change values (Figure 34, A). Even if *C. gibber* and *A. bilineata* remained among the five most dominant species, the trajectory underlined the shift in dominance by different *Ampelisca* spp. species, and the dominance of *V. gibba* and *A. alba* in recent surveys (Table II). The alternation of recovering and departing dynamics resulted in low directionality (0.359) and low net change ratio (10.11%).



C. Characterization of initial and final ecological states of trajectory clusters

Trajectory clusters		1987			2019	
A 20 st NC= 20,35 ±0.66	**Ind. sp**	*ns*			*ns*	
	Most num	*Ampharete spp.*	84.40 ±60.67	➡	*Varicorbula gibba*	85.2 ±18.36
		Ampelisca brevicornis	66.00 ±35.26		*Crepidula fornicata*	43.6 ±23.86
B 13 st NC= 16,59 ±1.09	**Ind. sp**	*Aponuphis bilineata*	0.622 / 0.0117		*Varicorbula gibba*	0.546 / 0.0214
	Most num	*Ampelisca brevicornis*	38.77 ±17.88	➡	*Varicorbula gibba*	127.38 ±31.55
		Aponuphis bilineata	34.46 ±8.89		*Ampelisca tenuicornis*	94.15 ±92.83
C 3 st NC= 27,82 ±1.67	**Ind. sp**	*Nemertea spp*	0.822 / 0.0037		*Pecten maximus*	0.724 / 0.0140
		Anapagurus hyndmanni	0.528 / 0.0438		*Syllis garciai*	0.667 / 0.0052
	Most num	*Ampharete spp*	21.33 ±17.49	➡	*Crepidula fornicata*	88.00 ±68.04
		Anapagurus hyndmanni	21.33 ±17.49		*Notomastus latericus*	21.33 ±9.61
D 2 st NC= 27.39 ±2.26	**Ind. sp**	*Protodorvillea kefersteini*	1.000 / 0.0019		*Timoclea ovata*	0.963 / 0.0041
		Nucula hanleyi	0.517 / 0.0192		*Glycymeris glycymeris*	0.500 / 0.0486
	Most num	*Crepidula fornicata*	168.00 ±168.00	➡	*Timoclea ovata*	64.00 ±56.00
		Notomastus latericus	44.00 ±20.00		*Notomastus latericeus*	52.00 ±20.00

Figure 33: Taxonomic trajectories. A: Map of local trajectories. Circle size corresponds to net change between 1987 and 2019 and colours to clusters of trajectories determined by Hierarchical Cluster Analysis on trajectory similarity analysis. All the dimensions of the multivariate space were considered in net change calculation and analysis of trajectory similarities. B: Trajectory ordination diagrams. Only two dimensions are shown. C: Characteristics of initial and final taxonomic ecological states of trajectory clusters. Taxonomic trajectory are coloured according to trajectory clusters (blue gradient), and described with distance-based metrics mean ± se (NC: net change, TP: Trajectory path), the two first indicative (Ind.sp.) and numerous species (1st. Num.)

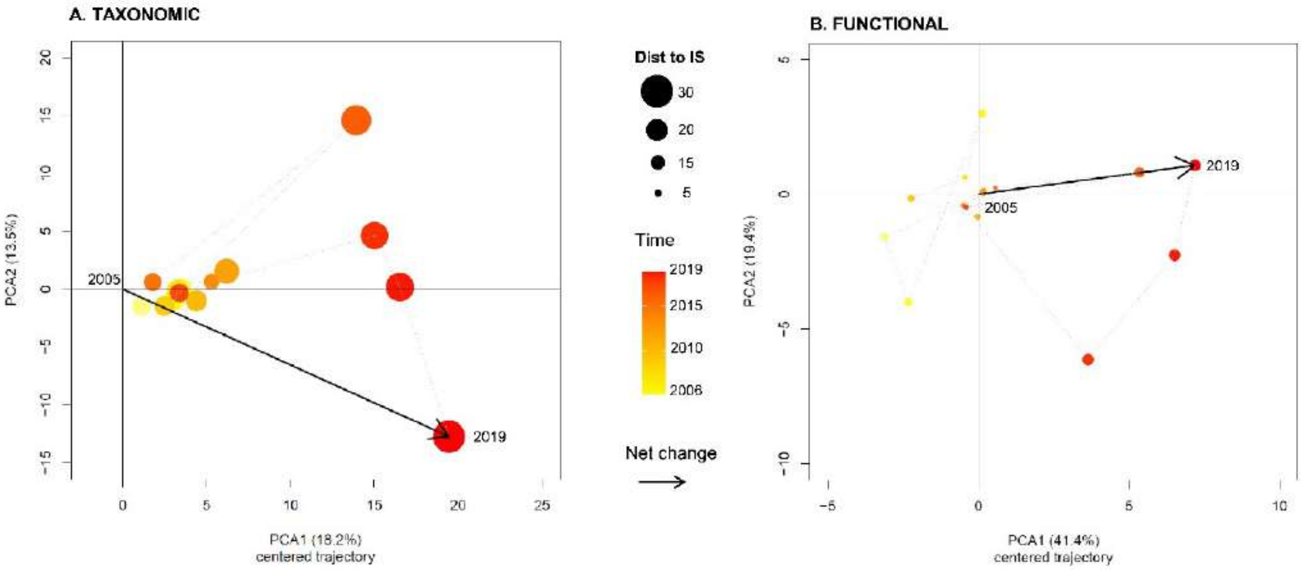
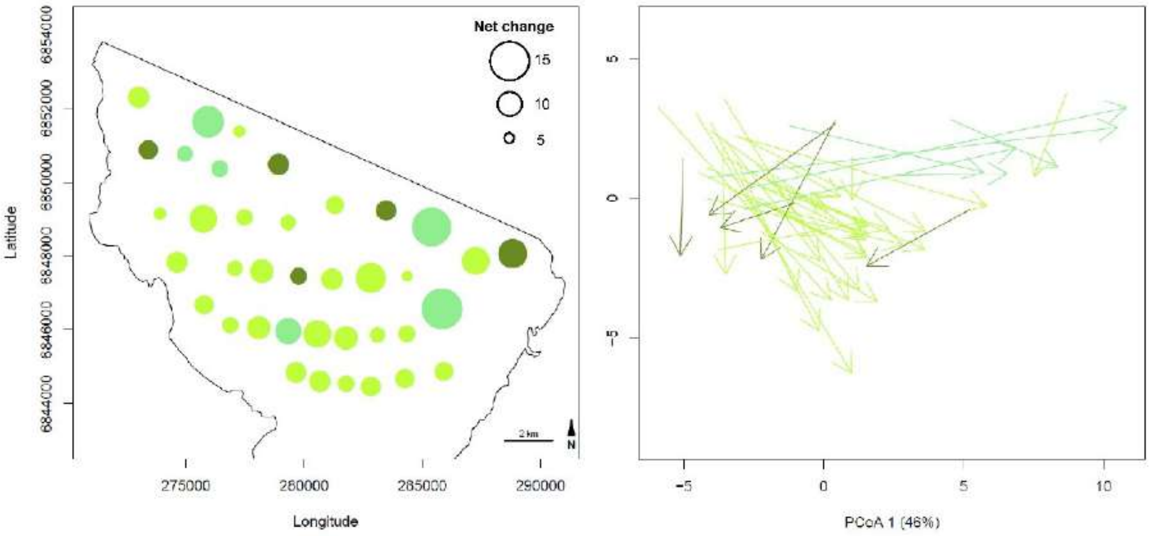


Figure 34: Trajectory of the station R between 2005 and 2019. The origin of the ordination diagram represents the initial state characterized in 2005 after trajectory centring. Only two dimensions are shown. Points correspond to intermediate ecological states (size= length of each state to initial state (IS) considering all PCA components) and are coloured according to time (yellow (2005) to red (2019)). Lines represent segments between transitional states. The black arrows represent the net change between 2005 and 2019.

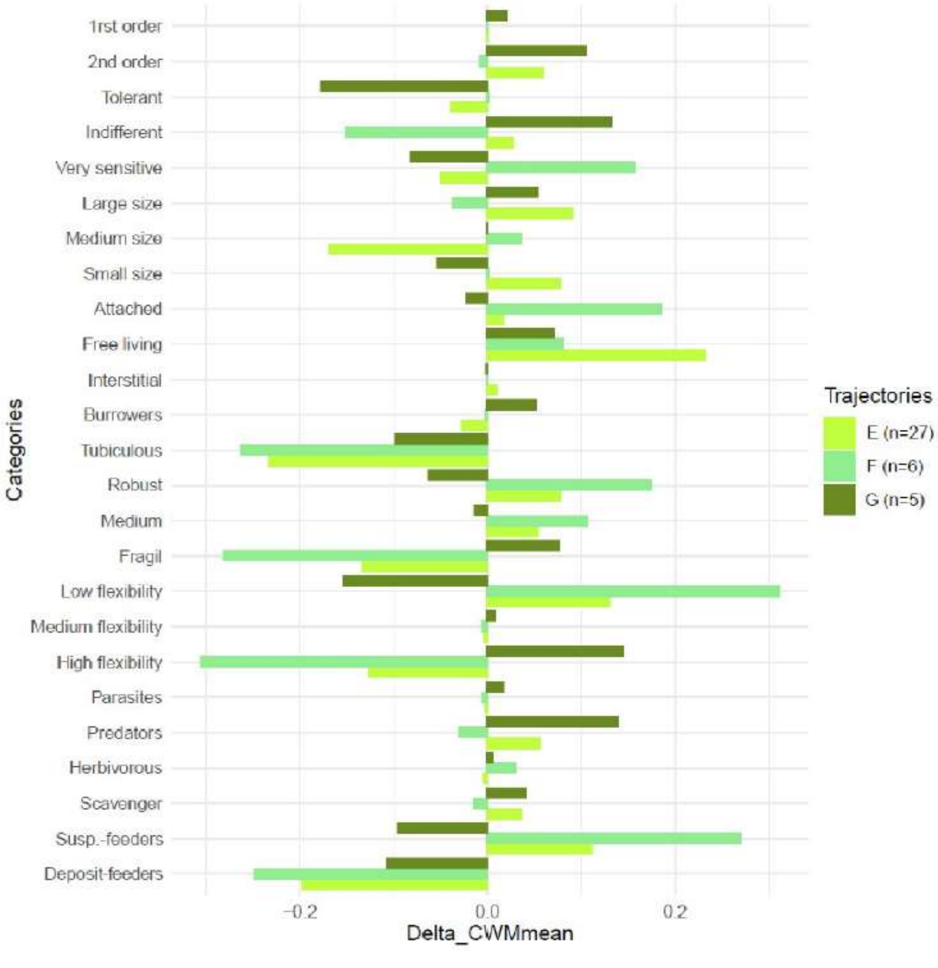
Functional trajectories

Long-term comparison. Net change was variable spatially (7.94 ± 2.53), ranging from 3.97 (station 87) to 15.24 (station 88). The HCA performed on CTA analysis of trajectory similarities separated three functional trajectory clusters (Figure 35, A, B & C). Trajectory length and direction were mainly responsible for the separation of clusters. Cluster E grouped 27 stations (7.34 ± 0.36) which highest net change values were mainly located in the southern part of the study area, and were characterized by a decrease in the relative contribution of the following categories: 1) medium size, flexible, fragile; and 2) tube-dwellers, burrowers and tolerant species. Simultaneously, the contribution of suspension-feeders, predators and scavengers increased, as well as rigid, robust, and large and small species. Free-living species became dominant and the contribution of second-order opportunistic species increased. Cluster F grouped six trajectories characterized by higher net changes (10.59 ± 1.64). The main functional changes consisted in a decrease of deposit-feeders, tube-dwellers, and flexible and fragile species. This group of trajectories was specifically characterized by an important increase of CWM values of very sensitive species, and attached species mainly represented by *A. ephippium*. Cluster G characterized five trajectories (7.96 ± 0.79). In addition to a similar pattern concerning deposit-feeders and tube-dwellers species, these trajectories were specifically characterized by an increase in the contribution of predator, flexible, fragile, and burrowing species and a decrease of rigid, suspension-feeders and tolerant species.



A. Local functional trajectories

B. Trajectory ordination diagram



C. Differences in mean CWM values of categories of traits within functional trajectory cluster

Figure 35: Functional trajectories. A: Map of local trajectories. Circle size corresponds to net change between 1987 and 2019 and colours to clusters of trajectories determined by HCA on CTA trajectory similarity analysis. All the dimensions of the multivariate space were considered in net change calculation and analysis of trajectory similarities. B: Trajectory ordination diagrams. Only two dimensions are shown. Functional trajectories are coloured according to trajectory clusters (green gradient). Characteristics of initial and final functional ecological states of trajectory clusters are detailed in table IV. C: Barplots of Community-weighted trait values (CWM) values shift for each categories of traits (mean 2019 – mean 1987). Bars are coloured according to functional trajectory clusters.

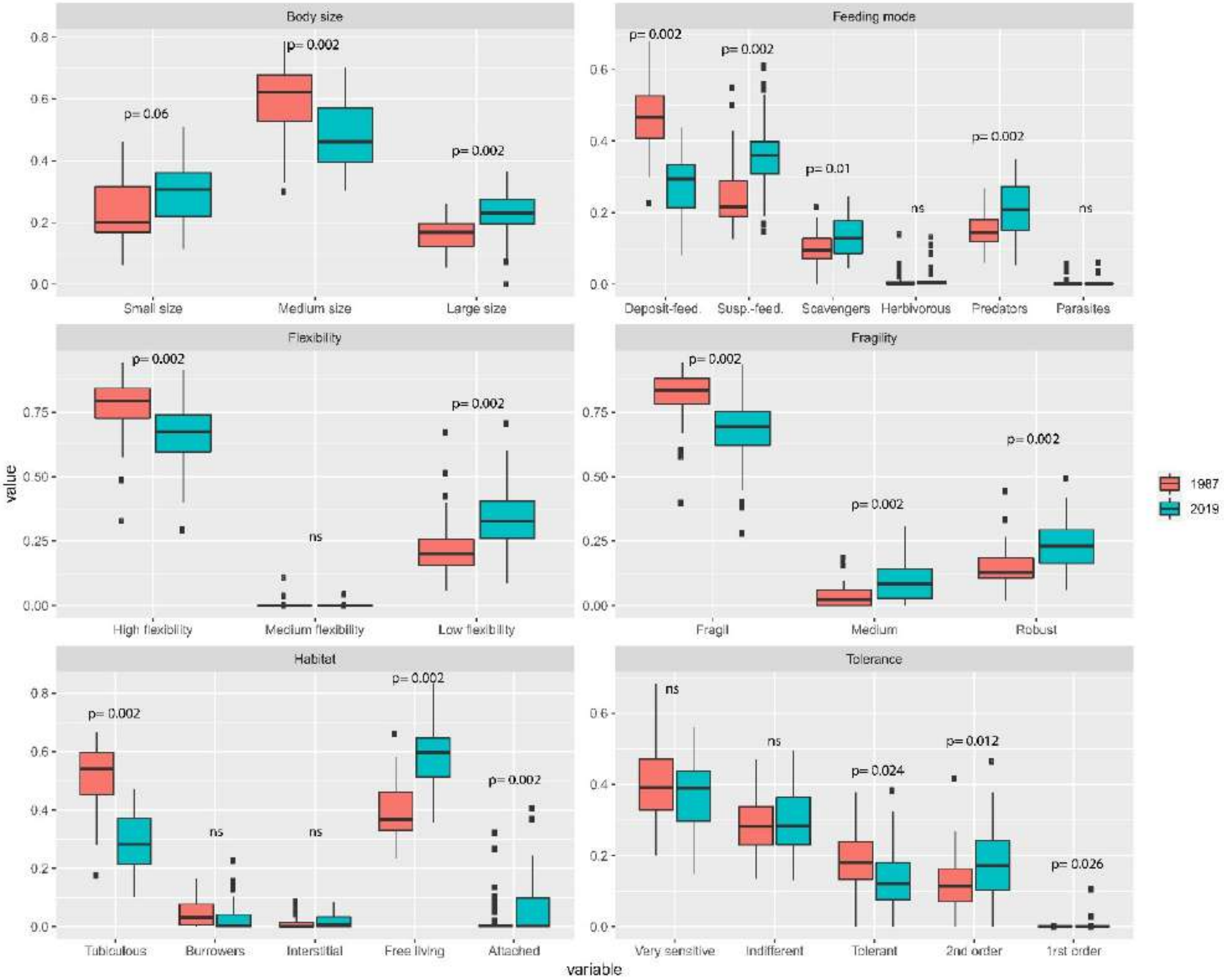


Figure 36: Boxplots of Community-weighted trait values (CWM) values for each category of traits and by year (1987: red; 2019: green). Boxplot indicates the median (line in the box), the first and third quartiles (hinges) and extreme data points (black points). Significance of student permutation paired-tests are indicated for each trait level.

At the scale of the whole study area, a similar global pattern was observed (Figure 36). Compared to 1987, the community was dominated by suspension-feeders and free-living species in 2019. Even if significant functional shifts in morphologic traits were observed over time, the fauna remained dominated by medium size, flexible and fragile species. According to the tolerance to nutrient enrichment trait, fauna remained dominated by very sensitive and indifferent species.

Inter-annual dynamics. Functional net change increased over time (Figure 34, B). Different categories of traits influenced the functional stability: axis I (41.4%) opposed filter feeders, living free, rigid and robust species to deposit feeders, tube-dwellers and highly flexible ones (Appendix H). The alternance of recovering and departing dynamics resulted in low directionality (0.387) and net change ratio (10.04%).

3.2.2.3| Discussion

Changes probably occurred recently. Among the four taxonomic clusters identified in 2019, two of them, representing 74% of stations, pointed towards a potential degradation of habitats indicated by 1) the numerical increase of the opportunistic species *V. gibba*, and 2) the lower species diversity in one of the two assemblages. This was further confirmed by the analysis of trajectory similarity, which revealed that 87% of the stations (clusters A and B) were notably characterized by increases in the density of *V. gibba* from 1987 to 2019. At the scale of the study area, however, decreases of β species diversity remained very moderate.

Inter-annual dynamics at station R suggests that these changes are very recent (Figures 30, 31 and 34). The lower variability observed at station R from 2005 to 2014 may depict natural dynamics, while recent changes since 2015 seem driven by a strong and cumulative disturbance regime. The recent shift in the taxonomic multivariate structure was driven by variations in the abundance of a few dominant species, among which *V. gibba*, *A. alba, C. chinensis* and *S. elliptica*. Interestingly, although benthic communities were highly variable over the last five years, sediment properties and organic matter content did not exhibit such variability, suggesting that the recent pattern in benthic community structure may not be strictly related to habitat characteristics.

Variocorbula gibba: an indicator of degradation processes but a response of ecosystems during the first recovering stages after a perturbation. Among the different species sampled in this study, *V. gibba* exhibited the strongest increase in abundance, especially in the southern part of the study area. Cabioch (1968) already reported an alternation between *V. gibba* and *A. alba* abundance peaks in the Western English channel, similar to what was observed at station R. Unstable conditions having been reported to promote *V. gibba* populations (Pranovi et al., 1998; Rosenberg, 1977), this species is considered as an indicator of environmental instability whose strong increase across Europe has been largely associated to disturbances (Hrs-Brenko, 2006), particularly pollution and sedimentary instability (FAO and UNEP, 1985; Pearson and Rosenberg, 1978; Pranovi et al., 2007; Salen-Picard, 1981). This species, which grows rapidly (Jensen, 1990), shows strong survival capacity to different abiotic (resistant to pollution, turbidity, hypoxia, and sedimentation) and biotic stressors. High larval settlement of *V. gibba* is known to frequently appear after catastrophic events (Hrs-Brenko, 2006).

The massive recruitment of *V. gibba* also characterizes the pioneer stages of benthic community dynamics following a perturbation (Pranovi et al., 1998). Bonvicini-Pagliai & Serpagli (1988) called this species “a time recorder of environmental stress”. As a dominant suspension-feeder, with rapid juvenile and adult growth, *V. gibba* plays an important role in the food web by transfering pelagic production to the benthic compartment (Hrs-Brenko, 2006). Once the disturbance regime decreases, biotic interactions will progressively regulate *V. gibba* populations (Olafsson et al., 1994). Knowledge on the level of disturbance required for the persistence of an abundant *V. gibba* population and its ability to increase in abundance in the absence of a primary disturbance factor is crucial to disentangle effects of natural and anthropogenic factors (Australian government, 2008).

In Australia, where this species is invasive, dramatic rises in abundance can have negative effects on the growth rate of *Pecten fumatus* juveniles, a commercial species, as demonstrated experimentally by Talman & Keough (2001). The bay of Saint-Brieuc, which suffers from eutrophication (but without hypoxic episodes) and supports intensive scallop dredging activities, appears to be a favourable area for the proliferation of this species.

Functional shifts suggest the degradation of benthic habitats. Ecological processes shaping energy flows in ecosystems are induced by a complex feedback system reflecting species adaption to their environment, while the environment is, in turn, constantly modified by biological activities (Díaz and Cabido, 2001; Levins and Lewontin, 1985; Pacheco et al., 2011).

Trait-based approaches have been widely used to characterize functional shifts, in response to different natural or human disturbance context (Bolam et al., 2017; Thrush and Dayton, 2002; van Denderen et al., 2015). The use of biological traits is expected to provide a good view of functional shifts over space and time (Pacheco et al., 2011). In our study, traits were chosen to assess the potential impacts of 1) fishing activities (size, flexibility, fragility, habitats, feeding habits) and 2) organic matter enrichment (tolerance, feeding habits).

Fishing activities. Trawling and dredging fishing activities are known to be responsible for many impacts on the seabed, such as the modification of benthic communities and sedimentary habitats (Eigaard et al., 2017; Ellis et al., 2000; Newell et al., 1998; Thrush and Dayton, 2002). Watling & Norse (1998) compared the consequences of disturbance induced on the seabed by mobile fishing gear to forest clear cutting. Scallop dredging in the Irish Sea has been shown to significantly modify benthic communities and *P. maximus* populations ((Morys et al., 2021). Dredging activities modify the structure of mounds, tubes, and burrows created by organisms living on the sediment surface, and limit small scale habitat structure heterogeneity (Thrush and Dayton, 2002). As underlined by Gray et al. (2006), the homogenization of heterogeneous habitats and the reduction of three-dimensional structures above and below the sediment-water interface constitute one of the most damaging effects of fishing activities.

In the study area, regulation of scallop fishing activities has changed in 2006-2007, resulting in an authorization to fishermen to dredge in the very coastal area (Figure 37), at the beginning of the scallop fishing season. Despite concentrating the highest scallop dredging pressure in Brittany (Figure 37), no accurate spatio-temporal assessment of fishing pressure is available for the bay of Saint-Brieuc. The existence of a potential impact of fishing activities on macrobenthos may seem at odds with the increase of suspension-feeder abundances over time in the study area. From our results, current functional shifts within assemblages led to a relative dominance of robust, rigid and free living species which suggests selective mortality processes of fragile, flexible, and sedentary species due to fishing pressure and human disturbances (Constantino et al., 2009; Duplisea et al., 2002; Jennings et al., 2001; Kaiser et al., 2006; Pedersen et al., 2009). However, results of Van Denderen et al. (2015) who studied benthic functional response to fishing activities according to natural disturbance regimes, invite to moderate such conclusions. They showed that fishing impacts are smaller or absent in areas exposed to high natural disturbance, leading to the hypothesis that, depending on local hydrodynamics, natural and fishing disturbances may affect benthic communities in similar ways. Same observations were made by Jac et al. (2020) who consider that the apparently higher trawling resistance of the benthic communities of coarse circalittoral sands in the English Channel, compared to the North Sea, could also be due to differences in hydrodynamics between the two basins. In the bay of Saint-Brieuc, the local wave regime has been broadly stable over the last 30 years, ruling out a strong influence of hydrodynamics on the observed patterns (H. Michaud and L. Seyfried com. pers.)

Overall sedimentary changes may also have contributed to the decrease of deposit-feeders in the study area. Beyond the potential natural variability, as dredging activities are known to homogenise the sediment. Mengual et al. (2019, 2016) showed an overall erosion of muddy areas in the bay of Biscay in relation with fishing activities, and a coarsening trend of surface sediments (5 cm). Morys et al. (2021) showed a significant decrease of surface organic matter content in a recent experimentation about the impact of bottom trawling on benthic biogeochemistry. Such organic matter content decrease was observed at station R from 2014 (Article IV). In our study, sedimentary parameters partly shaped the taxonomic multivariate structure of the benthic community, but the amount of explained variance decreased between 1987 and 2019 indicating that sedimentary variables explain only a limited part of the observed changes (Article IV).

Organic enrichment. The positive functional shift observed for second-order opportunistic species, and particularly *V. gibba,* seems to indicate an impact of organic matter enrichment in accordance with Hrs-Brenko (2006) who suggested that eutrophication increases the fecundity of *V. gibba*. During our sampling survey, small individuals of *V. gibba* were observed attached with their byssus to drifting *Ulva* sp., suggesting;

(1) a potential influence of algal mats offering new attachment substrates for early recruitment stages;

(2) that individuals could drift when attached to algal mats, and colonize new areas.

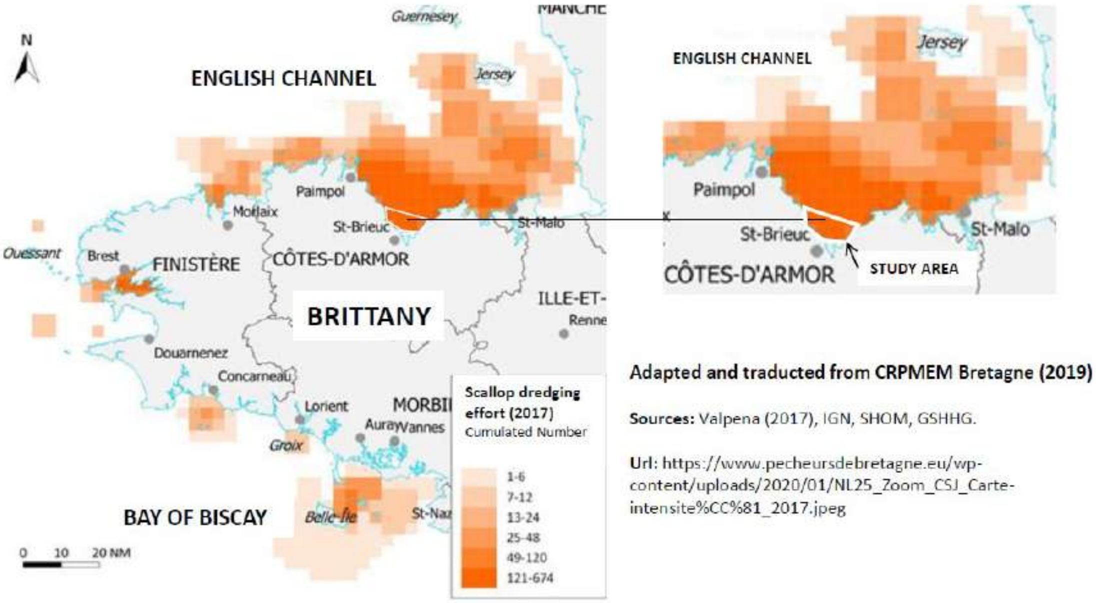
Eutrophication can also extend the spawning season of *Abra alba* (Dauvin and Gentil, 1989) which could be partly responsible for the high abundance of *A. alba* observed at station R in 2015 and 2017. Local disturbance, predation/competition, and climatic factors are also known to control *A. alba* populations (Dauvin et al., 1993). The persistence of the observed changes needs to be confirmed as *A. alba* and *V. gibba* are known to present high population variations in such soft-bottom communities (Cabioch, 1968). However, such high inter-annual variability was not observed until the mid 2010s.

Despite the fact the positive shift of second-order species was mainly driven by *V. gibba*, the community was still dominated by species very sensitive to nutrient enrichment in 2019, some molluscs having increased in abundance and occurrence (*B. incarnata*, *Laevicardium crassum*, *T. ovata*, *M. donacina*, *N. hanleyi, P. maximus*). The diversity of temporal dynamics suggests a complex gradient of sensitivity to organic matter enrichment (*i.e. Ulva* biomass, water columns enrichment) and the implication of additional driving factors. Indeed:

(1) discards from scallop dredging could promote opportunistic species and scavengers leading to increases in their abundances (Depestele et al., 2019);

(2) by capturing nutrients, green tides are particularly suspected to buffer the influence of nutrient enrichment on macrofauna as discussed by Ponsero & Le Mao (2011) and Sturbois et al. (Article III) concerning the neighbouring intertidal area. Such "buffered effect" may lead to a low to moderate level of eutrophication (i.e. enrichment of the water column). It could then contribute to explain the increase of some opportunistic species, despite the low sediment organic contents values suggesting that *Ulva* biomass were not integrated in sediments in these dynamic intertidal and subtidal areas. Interestingly, the maintenance or the increase of some sensitives species suggest that they probably beneficiate from moderately enriched conditions.

1. Distribution of scallop dredging effort in Brittany and in the Bay of Saint-Brieuc (2017)



Adapted and traducted from CRPMEM Bretagne (2019)

Sources: Valpena (2017), IGN, SHOM, GSHHG.

Url: https://www.pecheursdebretagne.eu/wp-content/uploads/2020/01/NL25_Zoom_CSJ_Carte-intensite%CC%81_2017.jpeg

2. Evolution of early dredging rules in the study area at the beginning of the fishing season

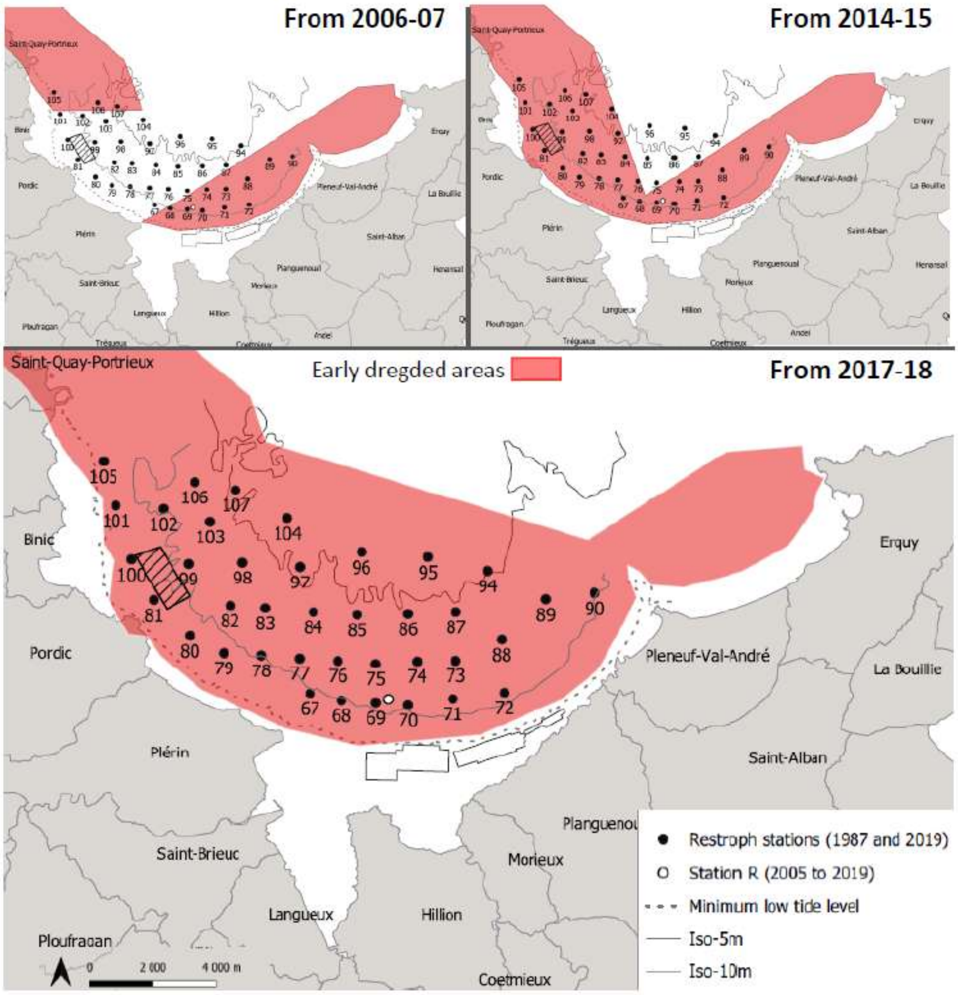


Figure 37: Fishing pressure and evolution of fishing rules in the study area.

Regional scale insights for mollusc populations. Recent fishing ground assessments have shown an important increase in the populations of *P. maximus* in the English channel, and particularly in the Normand-Breton gulf where landings have increased from 1200 tons in 1989 to an average of 7000 tons since the early 2000s (Foucher, 2017; Foucher et al., 2015; Le Mao et al., 2019). Over the last ten years, *P. maximus* densities across all age classes have increased in the lowest levels of the intertidal area (pers. obs.) suggesting a similar scenario in shallow bottoms between the low water mark and a depth of 5 m. The management of *P. maximus* populations by fishermen in collaboration with scientists, together with climate change, has favoured this stock increase (Shephard et al., 2010). Fishing activities in the bay, associated to recruitment fluctuations, may be involved in the drastic decline of other bivalve populations such as *Polititapes rhomboides,* which was commercially harvested in the Bay until recently (Huet and Pitel, 2006).
Among other bivalve species, *Moerella donacina* and to a lesser extent *Timoclea ovata* increased in abundance and occurrence. These trends are congruent with those reported by Gaudin et al. (2018) who tracked changes in response to climate change in the English Channel. They notably showed, between the 1960s and 2014, important and moderate increases in occurrence and eastward movements of populations (*i.e.* tracking colder conditions) for *M. donacina* and *T. ovata,* respectively. Climate change (temperature increase) is also suspected to be responsible for changes in the abundance of *Albra alba* at station R [Dauvin *et al.*, 1993 ; Thiébaut & Houbin (comm. pers.)], and of *Limecola balthica* in the adjacent intertidal mudflats of the bay of Saint-Brieuc (Article III).

In the past decades, the slipper limpet *Crepidula fornicata* has progressively become an important component of soft-bottom benthic ecosystems in the English channel (Blanchard, 2005; Blanchard et al., 2001). Total stock reached an estimated 450 000 tons in the bays of Saint-Brieuc and Mont Saint-Michel in the early 2000s (Blanchard and Hamon, 2006). Current trends are not documented, except in the bay of Brest, where Blanchet-Aurigny et al. (2012) reported that historical *Crepidula fornicata* beds collapsed and are currently mainly made up of dead shells. In our study, a decrease in the mean density of *C. fornicata* was observed (40.21 ind.m^{-2} ± 182.42 in 1987 vs 21.11 ind.m^{-2} ± 48.46 in 2019), but this overall trend is driven by change observed at a single station (105), while densities remained stable for the rest of the bay.

3.2.3 | Conclusions

Taxonomic and functional trajectories of intertidal and subtidal benthic assemblages were analysed in independent multivariate spaces, which limits the quantitative comparisons of trajectory metrics. However, the overall qualitative comparisons of spatio-temporal patterns show contrasted evolutions of these two neighbouring habitats from their respective initial states (stability for intertidal communities and increased variability for subtidal ones). Whatever the perennial contribution of dominant prevalent species at the site scale in the intertidal area, some species were highly variable over time and space, influencing the structuration of assemblages. Taxonomic changes were not systematically associated with significant changes in the functional properties at local and community scale. The consideration of local changes and variations at the species level explained the differences in composition observed at the scale of assemblages. Observed changes mainly reflected random population dynamics of structuring prevalent species in habitat under strong natural pressures, rather than specific changes of the community. Few species seem to reveal the long-term effect of green tides in some assemblages.

Overwintering birds also regulate benthic populations locally (Ponsero et al., 2016; Sturbois et al., 2015). The overall functional persistence was explained by the different functional trajectories exhibited by each station taken separately. This game of "functional musical chairs" reflect the mosaic of micro-habitats potentially composed of different recovering stages in a complex socio-ecosystem rather than strong changes in the community functional properties.

At the opposite, taxonomic trajectories in the subtidal area indicated changes in the structure and distribution of benthic assemblages, the homogenization of the assemblages and significant functional shifts, which concerned most of the stations in 2019. The scale at which the perturbation has been detected within the study area highlights the importance of the physical disturbance affecting the seabed. As wave regime was stable over the survey period, fishing activities and nutrient enrichment are probably (with climate change) strong drivers of the observed changes, as suggested by the higher mortality rate of fragile, flexible, tube-dwellers and burrowing species, and the increase in the abundance of opportunistic species in the assemblages. The magnitude of fishing influence is difficult to assess because of the lack of accurate data concerning dredging pressure.

These two studies provide an up-to-date assessment to policy makers and managers about the evolution of the composition, structure and functioning of benthic assemblages. This knowledge must integrate future governance rounds, in a multi-scale approach involving policy makers and stakeholders, and must make marine habitats, a central part of the future conservation processes.

3.3 | Spatio-temporal patterns in the intertidal foodweb (Article V)

3.3.1 | Introduction

The important productivity of coastal areas supports many ecological processes and ecosystems services (Costanza et al., 1997). The productivity of bays and estuaries is notably favoured by a wide diversity of primary producers, including phytoplankton seaweeds, seagrass, mangroves, salt marsh plants, macroalgae, and benthic diatoms (Bouillon et al., 2011).

All these primary producers contribute to an important pool of detrital organic matter, which plays a major role in the biogeochemistry and ecology of these ecosystems. Considering this diversity, understanding the fate of primary production within coastal ecosystems, and especially within food webs, is challenging (Mann, 1988). Furthermore, the contribution of these different producers to local food webs has been reported to vary within and among coastal systems (Chanton and Lewis, 2002; Deegan and Garritt, 1997; Domingos and Lana, 2017), leading to a lack of a commonly accepted paradigm for food web functioning across variable spatial and temporal scales.

Because coastal food webs potentially depend on primary food sources, which can be either sessile or mobile, assessing vertical (*i.e.* benthic-pelagic coupling) and horizontal (*i.e.* organic matter fluxes across habitats/ecosystems), trophic connectivity between adjacent habitat is important (Kang et al., 2015; Schaal et al., 2008). Trophic connectivity varies among systems, from near total isolation to strong mixing, and water motion facilitates the movement of carbon as dissolved or particulate matter in aquatic ecosystems (Guimond and Tamborski, 2021; Polis et al., 1997).

Hydrodynamics influences coastal productivity through a variety of mechanisms (Largier, 1993). In tidal environments, the periodic movement of the tide is responsible for organic matter redistribution, enhancing trophic connectivity among different habitats and assemblages (Polis et al., 1997). Redistribution range depends on tidal amplitude across meso, macro and megatidal systems (Domingos and Lana, 2017; Ziegler et al., 2019). Resulting hydrodynamics can lead to the accumulation and/or dispersal of water column constituents, including sediment, phytoplankton, and particulate detritus (Young et al., 2021), and potentially influence productivity pathways and food web structure. Strong water motion increases material processing (*e.g.* microphytobenthos resuspension) between benthic and pelagic compartments (Ubertini et al., 2012) which can be amplified by biological factors, such as bioturbation (Rakotomalala et al., 2015).

Bays and estuaries are known to be influenced by seasonal and inter-annual variability in marine and freshwater inputs. This variability affects the abundance and distribution of resources and consumers and may drive food web dynamics (Bouillon et al., 2011; Possamai et al., 2020). The consideration of the variability of food sources in terms of composition and availability is consequently crucial to take into account the spatio-temporal trophic dynamics.

In shallow bays under the influence of mega-tidal conditions, bathymetry influences submersion/emersion time of intertidal habitats, affecting the time available for feeding within each tidal cycle. Tidal conditions coupled with sediment characteristics have also a pronounced effect on benthic macrofauna species distribution (Blanchet et al., 2014; França et al., 2009). Such broad spatial-pattern in the distribution of intertidal benthic species can be strongly consistent over time, leading to the persistence of contrasted benthic assemblages along inshore/offshore and sheltered/exposed gradients in intertidal soft bottom-habitats (Article III).

Organic matter inputs (*e.g.* detrital plants or algae) from vegetated systems may diversify food web structures and energy pathways (Hyndes and Lavery, 2005; Nordström et al., 2015; Schaal et al., 2008). Such additional food resources may originate from close productive habitat such as salt marshes (Nordström et al., 2014), but also result from seasonal eutrophication with the proliferation of green algae, which may have important consequences on the structure of benthic food webs (Quillien et al. 2016) and fish assemblages (Jones et al., 2020).

For decades, stable isotope analysis has been widely used in trophic ecology studies to understand feeding behaviour, trophic relationship and organic matter flow through marine food webs (Fry, 2008; Peterson, B.J., 1999). More recently, the development of numerous isotopic metrics allowed to better integrate stable isotopes measurements at the community scale, providing relevant information about ecosystems structure and functioning (Cucherousset and Villéger, 2015; Layman et al., 2012, 2007; Rigolet et al., 2015).

The aim of this study was to investigate the structure and the composition of the food web in an intertidal sandflat influenced by mega-tidal conditions and characterised by a variety of primary producers. δ^{13}C and δ^{15}N values from sources to benthic consumers at the scale of the entire sandflat and for benthic assemblages which constitute the mosaic of habitat within the bay were specifically explored. Traditional analyses were coupled with distance- and direction-based metrics of the new stable isotope trajectory analysis framework (Article II). This new method provides an assessment of stable isotope data at different levels of biological organization, from individuals to ecosystems to derive structural and functional trajectories in a new approach referred to as Stable Isotope Trajectory Analysis (SITA). We hypothesized that:

(1) due to the aforementioned characteristics of the bay, spatial gradient and temporal variability drive the sources supporting the food web;

(2) the variability induces spatial and temporal difference in the food web structure among habitats;

(3) temporal trophic trajectories may vary between trophic groups as these differences may originate from the availability in food sources;

(4) looking for spatio-temporal patterns though stable isotope trajectories may offer interesting perspectives, notably in complex ecosystems characterised by similar basal sources with dynamic stable isotope compositions.

3.3.2 | Material et methods

Sample collection and laboratory processes

Sources and consumers were collected in early March and September 2019. Sampling of benthic macrofauna was carried out in four soft-bottom habitats in the bay of Saint-Brieuc: salt marsh muddy creeks (2 stations), and the succession of muddy (5 stations), fine (9 stations) and medium sands (6 stations) from the high to the low shore (Figure 38). Samples were then prepared (powders packed into 5 x 8 mm ultra-clean tin capsules) for δ^{13}C vs δ^{15}N stable isotope analyses. (See article V, for more details).

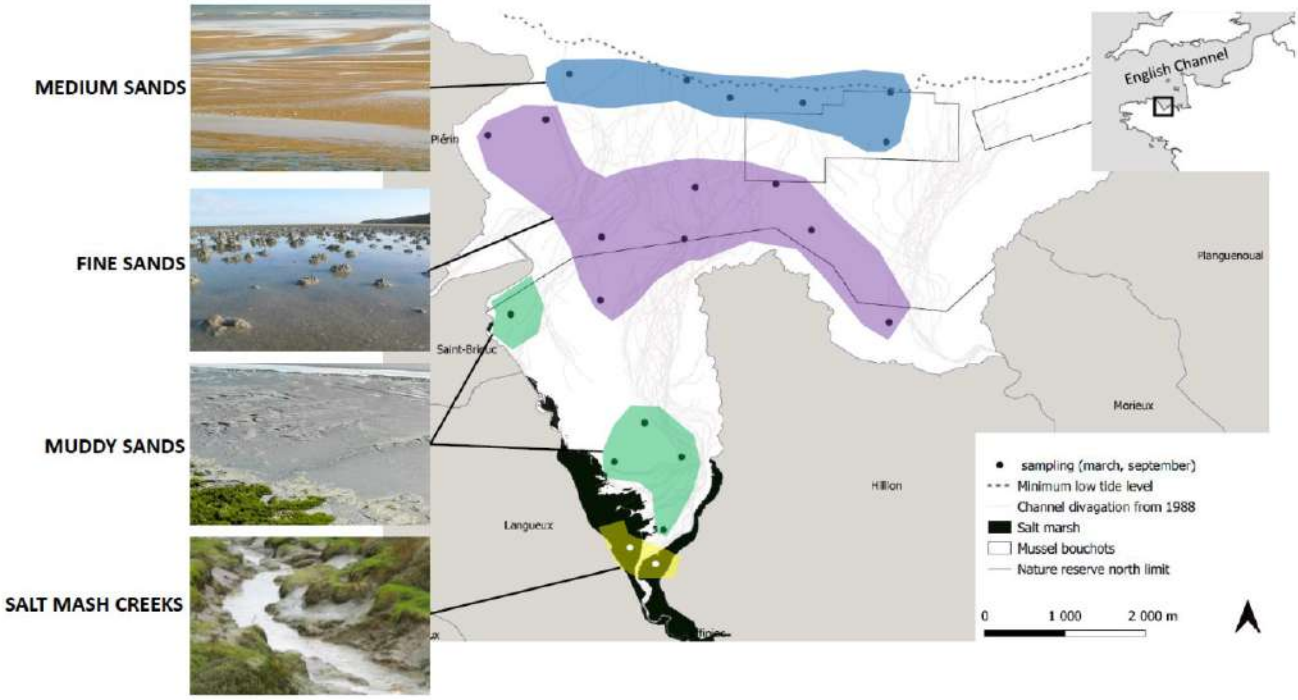


Figure 38: Location of the study area and sampling strategy. Dots correspond to the stations sampled in the different habitats. Colors of polygons correspond to the four habitats sampled for δ^{13}C and δ^{15}N values: salt marsh creeks (yellow), muddy sands (green), fine sands (purple) and medium sands (blue). A black line indicates the northern limit of the Nature reserve.

Data analysis

Data sets were investigated to analyse spatial patterns and seasonal variability of the intertidal benthic food web. Analyses were conducted in term of composition and structure at the bay scale (*i.e.* entire community) and at the finer scale of the different benthic assemblages.

Differences in δ^{13}C and δ^{15}N were tested with a one-way ANOVA for the factor 'Assemblages' for each species. The food web structure was analysed though community-wide metrics (Layman et al., 2007):

- δ^{13}C range (CR): Distance between the highest and the lowest δ^{13}C values of the community (*i.e.*, maximum δ^{13}C - minimum δ^{13}C). CR is one representation of basal source diversity within a food web;
- δ^{15}N Range (NR): Distance between highest and the lowest δ^{15}N values of the community (*i.e.*, maximum δ^{15}N - minimum δ^{15}N). NR is one representation of the total length (*i.e.* total number of trophic levels) within a food web;
- Total Area (TA): Convex hull area encompassed by all species in the δ^{13}C-δ^{15}N 2D δ space. This represents a measure of the total amount of niche space occupied, and thus a proxy for the total extent of trophic diversity within a food web;
- Mean distance to centroid (CD): Average Euclidean distance of each species to the δ^{13}C-δ^{15}N centroid, where the centroid is the mean δ^{13}C and δ^{15}N values for all species in the food web. This metric measures the average degree of trophic diversity within a food web;
- Mean nearest neighbor distance (NND): Mean of the Euclidean distances to each species' nearest neighbor in bi-plot space, and thus a measure of the overall density of species packing.

Three other indices from Cucherousset and Villéger (2015) were also calculated to analyse the similarity between March and September and among assemblages:

- Isotopic similarity (ISim): Overlap in the total isotopic niches as the ratio between the isotopic niche of the intersection and of the union off the two groups considered. It ranges from 0 when there is no isotopic overlap to 1 when the group with the lowest isotopic richness fills a subset of the isotopic space filled by the group with the highest isotopic richness;

- Isotopic divergence (IDiv): Distribution of points (close to the centroid or edges) within the convexhull. IDiv is minimal (*i.e.* tends to 0) when most of the points are close to the centre of gravity of the convex hull, and organisms with the most extreme stable isotope values are rare in a community. IDiv tends to 1 when all the points are located on the edges of the convex hull and organisms with the most extreme stable isotope value(s) dominate the foodweb;

- Isotopic Eveness (IEve): Regularity in the distribution of organisms along the shortest tree that links all the points. IEve tends to 0 when most of organisms are packed within a small region of the stable isotope space while a few others are far from this cluster. IEve tends to 1 when organisms are evenly distributed in the stable isotope space.

We used the stable isotope trajectory analysis (SITA) to quantify and characterize the magnitude (distance) and the nature (direction) of seasonal shift in the δ^{13}C/δ^{15}N-space for sources and trophic groups (Article II). The net change (Euclidian distance between March and September for a given group) and the angle α (0-360° direction in the δ-space considering the Y axis, δ^{15}N, as the North, *i.e.* 0°) were calculated to assess the magnitude and the nature of change in the δ^{13}C/δ^{15}N-space, respectively. Net changes and angle α were represented through trajectory diagrams and trajectory roses and seasonal differences in δ^{13}C and δ^{15}N mean values for sources and trophic groups were represented through bar plots and tested with permutation Student's t-tests.

3.3.3 | Results

Primary food sources

Contrasts were observed in primary food sources stable isotope values (Figure 39). δ^{13}C values were lower for terrestrial POM (-30.13 ‰± 0.98). Salt marsh plants exhibited among the lowest δ^{13}C values, excepted *Spartina anglica* characterised by the highest δ^{13}C (-12.89 ‰) typical of C4 plants (Currin et al., 1995). Higher δ^{15}N values were observed for *Halimione portulacoides* in March (12.98 ‰ ± 1.74), and September (11.94 ‰ ± 0.44).

SOM of all assemblages were characterized by the lowest variability in δ^{13}C and δ^{15}N values (Figure 40). *Ulva* stable isotope values showed an increase in both isotopes (angle α: 50.57°, trajectory length : 6.49), although this variation was not significant for δ^{13}C (p=0.094). POMs followed an inverse pattern (243.49°, 7.41). Significant δ^{13}C shifts between March and September were observed, with a decrease for POM_SEA (*p*=0.004), and an increase for terrestrial POM (*p*=0.032).

Consumers

Benthic consumers displayed a wide range of stable isotope values in both seasons. In March, δ^{13}C mean values ranged from -21.90 ‰ ± 0.30 for the grazer *Orchestia gammarellus* to -12.58 ‰ ± 0.94 for the deposit-feeder *Peringia ulvae* (Figure 39, A.). δ^{15}N mean values ranged from 8.81 ‰ ± 0.50 for the deposit-feeder *Bathyporeia sarsi* to 13.46 ‰ ± 0.73 for the predator polychaete *Sigalion mathildae*. In

September, mean $\delta^{13}C$ values ranged from -21.39 ‰ ± 0.93 for *Orchestia gammarellus,* to -11.88 ‰ ± 0.94 for the deposit-feeder *Bathyporeia pilosa* (Figure 39, B.). $\delta^{15}N$ mean values ranged from 9.08 ‰ ± 0.50 for the deposit-feeder *Bathyporeia pilosa,* to 14.37 ‰ ± 0.29 for the omnivore *Hediste diversicolor*. Omnivores and carnivores exhibited among the highest $\delta^{15}N$ values while deposit-feeders and suspension-feeders among the lowest with an important variability (Figure 39).

Total areas were similar in March (43.46 ‰²) and September (46.64 ‰²). The food web centroid was characterized by a $\delta^{13}C$ decrease (-0.95‰) but the food web still strongly overlapped in March and September (Isotopic Similarity = 0.728). CD remained similar over time (1.99 vs 2.02) revealing a stable trophic diversity. In September, species were more evenly distributed, decreasing the trophic redundancy as shown by the increase in NND (0.28 vs 0.36), SDNND (0.24 vs 0.31), and IEve (0.61 vs 0.80).

Assemblages scale

Species sampled in the salt marsh were characterised by the lowest $\delta^{13}C$ values at both seasons. $\delta^{13}C$ values showed significant spatio-temporal variability characterised by a ^{13}C-depletion gradient from muddy to medium sands (F: 54.38, p-value < 0.0001) which was consistent over time, and followed the previously mentioned emersion time gradient (Figure 41). CR increased between March and September (2.74 vs 5.20) in medium sands and remained stable in other assemblages. $\delta^{15}N$ was significantly different between assemblages.

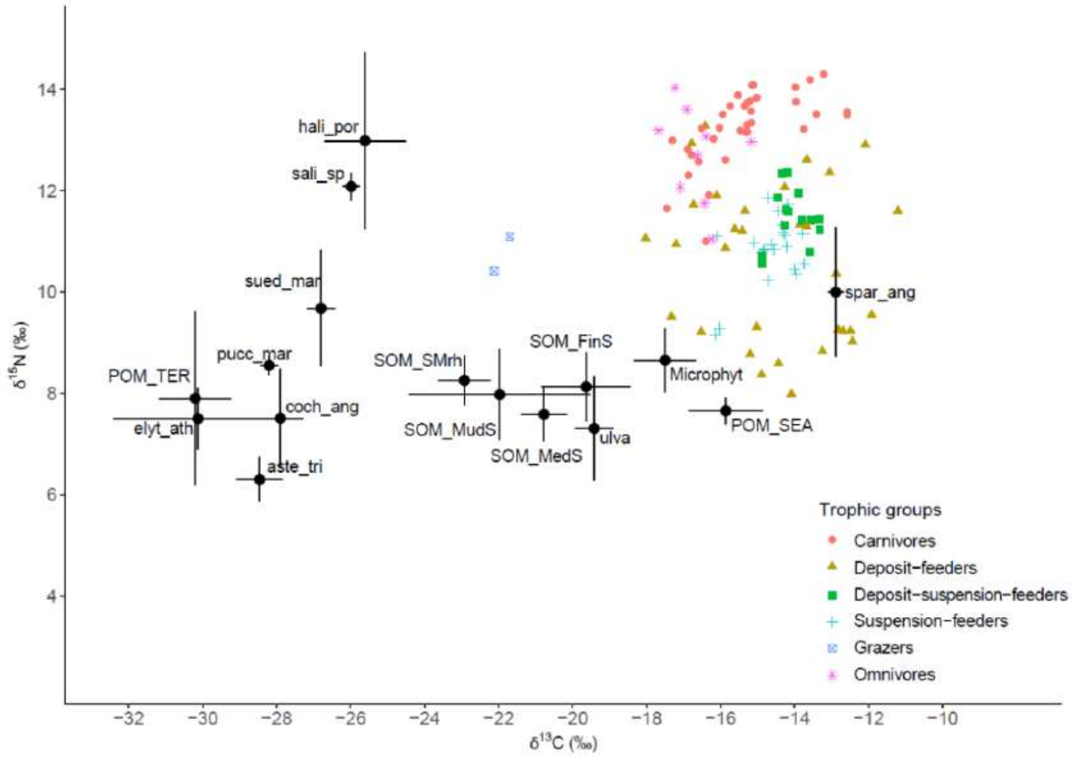
Some spatial patterns in the stable isotope composition of trophic groups were also identified at the scale of trophic groups and correlated with emersion time. Deposit-suspension-feeder $\delta^{13}C$ values were negatively correlated with emersion time in March (-0.674, p<0.01, Pearson), while suspension-feeders (0.720, p<0.001), deposit-feeders (0.635, p<0.01), and carnivores (-0.588, p<0.01) showed a positive correlation in September.

TA was higher in March for muddy (21.92 ‰²) and fine sands (23.16 ‰²) compared to medium sands (9.12 ‰²) and salt marsh (9.59 ‰²) (Figure 41). In September, TA were similar for sand assemblages, following a decrease for muddy and fine sands and an increase for medium sands.

No major convex hull overlap was observed between the salt marsh and other assemblages. An overall decreasing gradient of values from muddy ($\delta^{13}C$ centroids in March: -13.93 ‰, September: -14.46 ‰), to fine (-15.01 ‰, -15.08 ‰) and medium (-16.41 ‰, -17.34 ‰) sands assemblages led to a partial convex hull overlap. The lowest isotopic similarity among sand assemblages were observed between muddy and medium sands in both seasons (March: 0.139, September: 0.149). In March, fine sands were more similar to muddy sands (0.607) than medium sands (0.351). In September, overlap became more balanced (0.401 vs 0.441, respectively), revealing more similarity in isotopic niche between assemblages. More specifically, dissimilarity at the lower levels of the food web increased in September between muddy and medium sands indicating some differences in stables isotopes values mainly involving suspension-feeders.

In sand assemblages, CD ranged from 1.40 to 1.76 in March, and 1.50 to 1.91 in September. Species sampled in muddy and medium sands were more evenly distributed in the δ-space in September as shown by the increase in NND, SDNND, IDiv and IEve values.

A. March



B. September

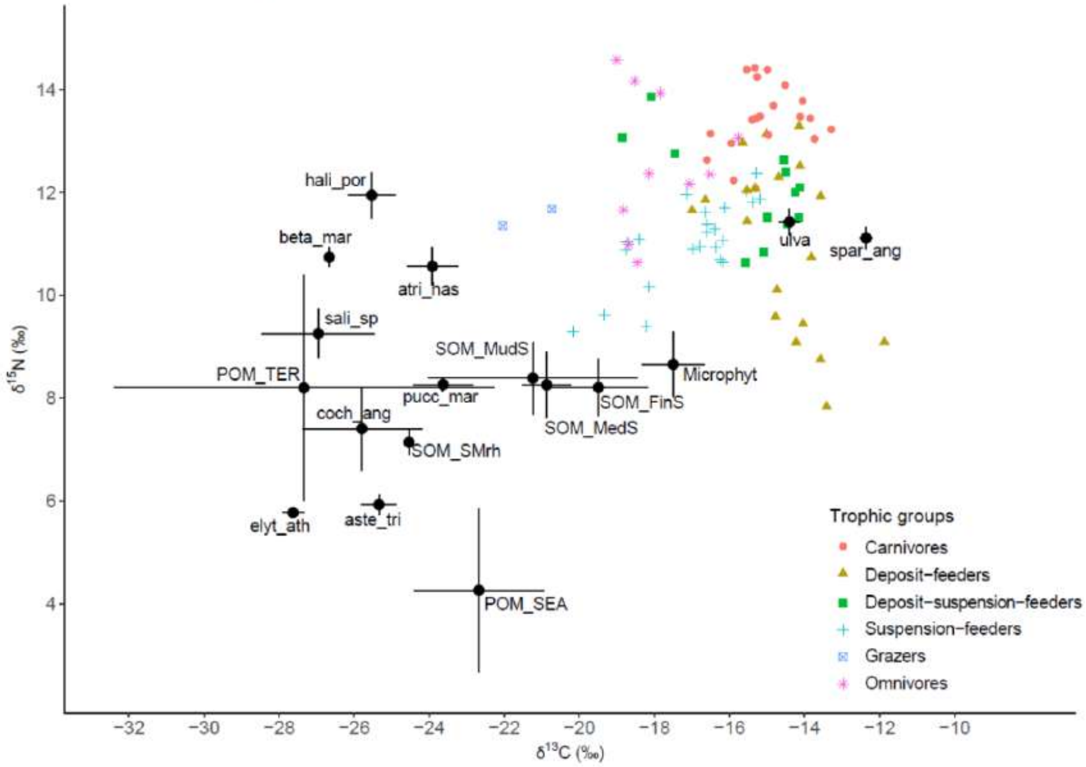


Figure 39: $\delta^{13}C$ and $\delta^{15}N$ of consumers and potential dietary sources in March (A) and September (B) in intertidal soft-bottom sediments of the bay of Saint-Brieuc. $\delta^{13}C$ and $\delta^{15}N$ values are plotted for each individual of consumers. Colors and shapes represent trophic groups. Mean $\delta^{13}C$ and $\delta^{15}N$ values of potential dietary sources are represented with black dots with error bars. Marine and terrestrial particulate organic matter (POM_SEA, POM_TER). Sedimentary organic matter in the different habitat from salt marsh to muddy, fine and medium sands (SOM_SMrh, SOM_MudS, SOM_FinS, SOM_MedS). Microphytobenthos (Microphyt). C3 plants: *Halimione protulacoides* (hali_por), *Beta maritima* (beta_mar), *Atriplex hastata* (atri_has), *Salicornia sp* (salic), *Puccinelia maritima* (pucc_mar), *Cochlearia anglica* (coch_ang), *Elytrigia atherica* (Elyt_ath), *Aster Tripol*ium (aste_tri). C4 plant: *Spartina anglica* (spar_ang). Algae: *Ulva sp* (ulva).

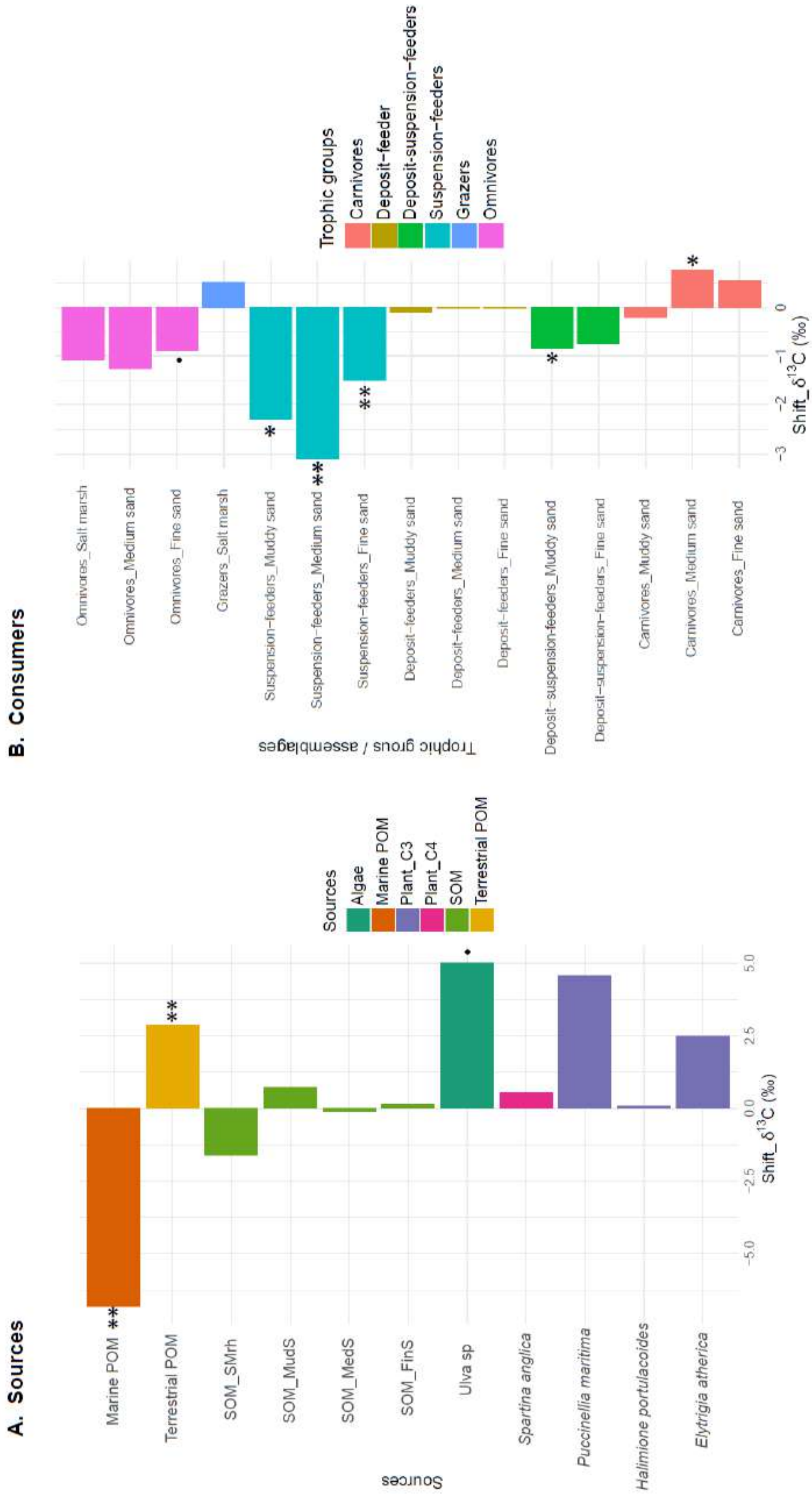


Figure 40: Seasonal variation of δ^{13}C values between March and September. Sources (A): main primary food sources are represented by colors: marine POM, terrestrial POM, SOM for the four habitats (Salt marsh creeks (SOM_SMrh), and muddy (SOM_MudS), fine (SOM_FinS), and medium (SOM_MedS) sands), Ulva sp, and the four main C3 (*Puccinellia maritima, Halimione portulacoides, Elytrigia atherica*) and C4 salt marsh plants (*Spartina anglica*). Consumers (B): consumers are represented by colors and seasonal shift in δ^{13}C values is provided for each habitat. Mean significant differences tested with Permutation Student's t-tests are summarized as *** (P<0.001), ** (P<0.01), * (P<0.05). Mean differences near the significant level are also represented (·, P<0.1).

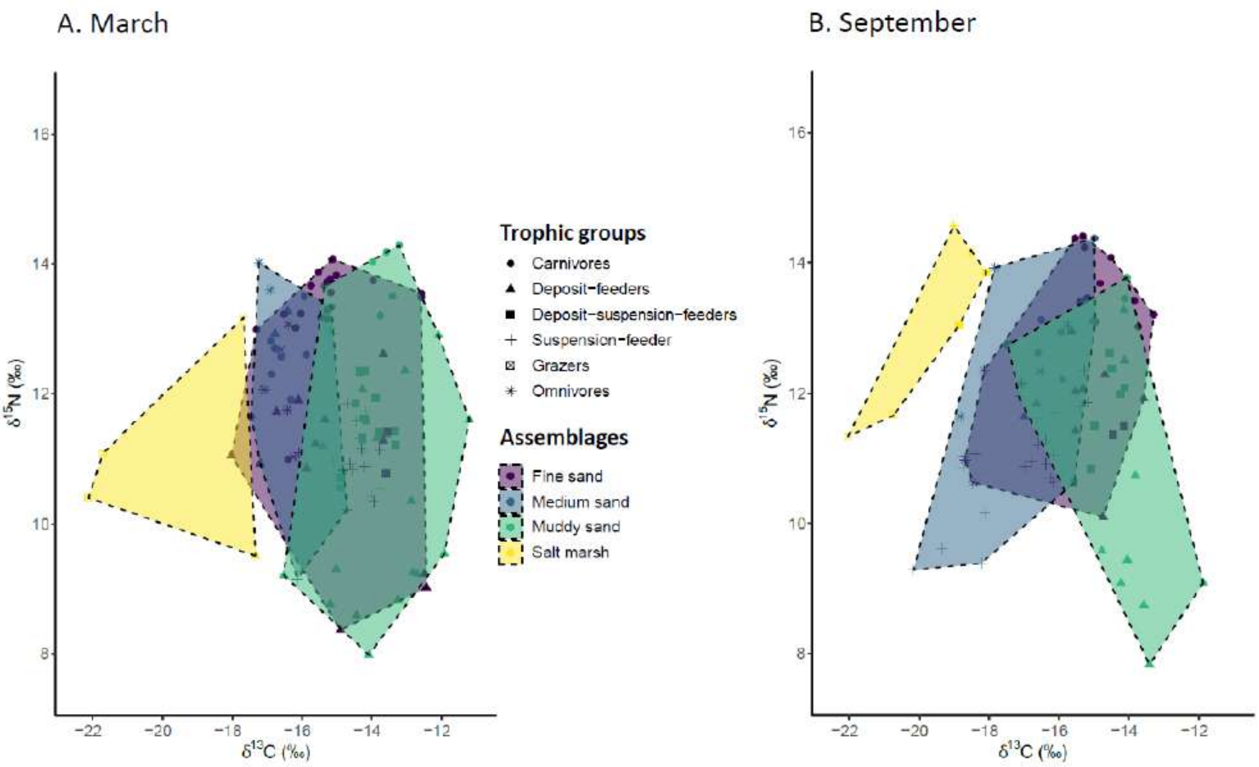
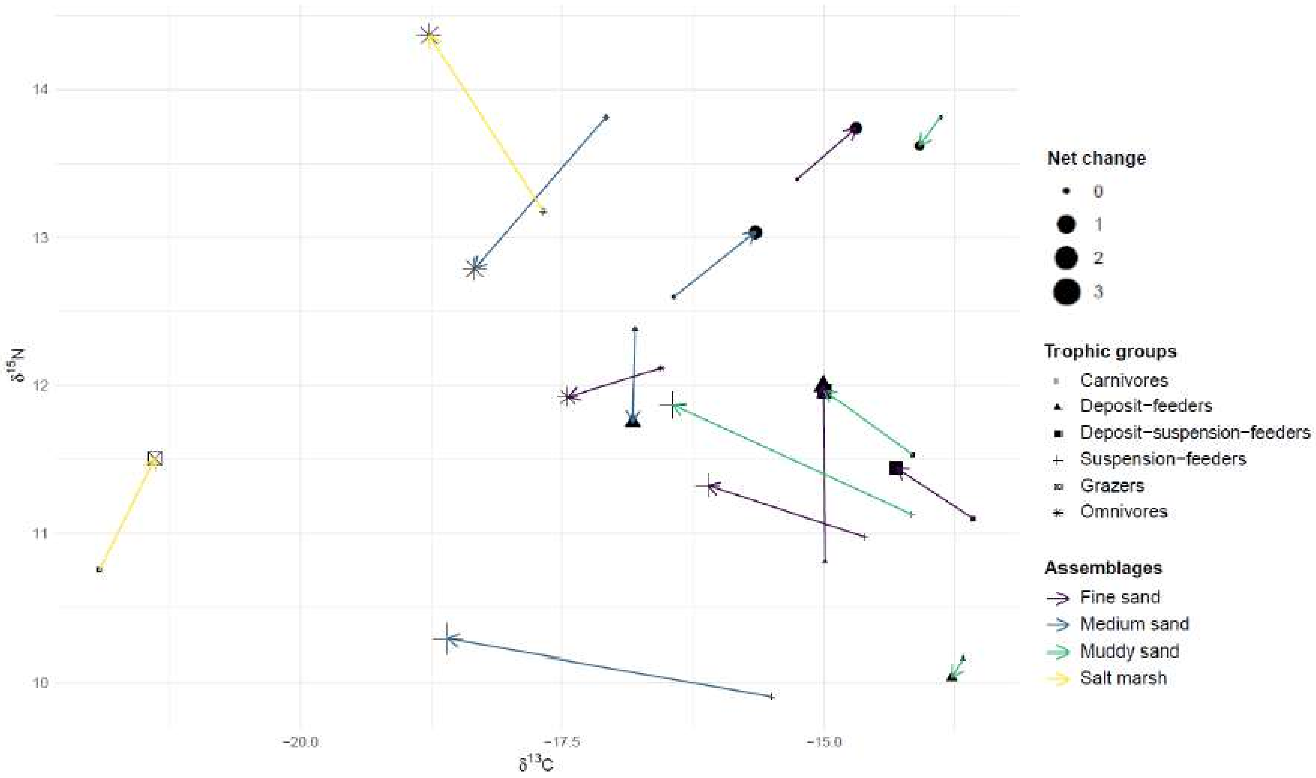


Figure 41: $\delta^{13}C$ and $\delta^{15}N$ stable isotope composition of the food web in March (A) and September (B) in the four habitats. $\delta^{13}C$ and $\delta^{15}N$ are plotted for each individual of consumers. Shapes represent trophic groups. Isotopic niche (Total area) is represented by convex hull polygons for each habitat: salt marsh creeks (yellow), muddy sands (green), fine sands (purple) and medium sands (blue).

Trajectories of trophic groups

Significant decreases in $\delta^{13}C$ value were observed between March and September in muddy sands for suspension-feeders (*p*=0.012) and deposit-suspension-feeders (*p*=0.020), and for suspension-feeders in fine (*p*=0.002) and medium sands (*p*=0.002) (Figure 42). A moderate increase in $\delta^{13}C$ value was observed for carnivores in medium sands (*p*=0.022). Contrasts among assemblages were observed in trophic groups stable isotope values between March and September. Medium sands suspension-feeders exhibited the longest trajectory (Euclidean distance= 3.12) while muddy sand deposit-feeders were characterized by the lower shift (0.16) (Figure 42). Stable isotopes values of trophic groups remained contrasted between assemblages but the seasonal shifts of both $\delta^{13}C$ and $\delta^{15}N$, could be similar for given trophic group among assemblages. Suspension-feeders exhibited very similar directions (283.90°±3.70) and among the highest changes (2.27±0.68), characterized by a ^{13}C-depletion and a moderate increase in $\delta^{15}N$. Similarities of seasonal pattern between assemblages were also observed for deposit/suspension-feeders in muddy (0.95, 297.24°) and fine (0.81, 294.95°) sands, and for omnivores and carnivores in fine and medium sands respectively. Inversely, deposit-feeders exhibited contrasted trajectories in muddy (0.16, 221.10°), fine (1.19, 359.20°) and medium sands (0.63, 182.00°) mainly influenced by shift in $\delta^{15}N$. In salt marsh creeks, omnivores and grazers both exhibited singular trajectories.

A. Trophic trajectory diagram



B. Trophic trajectory roses

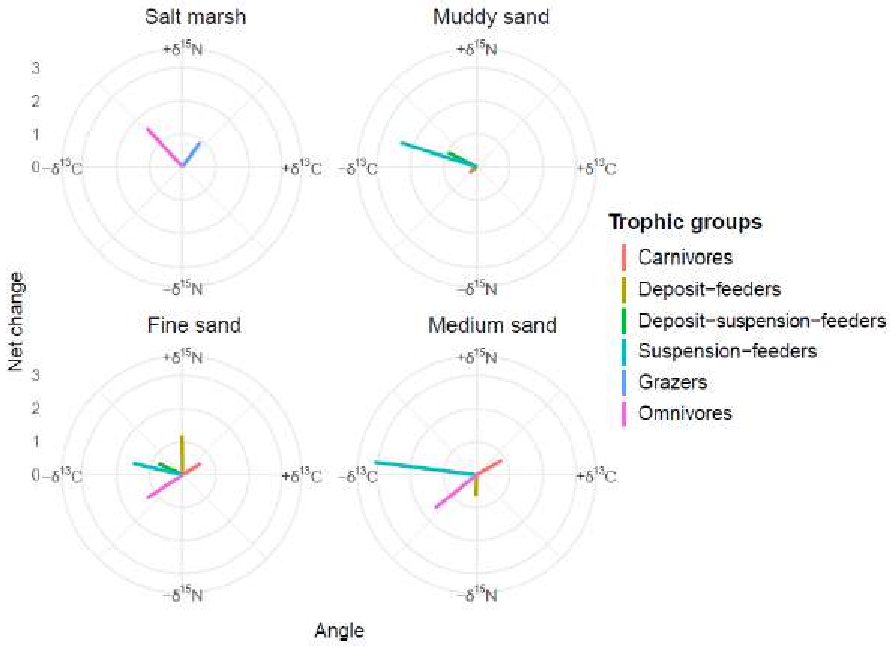


Figure 42: Seasonal trajectories of trophic groups between March and September. Stable Trophic trajectory diagram A: Arrows represent trophic trajectory in the $\delta^{13}C/\delta^{15}N$ space between March and September for each trophic group in each habitat (color). Length of arrows and size of dots corresponds to the net change (Euclidean distance) and inform about the magnitude of change. Shape of dots correspond to trophic groups. Trophic trajectory roses B: Angles α and net changes are represented in trophic trajectory rose for each trophic group (color) in each habitat (panel). Angle α values (0-360°) represent the nature of change in the δ-space (0-90°: + $\delta^{13}C$ and + $\delta^{15}N$; 90-180°: + $\delta^{13}C$ and - $\delta^{15}N$; 180-270°: - $\delta^{13}C$ and - $\delta^{15}N$; 270-360°: - $\delta^{13}C$ and + $\delta^{15}N$).

3.3.4 | Discussion

Spatio-temporal patterns as a potential alternative to track trophic links

Stable isotopic composition of consumers and their food sources are commonly used to unravel trophic interactions within natural communities. The use of isotopic mixing models is a way to convert isotopic data into estimates of food source contributions from the various components of a consumer's diet (Phillips et al., 2014). Source pools with distinct isotope values is a necessary prerequisite to the use of these tools, while multiple sources or strong similarity in their stable isotope composition affects their relevance in answering questions about trophic relationships (Fry, 2013; Layman et al., 2012). The sources pools described in this study were highly diversified and characterised by strong overlap and high dynamics, limiting the relevance of mixing models and claiming for an alternative approach. Therefore, we focused on stable isotope trajectories of sources and consumers. Covariation of stable isotope composition between sources and consumers were used to help to identify sources supporting food webs (Leclerc et al., 2013; Melville and Connolly, 2003; Vanderklift and Wernberg, 2010).

Salt marsh influence on the coastal food web

From the estimation calculated on the Mont-Saint-Michel bay, the productivity of salt marshes during summer is high, reaching 30 tonnes of dry matter per ha per year (Lefeuvre et al., 2000). The outwelling hypothesis states that salt marshes export organic matter, dissolved carbon and nutrients to tidal adjacent habitats from tidal channels to estuaries and coastal ocean (Odum, 1968; Teal, 1962). The influence of salt marsh vegetation on food webs is highly variable, ranging from almost insignificant (Christianen et al., 2017) to very important, and reflected in the stable isotope composition of marshes inhabiting consumers (Nordström et al., 2014; Riera et al., 1999), or adjacent habitats assemblages (Conway-Cranos et al., 2015).

In our study area, the salt marsh is characterised by a good conservation status but only covers small surfaces [125 ha, Sturbois and Bioret (2019)], compared to other coastal bays of the French Atlantic coast, such as the bay of Mont-Saint-Michel [4000 ha, Lafage et al., (2021)], the bay of Seine [1200 ha, Lafage et al., 2021)], or the bay of Aiguillon [1100 ha, Joyeux et al., (2017)]. Trophic connectivity depends on the relative proportion of allochthonous and autochthonous resources rather than only on asymmetric productivity between habitats. Differences in the proportion of resources result from interaction among productivity, permeability, and transport vectors that lead to many states of trophic connectivity (Domingos and Lana, 2017).

The influence of salt marsh C3 plants was limited to the grazer *O. gammarellus*, the omnivore *H. diversicolor* and the deposit-suspension-feeder *Scrobicularia plana* when specifically sampled in the muddy salt marsh creeks. *O. gammarellus* is known as a consumer of salt marsh detritus [*H. portulacoides* in particular (Joyeux et al., 2017; Laffaille et al., 2001)]. *H. diversicolor* is a very polyvalent omnivore able to:

(1) feed on sediment, microphytobenthos, macroalgae, detritus and plant material;
(2) predate small invertebrates;
(3) suspension feed by secreting and using a mucobag as a filter when drawing down particles in its burrow;
(4) garden by sprouting seeds (Durou et al., 2007; Scaps, 2002; Zhu et al., 2016).

Only few evidence exist about the local use of marsh resources: juveniles of *Dicentrachus labrax* were proved to feed on ^{13}C-depleted preys inhabited the salt marsh (Sturbois et al., 2016), or *Branta bernicla*, on *Puccinellia maritima* (Ponsero et al., 2009b). As no species displayed a ^{13}C depletion, which would be consistent with the significant assimilation of such sources further on the shore, no evidence was found that salt marsh plants support the benthic food webs in unvegetated sandy habitats. The influence of the enriched C4 plant *S. anglica* was also discarded. The capacity of salt marsh plants to fuel intertidal benthic habitat seems limited, especially for macrofauna species that exhibit a very restricted mobility in a large flat characterised by megatidal and dispersive conditions.

Consequently, we believe that salt marsh organic matter is either transferred into coastal food webs through highly mobile consumers (fish, shorebirds), thereby overpassing the intertidal benthic food web, or exported over spatial scales which exceed the bay, contributing to the overall detrital pool (Lopez and Levinton, 2011). It results in a strong dilution and the impossibility to assess its influence through stable isotopes.
Salt marsh muddy creeks are characterised by a high production of benthic diatoms. Mullets (*Chelon spp.)* feeding on biofilm and associated meiofauna, contribute to the exportation pathway of the biofilm (Carpentier et al., 2014). Regularly submerged at high tide, salt marshes are reached by a water height of more than 10.70 metres, which represents 45% of the tides [76% for associated creeks, Sturbois et al. (2016)]. Megatidal conditions associated with strong currents may also contribute to the effective resuspension of sediments and microphytobenthos (personal observation), exporting benthic diatoms in the water column and further away in the bay. The importance of resuspended microphytobenthos as a major food source for macrobenthos in mudflat environments is a long known process in those environments (De Jonge and Van Beuselom, 1992; Riera and Richard, 1996).

Sources supporting the food web: limited influence of *Ulva*

The year 2019 was characterised by an important *Ulva sp.* biomass, which progressively accumulated during summer.

Ulva sp. was ^{13}C- and ^{15}N-enriched in September compared to March, which provided an opportunity to investigate its potential role in the food web. Our results showed that a major influence of *Ulva* on the entire food web was excluded regarding negligible quantities in February (12 ha), and the absence of graphical evidence of potential trophic links in September. From this last point of view, no evidence of the use of *Ulva* by consumers were observed. For example, *A. spatulispina* sampled in September were ^{13}C-depleted, suggesting no *Ulva* sp. influence and contrasting with the results of Quillien et al. (2016) who showed, in another coastal bay of Brittany, the bay of Douarnenez:

(1) a direct consumption of *Ulva sp.* fragments by a few species (*Owenia fusiformis, Acrocnida spatulispina*);
(2) an indirect influence on the whole food web through the isotopic modification of SOM and POM due to *Ulva sp*. presence.

The moderate ^{13}C- and ^{15}N-enrichment observed for carnivores may reveal accidental ingestion of *Ulva* fragments when hunting and feeding on preys and/or a reduced omnivorous component in their feeding, but the low magnitude of the trophic trajectory suggest a very limited influence. Such low influence of *Ulva* in the diet and stable isotope composition of marine crustaceans has also been demonstrated through experimental (Karez et al., 2000; Salathé and Riera, 2012) and *in situ* (Adin and Riera, 2003) studies.

On the western coast of Korea, Park et al. (2016) showed that blooming green macroalgae support an intertidal macrobenthic food web with a certain variability depending on both feeding strategies of consumers and resource availability. From field experiments with varying macroalgal mat thickness (0.5, 1.5 and 4 cm) over eight weeks, Green and Fong (2016) quantified the effects on macrofauna in a lagoon mudflat in California. They found that the mechanism of negative effects for the highest macroalgal subsidies was linked to the development of anoxic conditions. Sulfide accumulation for the 4 cm treatment altered ecosystem functioning, favouring subsurface deposit feeding as capitellids.

Contrast with the results of Quillien et al. (2016), Park et al. (2016) and Green and Fong (2016), may be explained by the mega-tidal conditions occurring in the study area. In the bay of Saint-Brieuc, tide is a strong driving factor, daily redistributing algal mats and limiting long-term static accumulation of algae and potential anoxic episodes to very limited zones (*i.e.* beaches on the upper shore), where *Ulva* are collected by local authorities as part of precautionary sanitary measures. This process potentially limits the integration of *Ulva* in the food web. Furthermore, the bay of Saint-Brieuc shelters benthic producers on muddy and muddy sand habitats, which contrasts from the sandy beaches located in the bay of Douarnenez.

Marine POM and MPB stable isotope compositions were the most likely bases of food webs within the different habitats, regarding $\delta^{13}C$ ranges displayed by benthic communities. Marine POM was the only source exhibiting a significant ^{13}C-depletion between March and September, which was also observed for suspension-feeders from all habitats, as well as by mixed deposit/suspension-feeders and some omnivores. The low shift in $\delta^{13}C$ values of deposit-feeders between March and September suggests a low seasonal variability in the composition of benthic producers.

Christianen et al. (2017) reported that energy for the Wadden sea ecosystem is mainly provided by locally produced organic matter and, in a lesser extent, by pelagic producers. Such contribution of MPB has also been highlighted, at lower geographic scales, in salt marsh consumers in the Mont Saint-Michel bay (Créach et al., 1997), and for cockles in Marennes-Oléron (Kang et al., 1999). Other intertidal studies also revealed the fuelling of main higher trophic levels by MPB and pelagic primary production (van Oevelen et al., 2006). In the bay of Saint-Brieuc, where muddy habitats are limited (64 ha), our results suggest that the food web is mainly fuelled by pelagic producers and, in a lesser extent, by benthic producers. However, salt marsh muddy creeks could also support a part of the MPB production, in addition with muddy sands. Such assumption will require further investigations to be accurately quantified (Méléder et al., 2020; Morelle et al., 2020). Such overall considerations and assumptions do not exclude contributions of other food sources at finer local scale in this highly dynamic system as suggested in the Roscoff bay (Ouisse et al., 2011), in the Wadden Sea (Christianen et al., 2017) or in this study for the macrofauna inhabiting salt marsh creeks.

Spatial patterns in benthic-pelagic coupling

Large scale spatial heterogeneity in the carbon stable isotope composition of consumers has been revealed by Christianen et al. (2017) in the Wadden Sea for species that foraged either on benthic or pelagic sources. For the suspension-feeder *Cerastoderma edule,* the dominance of pelagic food sources was underlined for a large part of the Wadden sea, while the dominance of benthic producer was suggested for some spatially limited areas. Conversely, for the deposit-suspension-feeder *Limecola balthica*, $\delta^{13}C$ indicated a high benthic contribution to its diet in most of the flat, contrasting with a dominant pelagic contribution in some limited areas.

In the study, spatial patterns were revealed within trophic groups, with higher $\delta^{13}C$ for suspension-feeders, deposit-suspension-feeders and carnivores in muddy and fine sands compared to medium sands. These patterns were maintained between March and September and confirmed by the correlation between $\delta^{13}C$ values and emersion time for some trophic groups. In addition, some contrasted temporal trophic trajectories among habitat were evidenced. Trajectory metrics (Net changes and angle α) revealed a congruent negative shift between marine POM and suspension-feeders $\delta^{13}C$ values between March and September. However, while direction in the δ space was similar, differences were observed in net changes values. This contrasted pattern in the magnitude of change suggests a decreasing influence of pelagic sources in the diet of suspension-feeders from muddy and sandy habitats compared to medium sands. Deposit-suspension-feeders showed similar direction but lower net changes than suspension-feeders, confirming both their higher dependence to benthic primary producers and their ability to feed on pelagic producers. The low variability of deposit-feeder $\delta^{13}C$ values was in accordance with the temporal stability observed for sedimentary organic matter in medium sands and suggested a low temporal variability in the stable isotope composition of MPB.

Lower net changes exhibited by suspension-feeders in muddy and fine sands habitat suggests a significant resuspension of MPB in the water column as already shown in different intertidal areas (De Jonge and Van Beuselom, 1992; Liénart et al., 2017; Riera and Richard, 1996; Sauriau and Kang, 2000; Underwood and Chapman, 1998). Suspended particulate organic matter is a dynamic mixture of pelagic and benthic algae due to the resuspension of MPB. Microphytobenthos growth is favoured in muddy and muddy sands habitats (Morelle et al., 2020), and its spatio-temporal distribution is driven by highly variable physical and biological factors (Méléder et al., 2020). MPB resuspension is known to be favoured by hydrodynamics and bioturbation activities of some macrofauna species such as *C. edule* (Rakotomalala et al., 2015). The bay of Saint-Brieuc is characterised by megatidal conditions and high density of *C. edule* reaching 2000 ind.m^{-2} in muddy sands. MPB can be easily resuspended at relatively weak current velocities (~10 cm.s^{-1}) on silty sediment (Blanchard et al., 1997; Kang et al., 2015; Ubertini et al., 2015). Resuspension is increased by the coverage and the important dynamics of tidal channels (Article III), which may contribute to organic matter fluxes. Emersion time regulates the trophic availability of MPB for some consumers (suspension and surface deposit feeders). Overall, our results suggest a contrasted trophic link between the benthic diatoms of muddy sand and suspension vs deposit-feeders. Hydrodynamics and tides favour the trophic connectivity between muddy sands and fine sands located at lower levels through the exportation of microphytobenthos in the water column. However, the exportation of the tidally resuspended MPB seems limited to fine sands habitats and suggests spatial contrast in benthic-pelagic coupling. De Jonge and Van Beuselom (1992) and Riera and Richard (1996) find similar results, demonstrating that the influence of the MPB exported in the water column is limited to nearby habitats.

Small spatial scale variability in food web structure.

Despite a slight increase in IEve in relation to the ^{13}C-depletion of suspension and deposit-suspension-feeders, the stability of structural properties and the strong overlap observed at site scale between March and September highlight the seasonal stability of the system. Dissimilarity among assemblages was strongly influenced by the δ^{13}C decreasing gradient of consumers from muddy to fine and medium sands assemblages, while no such pattern was observed for δ^{15}N. This gradient illustrates the spatial variability in the benthic pelagic coupling, with a higher influence of MPB in the upper level compared to low shore habitats. The decrease in the similarity between the low levels of the muddy and medium sands observed between March and September (in relation with the trophic trajectory of suspension-feeders in medium sands) highlights the two main energy pathways supported by pelagic and benthic producers.

Quillien et al. (2016) showed an overall simplification of community-wide food web structure and functioning in sandy beach harbouring green tides. They notably highlighted a significant community-wide shift in δ^{13}C over time progressively splitting up into two distinct isotopic niches. A linear arrangement of trophic web components indicated a single carbon pathway where *Ulva* mats were present on the shore. In the study area, no such simplification was observed at site or assemblages scale. Conversely, the selected indices of trophic structure and functioning were stable or increased during the year. Assemblages still overlapped over time and no overall ^{13}C enrichment of consumers was observed in accordance with δ^{13}C composition of *Ulva.* Overall, the temporal consistency observed in the food web structure in the different habitats confirm that the summer *Ulva* bloom did not play a major role in the trophic functioning off the bay of Saint-Brieuc.

CHAPTER IV

Main contributions and perspectives

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4.1 | Conservation and management implications in the bay of Saint-Brieuc

Marine protected areas (MPAs) are clearly defined geographical areas dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature and associated ecosystem services and cultural values (Day et al., 2012). MPAs are important tools in the protection of the marine environment (Klein et al., 2015): their designation potentially influence the dynamics of multiple species because of the extended protection from anthropogenic activity. Their influence can benefit, in certain areas, to all species residing within a geographically bound region (Bevilacqua et al., 2006; Thompson et al., 2012; Appolloni et al., 2017). Among the different declinations of the MPA concept, Nature reserves are strictly dedicated to the protection of biodiversity from human disturbances, and control impacts to ensure the protection of the conservation values (Day et al., 2012).

Benefits from the natural reserve on the intertidal area

An overarching question in conservation biology is the assessment of the effects of marine protected areas on marine habitats (Appolloni et al., 2017; Bevilacqua et al., 2006; Day et al., 2012; Klein et al., 2015; Thompson et al., 2012). The National Nature Reserve of Saint-Brieuc was initially devoted to the protection of birds. Because overwintering waders forage on macrofauna (Ponsero et al., 2011), their protection involves the conservation of marine habitats and benthic resources. By considering benthic macrofauna and its interaction with shorebirds at the scale of the whole flat, the reserve may have favoured some of the positive trends observed, such as increases in richness and species diversity observed in 2019 (Grorud-Colvert et al., 2021), and contributed to the persistence of functional properties.

Long-term monitoring extends beyond the MPA boundaries and contributes to improve the consideration of the importance of macrofauna in the governance process. For example, the MPA takes part in the cockles (*Ceratoderma edule*) fishing ground committee, which regulates fishing activity and determines the legal fishing season in delivering professional license adjustment according to monitoring results. Managers of the MPA also work with local authorities to avoid any impacts on sediment and macrofauna of mechanical collection of stranded macroalgae in the upper shore. Interventions of the nature reserve managers have significantly contributed to the recent regulation (2020) about dredged sediment disposal in Saint-Brieuc harbour (Figure 43). Such implications of the reserve managers undeniably contribute to the conservation of benthic habitats and the long-term stability of the benthic resource (van Gils et al., 2006) and, depending on species, to the stability or the increase of wader populations (Sturbois and Ponsero, 2019). In this context, the scale at which the MPA did implement the different monitoring programs provides a good baseline knowledge of the species and habitats, relevant in a MPA extension scenario as recommend by Greathead et al. (2020), since siting and design are frequently based on opportunities rather than ecological criteria and information (Sala, 2002). Local development of sampling design characterized by higher frequencies and experimental studies is then essential.

The nature reserve currently covers only one third of the intertidal area, which is assumed to be a functional unit from waders perspectives (Ponsero et al., 2016; Sturbois et al., 2015). There is no specific regulation outside of MPA. This insufficient size for including wider support systems for the benthos has been underlined in Europe and is part of the improvement recommendation of Greathead et al. (2020). On the intertidal flat of the bay of Saint-Brieuc, it remains difficult to formally and quantitatively conclude on any reserve effect because of:

(1) the high specific differences between protected and unprotected assemblages;
(2) the strong influence of bathymetry on ecological community properties and variability;
(3) the difficulty to disentangle natural from anthropogenic variability under natural constrains;
(4) the need of an assessment on a global network of protected and unprotected areas.

Then, assessing the role of the reserve at a wider scale, the bay eco-socio-system, is all the more difficult because some pressures such as eutrophication depend on terrestrial activities prevailing beyond the reserve limits, with no possible regulation at the natural reserve scale. Even more, despite a decrease in nutrient inputs, green tides still regularly occur in the bay of Saint-Brieuc (Figure 43). MPA appears as a very limited tool for the management of external pressures that lead to endogenic disturbances (Elliott and Whitfield, 2011) such as eutrophication and inherent green tides events. Paradoxically, despite green tides have indisputable effects on the environment and notably human health, the proliferation of *Ulva sp.* may be beneficial for birds populations as already shown for the herbivorous Brent goose *Branta bernicla* (Ponsero et al., 2009b), and the molluscs feeder Red knot *Calidris canutus* by favouring *Donax vittatus* populations (Sturbois et al., 2015).

Food webs studies: a baseline for conservation process

As the first attempt to characterize intertidal benthic food webs of the bay of Saint-Brieuc this thesis provides valuable information about the structure, functioning and energy pathways supporting benthic communities. The first information, useful for managers, concerns the limited influence of salt marsh plants for benthic macrofauna. Such result remains fundamental for the consideration of trophic functioning at larger scale in the bay. However, it does not question the value of salt marsh already shown for juveniles of some fish species (Carpentier et al.,2014; Joyeux et al., 2017; Lafage et al., 2021; Sturbois et al., 2016) or birds (Ponsero et al., 2009b, 2019a), two functions which rely on the good conservation status of the salt marsh (Bioret et al., 2009), which contrasts with other salt marsh under anthropogenic influence (Joyeux et al., 2017; Laffaille et al., 2005). The second main lesson is that, while the consumption of *Ulva sp.* was shown for two bird species in the bay of Saint-Brieuc, *Mareca penelope* and *Branta bernicla* (Ponsero et al., 2009b), the lack of influence of *Ulva* sp. seasonal increasing biomass on the trophic functioning of benthic habitats was unexpected. Despite some limited degraded area located up on the shore, where *Ulva* mats strands for a long time leading to sanitary problems, the presence of *Ulva* do not seem to affect the food web as shown with seasonal comparisons. This perturbation is even more limited by the fact that *Ulva* are collected by local authorities on the shore (close to 11 000 tons of *Ulva* in 2021, after field redrying). This important collection confers on *Ulva* a partial trophic dead end status especially with respect to the benthic macrofauna.

Conversely, as observed in many others bays and estuaries [e.g. Wadden sea (Christianen et al., 2017); Chesapeake bay (Semcheski et al., 2016), Oosterschelde estuary (Riera et al., 2002); Mont Saint-Michel bay (Kostecki et al., 2012); Marennes-Oléron estuary (Riera and Richard, 1996), in addition to benthic producers of the salt marsh muddy creeks, MPB partially supports the food web in muddy sands. By the way of resuspension, MPB is exported towards fine sand assemblages and support their production, notably the growth of young cockles on areas suitable for their recruitment, as shown by Sauriau and Kang (2000) on the Atlantic coast (Pertuis Charentais). In their conservation strategy, managers should also considers that MPB is largely produced in muddy salt marsh creeks. Maintaining benthic pelagic coupling involves salt marsh protection and conservation.

Despite all habitats are used by birds, muddy and fine sand assemblages are the most available due to their emersion time (Ponsero et al., 2016; Sturbois et al., 2015). This study highlights that wader food resources are supported by pelagic and benthic producers with a decreasing inshore/offshore gradient of MPB influence.

Such an updated knowledge must integrate governance process to inform and sensitize stakeholders, users and managers about the importance of muddy habitats to avoid cascading effect further up the food webs leading to potential ecological and economical consequences.

What conservation perspectives in the subtidal area?

On the opposite of the intertidal area, managers of the "Baie de Saint-Brieuc-Est" Natura 2000 site had a poor knowledge of the subtidal area, as the last global ecological assessment goes back to 1987. Since this date, only one station (R) was sampled from 2005 to 2019 as part of the WFD framework and the Rebent network. The use of the station R data set was essential to the better understanding of long-term changes observed between only two sampling dates (1987 *vs* 2019). It confirms that the development of such monitoring strategies coupling different spatial and temporal scales is essential for the future. The knowledge about the evolution of benthic communities inhabiting this area is all the more important because of the absence of strong regulations of human activities within the Natura 2000 site compared to MPA such as National nature reserve. As evidence, the evolution from subtidal benthic assemblages dominated by polychaetes to assemblages dominated by an opportunistic mollusc species, and characterised by important functional shifts, points out the strong dynamics occurring in the subtidal area.

Among the different species sampled in the subtidal area, *V. gibba* experienced the strongest increase in abundance, especially in the southern part of the study area. *V. gibba* is considered as an indicator of environmental instability whose strong increase across Europe has been largely associated to disturbances (Hrs-Brenko, 2006), particularly pollution and sedimentary instability (FAO and UNEP, 1985; Pearson and Rosenberg, 1978; Pranovi et al., 2007; Salen-Picard, 1981). Massive recruitments of *V. gibba* characterize pioneer stages of benthic community dynamics following a perturbation (Pranovi et al., 1998). Bonvicini-Pagliai & Serpagli (1988) called this species "*a time recorder of environmental stress*". Once the disturbance regime decreases, biotic interactions progressively regulate *V. gibba* populations (Olafsson et al., 1994). Knowledge on the level of disturbance required for the persistence of an abundant *V. gibba* population and its ability to increase in abundance in the absence of a primary disturbance factor is crucial to disentangle effects of natural (among which hydrodynamics) and anthropogenic (among which dredging activities) factors (Australian government, 2008).

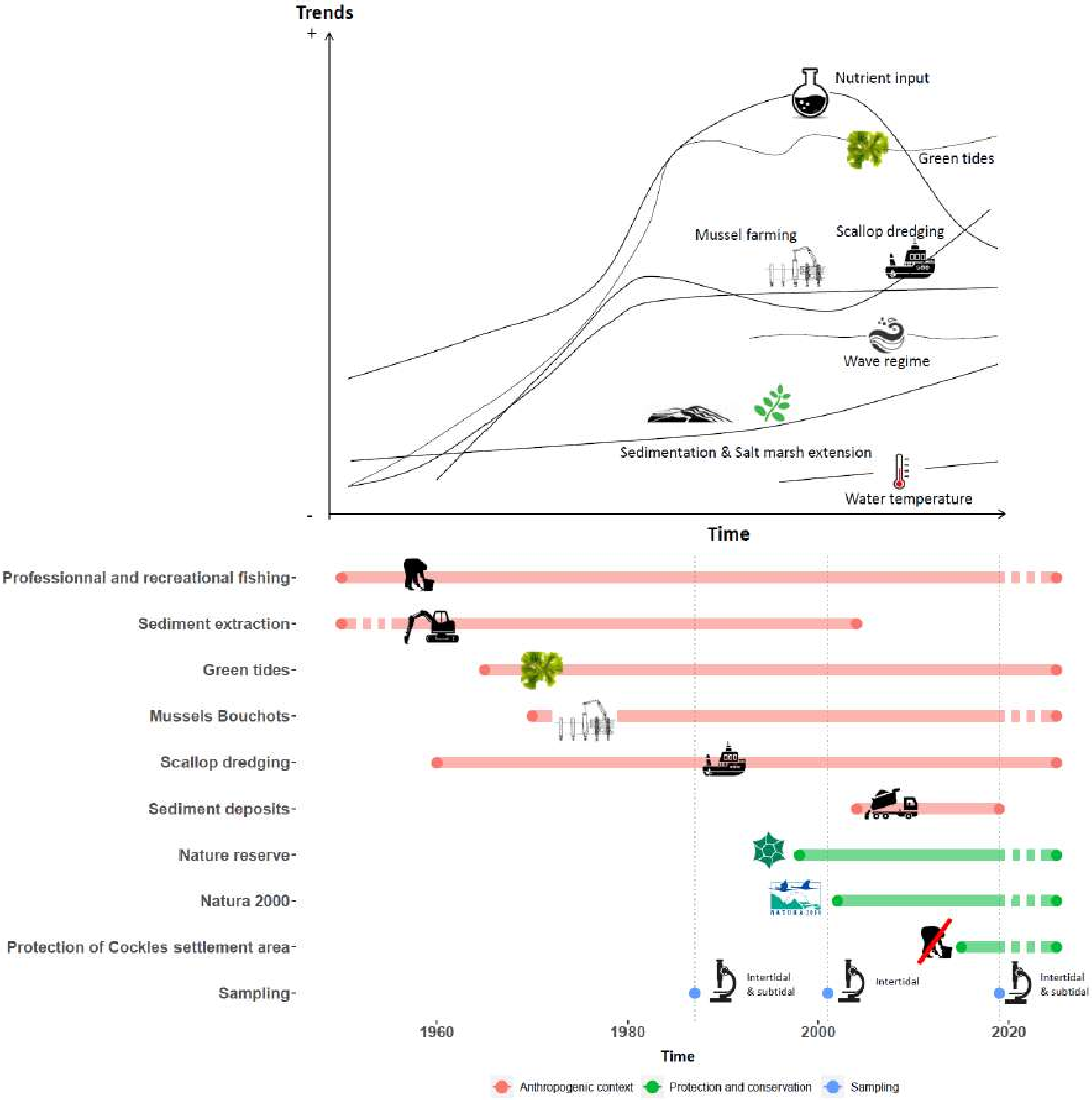


Figure 43: Time line of sampling dates with respect to main anthropogenic uses, pressures, natural factors, and conservation and protection regulations. Note that the overall trends of pressure was schematize by lines for each categories and may derive form expert opinions. The absolute position of each pressure or factor in the chart respectively to each other is not informative. (Sources: Nutrient input: Shéma d'aménagement et de gestion des eaux (SAGE), Centre d'étude et de valorisation des algues (CEVA); Green tides: CEVA; Mussel farming: Direction départemental des territoires et de la mer 22 (DDTM 22); Scallop dredging: Comité départemental des pêches maritimes et des élévages marins 22, DDTM 22 ; Wave regime : Service hydrographique et océanographique de la Marine, Sedimentation & salt marsh extension : Réserve naturelle nationale de la baie de Saint-Brieuc (RNNBSB), Water temperature : RNNBSB)

When developing management plans for marine areas and benthic resources, stakeholders must consider that benthic communities have the capacity to adapt to a predictable and moderate level of anthropogenic disturbance. However, there is a threshold beyond which populations, even composed of 'resistant' species, will collapse and cause the impoverishment of communities, with loss of major ecological functions and inevitable negative feedbacks, even on target species (Pranovi et al., 1998). In the "Baie de Saint-Brieuc-Est" Natura 2000 site, dredging activities may appear at odds with the conservation imperatives of benthic habitat. In the bay, the creation of the early dredged area in 2006-07 and its progressive extension in 2014-15 and 2017-18 illustrate the attractiveness of this zone for scallop dredging (Figure 37). The assessment of fishing impacts on Natura 2000 sites requires high-resolution spatial environmental data, including distribution of natural habitats and species, as well as fine-scale data on the distribution of ongoing fishing activities that overlap with high-value conservation zones (AFB et al., 2019; Lusenius et al., 2019; Pedersen et al., 2009). In this context, this study confirms the necessity of correctly evaluate the fishing pressure to interpret changes in marine ecosystems attributable to human activities.

There is no area free of dredging activity in the study site or in peripheral areas, which could be considered an un-impacted reference for the evaluation of dredging consequences on the benthic compartment. Alternatives to characterize the impact of fishing activities in the study area could consist in studying the response of benthic communities to a gradient of fishing pressures as proposed by van Denderen et al. (2015), or within an experimental area closed to commercial fishing as tested by Bradshaw et al. (2001) in the North and Irish seas. Further works are needed to quantify fishing efforts in the shallow area (*e.g. via* abrasion maps) as such accurate information is lacking, and to design a sampling based on the comparison between dredged and un-dredged areas.

Overall, access to highly resolved information about dredging activities is essential to understand changes in benthic communities and assess the impact of fishing activities and other driving factors (nutrient enrichment, sediment instability, climate change). Up-to-date documented reports on ecological changes and conservation status must be shared with stakeholders to effectively inform public debates (Eastwood et al., 2007; Pedersen et al., 2009). Consultation processes should involve policy makers, members of fishing institutions, fishermen, environmental organizations, and managers of MPAs when present. This step should ideally lead to the implementation of fishery management measures to reduce threats, and achieve conservation objectives (AFB et al., 2019; Lusenius et al., 2019; Pedersen et al., 2009). Although progress in expanding the coverage of MPAs has been made, the application of management tools has not yet been implemented in most of these areas (Torriente et al., 2019). Conservation of the marine environment is a relatively new field and is currently catching-up with its terrestrial counterpart where protected areas have been established for many decades (Morris et al., 2014). Despite the need for a worldwide improvement in the designation and management processes of marine areas, it has already been demonstrated that local human impacts on the marine environment could be effectively reduced within networks of Natura 2000 and marine protected areas (Fraschetti et al., 2018; Zupan et al., 2018). Management plans are recommended for Natura 2000 sites but are not mandatory under the Habitats Directive. Nevertheless, they appear to be an appropriate solution to reflect transparent conservation objectives (European Commission, 2011). Despite their complexity, fishing regulations implemented through a consultation process and management scheme have been shown to represent win-win scenarios between economic and conservation goals in different marine protected areas around the world (N2K group, 2018). In the bay of Saint-Brieuc, the implementation of such win-win scenarios enabled the long-term management of *P. maximus* population with benefits for the fishermen, and more modestly, promoted cockle fishing grounds (Ponsero et al., 2009a). Similar trends were reported in the Irish sea by Bradshaw et al. (2001), who showed positive effects of commercial fishing area closures on *P. maximus* (and indirectly on fishermen) and on benthic communities which became more diverse.

The need of collective representations and knowledge to facilitate governance and conservation processes

Faced with these results, which clearly underlined contrasted evolutions of the composition, structure and functioning of benthic assemblages in the bay of Saint-Brieuc, pointing a degradation of subtidal soft-bottom macrobenthos, the ball is in stakeholder's court to integrate this new knowledge into governance processes and impulse an ambitious conservation strategy, especially in the Natura 2000 site. A recent social-diagnostic pointed that key players in the local governance are characterised by a diversity of representations and a poor knowledge level about habitats and associated food web (Alavoine et al., 2021). However, they all shared an important attachment and a common vision of a bay under anthropogenic pressures. Collective representation and knowledge on the evolution and functioning of benthic habitat is consequently an important issue in this coastal area. This knowledge will rapidly be completed by other studies currently in progress in the bay of Saint-brieuc in complementary topics (marine geophysics and coastal geomorphology, human and social science).

These new knowledges must be considered for future governance rounds, in a multi-scale approach involving policy makers and stakeholders, and must make marine habitats, a central part of the conservation process (Greathead et al., 2020). As part of the national strategy for protected areas, a future project will focus on the extension of the National nature reserve of the bay of Saint-Brieuc. Among the different extension scenario, the inclusion of the whole intertidal area as an important zone for the functioning of benthic and bird communities appears as a promising and relevant goal. I also strongly believe that a scenario including the protection and the conservation of subtidal habitats should be debated publicly, especially in relation with the adjacent Natura 2000 site.

Such approaches should not only focus on aggregating local current practices, but also on exploring future visions and potential *scenarii* (Pereira et al., 2021). Further scientific studies should keep improve the understanding of benthic communities (*e.g.* functional approach including biomass) and food webs (*e.g.* tracking sources with fatty acids and heavy metals) in the bay of Saint-Brieuc. The existence of the MPA, strongly involved in the ResTroph research program, constitutes an interesting breeding ground.

4.2 | Ecological trajectory analysis frameworks

Methodological innovations, in terms of data collection, analysis and visualization, have an important influence on the ability of ecologists to advance understanding of biodiversity changes (Magurran et al., 2019). With the Community Trajectory Analysis framework, De Cáceres et al. (2019) provided a relevant contribution and a complementary tool to available methods for the analysis of temporal community dynamics (Buckley et al., 2021a, 2021b). Since its creation, some authors have suggested its use for the analysis of temporal dynamics data (Buckley et al., 2021a, 2021b; García-Callejas and Torres, 2019; Inouye et al., 2019; Lamy et al., 2021; Magurran et al., 2019; Yang, 2020). Others authors have applied the CTA framework to taxonomic community dynamics on species*sites matrices in terrestrial (Koshelev et al., 2021; Sánchez-Pinillos et al., 2019a; VanWallendael et al., 2021; Zald et al., 2020), freshwater (Li et al., 2021; Mota-Ferreira et al., 2021), and marine ecosystems (Boyé, 2018; Lefran et al., 2021). Cardou (2020) suggests the use of functional trajectory analysis in human-affected environment while Fernandes Neto et al. (2019) applied it to a community-weighted mean*sites functional matrix along succession after different land uses in central Amazonia. The speed at witch this framework have been used since its creation highlights the relevance of temporal trajectory analysis in different ecosystems and study contexts.

Building on the CTA framework, the results of this thesis went further than previous utilisations by a wider exploration and the development of Ecological Trajectory Analysis concepts and metrics by:

(1) providing new distance- and direction- based metrics and data visualization concepts (Articles I and II);

(2) implementing widely the exploration of trajectory analysis beyond sites*species matrices to bridge a gap identified in the consideration of dynamics in different fields in ecology (Articles I-V).

These new metrics and data visualization concepts have proved to be relevant to the analysis of taxonomic, functional and stable isotope dynamics in different context and at different spatial and temporal scales (Figures 3 and 11).

ETA analysis requires the definition of Ω defined by the resemblance between pairs of observations, measured using a dissimilarity coefficient *d*. Trajectory analysis is based on dissimilarity values contained in a distance matrix Δ=[*d*] (De Cáceres et al., 2019). The importance of choosing an appropriate dissimilarity index has been a concern for community ecologists for a long time when comparing composition. As ordination spaces are specifically constructed for each given data set, any data transformation on the raw data or sampling decision is likely to affect trajectories, and subsequently, all metrics to be calculated. This effect should be tested before any overall transformations. Such considerations, are also relevant in a functional purpose (Martini et al., 2021) where Ω may be defined by different types of raw data including Community-weighted trait values or functional indices.

Further use of the ETA frameworks should bring new improvements in metrics or data visualization. Similarly, other ETA metrics have to be explored more widely, such as convergence/divergence that may bring interesting issues to compare effective trajectories to potential modelled trajectories of reference or to explore ecological stability at regional spatial scales, where interconnected local communities form metacommunities (Lamy et al., 2021). Ecological trajectories can be performed at station or landscape scales within sites or in larger scale meta-analyses, comparing lengths and direction metrics between similar habitats along geographical gradients underpinning analysis in a same space of analysis. In this last case, the calculation of distance between pairs of trajectories and the definition of trajectory clusters may be influenced by differences in site characteristics, a situation that can be tested by the comparison of community dissimilarity matrix at a given sampling date to the overall trajectory dissimilarity matrix, or by centering trajectories to focus the analysis on the shape of the trajectory ignoring their respective position in the space of analysis.

Uses of this young approach need to be analysed and compared to look, for example, for differences in the behaviour of metrics depending on the field and/or study context. For instance, strong directional trajectories are more likely to occur in a plant community composed of few perennial species under a restoration process, than in benthic communities involving several dozen or hundred of species in a dynamic marine environment. Such contrasts in the studied community may for example dramatically influence the calculation of Directionality or Net change ratio and the overall shape of trajectories. Simulation studies may help to go further in the behaviour of trajectory metrics. Similarly, direction-based metrics calculated from a community characterised by a wide stability with respect to initial state, or on the contrary from a community characterised by a catastrophic event will not have the same ecological meaning, even if their absolute values are similar. This is why both distance- and direction-based trajectory metrics have to be used together and associated with a strong examination of underlying datasets. Doing this, the interpretation of the directional, non-directional or disruptive shape of the trajectory (Lamothe et al., 2019; Matthews et al., 2013) will avoid potential wrong interpretation, which may lead to misdirecting conservation actions or overstating conservation progress.

As written by Layman and Post (2008), "*A carpenter would never use a screwdriver to pound a nail*": ETA concepts and metrics were not intended as a universal tool to be applied in all situations or to be opposed to other available methods (Buckley et al., 2021a), but as a new tool for the ecologists which could be useful in situations suitable for trajectory analysis. Similarly to all analytical tools, there is a high probability that the ETA frameworks may be applied to data sets to which it is not well suited or that inexperienced users may misinterpret the results. Indeed, there is a considerable history of this in the literature concerning for example mixing models in stable isotope ecology (Fry, 2013; Jackson et al., 2009; Phillips, 2001; Phillips et al., 2014). Users must consequently be aware of the assumptions, fields of application and limitations associated with the ETA frameworks.

Despite the speed of changes allows dealing with variations in frequency of surveys or that metrics can be calculated between different states, users are encouraged to establish sampling strategy implying synchronous sampling and similar frequency of surveys. It makes trajectory analysis data-gourmand but it is an essential condition to take the most of the ETA frameworks. Future potential users should also be aware of that when looking for the reanalyse of previous dataset not specifically computed for trajectory analysis.

The ecological datasets called in this thesis participate to the audience and the exportation of ETA in different fields in ecology underpinning understanding and appropriate uses of the framework. At many occasions during the thesis, I experienced the presentation of trajectory concepts and metrics to different profiles of ecologists in working groups, conferences or seminars (see the "List of contributions" section). I consequently had the occasion to test and realize the necessary level of information about trajectory analysis and concepts and to see that some missing background information dramatically limit the understanding of the framework. Some scientists or managers may be not familiar with multivariate and/or dynamics analyses, and I think that the exportation of ETA frameworks would be facilitated by training sessions that could be tested as a first step within the programs proposed by the Observatoire du patrimoine naturel littoral or the Agence Bretonne de la Biodiversité. Some other interesting perspectives already appeared such as the analysis on stable isotope dynamics at the scale of the nort-east Atlantic water body, in landscape phytosociology (Géhu, 1979), or in a macrobenthic communities along a network of bay and estuaries along the English Channel and Atlantic coast as part of the the Observatoire du patrimoine naturel littoral coordinated by Reserves Naturelles de France.

4.3 | Reporting ecological status quality

For a long time, biodiversity indices have been privileged for reporting biodiversity ecological states. Scientists and stakeholders desire for a reductionist approach to the assessment of habitat quality have favoured a still ongoing development of biotic indices devoted to synthetize community response to perturbations and ecological quality status (Buckland et al., 2005; Diaz et al., 2004; Labrune et al., 2021; Washington, 1984). A common approach followed by scientists consists in the integration of multivariate data into a single site-specific numeric score that can be interpreted by a non-specialist within a 'good' versus 'bad' continuum, most often in relation with legislative requirement (Diaz et al., 2004). The common advantages of most of these biotic indices is their ability to combine multiple attributes into a single measure allowing the distinction between impacted and non-impacted habitat. In practice, some biotic indices based on a classification of taxa on a scale of sensitivity/tolerance to a defined pressure [*e.g.* M-AMBI (Borja et al., 2008), TDI (de Juan and Demestre, 2012)] have proved to be limited in some situations because the knowledge used for linking the species sensibility to a range of pressure is partial, and their use is limited to a specific type of pressure. In response, indices based on the deviation of the taxonomic composition of tested community with respect to stations of reference offer interesting alternatives (Flåten et al., 2007; Johnson et al., 2008; Labrune et al., 2021). What is an acceptable index? What is a good or bad ecological status? What level of synthesis can satisfy scientist, managers and stakeholders? In aquatic habitats, the high diversity of indices reveals that the unanimity of any specific single metric by managers and scientists remains a complex task (Diaz et al., 2004) for reporting ecological status as part of intergovernmental engagement or European directives .

The adoption of conservation policies by many countries (Convention on Biological Diversity, 2010; UNEP, 2011) has influenced the story of biotic indices as it often requires reporting synthetic information about the quality of the ecological status of biodiversity. For marine habitats, the European Water Framework Directive (WFD, Directive 2000/60/EC) and the Marine Strategy Framework Directive (European MSFD, Directive 2008/56/EC) require that European Member States implement measures to achieve a good environmental status of their water bodies. It requires assessing ecological status of habitats with respect to reference conditions, and claims for a general framework to determine if habitats meet the chosen reference conditions defined as a conservation target.

Benthic macrofauna has been considered a relevant descriptor to characterize the biological status of water bodies by the European WFD (Borja et al., 2012, 2009; Diaz et al., 2004; Labrune et al., 2021), as this compartment influences nutrient cycling, represents an important food resource for higher trophic levels (McLusky and Elliott, 2004; Snelgrove, 1997), and reacts rapidly to disturbances (Claudet and Fraschetti, 2010; Gray, 1997). In the bay of Saint-Brieuc case study, the interest of trajectory metrics coupled with other complementary methods to track for long-term taxonomic and functional changes in benthic habitats has been explored with respect to an initial state defined in 1987 and coupled with a more recent long-term dataset (Rebent) in the subtidal area (Articles III and IV). The ability of the ETA frameworks to provide synthetic metrics and data visualization such as trajectory map and roses, and the definition of qualitative recovering or departing patterns has been demonstrated. This approach could become relevant within WFD and MSFD to assess the ecological distance between current and reference status, by measuring net changes with respect to predefined reference conditions. Such ecological baseline should be defined within an ecological entity (*i.e.* habitat), in unaffected areas or using historical data. In the absence of a local pristine state, or of an ecological state that could be considered as a conservation target, it should be possible to include in the analysis data from similar ecosystems located in the same habitat and region to define a reference state in the multivariate space.

The reference state can be conceptualized, from a set of samples considered as potential conservation targets, by both:
(1) a reference envelope;
(2) its centroid in the multivariate space.
Doing this, the natural variability of healthy habitats defined by all reference stations is integrated and takes a central part in the analysis.

Coupling this concept with Hierarchical Cluster Analysis (HAC) allows separating stations which meet reference conditions from the others, based on the inclusion or the exclusion with respect to a cluster of reference. Technically, I propose to cut the HAC dendrogram at a height which includes all of the stations considered as reference in the analysis. The tested stations included in this cluster can be considered as meeting the chosen condition of reference. Consequently, stations, which do not meet the chosen conditions of reference are grouped in additional clusters that can be used to describe different states, which deviate from reference conditions. Additionally, I propose the calculation of net changes between the centroid of reference and tested stations to complement the inclusion test in the cluster of reference. For instance, in temporal analysis, net change calculations over time, with respect to the reference conditions, may allow the accurate measurement of restoration or degradation processes through recovering or departing trajectories respectively.

This data-driven reference state concept proposed to track for ecological status quality focusing on the deviation of tested stations with respect to a reference state using ETA is very similar to the underlying principles of indices based on the deviation of the taxonomic composition of tested community with respect to a set of stations of reference (Flåten et al., 2007; Johnson et al., 2008; Labrune et al., 2021). Coupling these two approaches needs to be tested to quantify biodiversity targets and contribute to the objectivity of ecological status quality assessments in a repeatable and real-time measurement (*i.e.* after each survey).

As a perspective of this thesis, I propose some potential directions for the use of ETA and biotic indices together for the reporting of ecological quality status as part of the WFD and MSFD European Directives (Figure 44). To illustrate my purpose, I have chosen to consider an index, which is, as the proposed data-driven reference state concept, free from an a priori classification of variables, on the basis of their degree of sensitivity/tolerance to pressure gradients (as AMBI, M-AMBI and all derived indices). Based on a measure of deviation with respect to reference conditions, the recent General-Purpose Biotic Index (GPBI) proposed by Labrune et al. (2021) to measure changes in benthic habitat quality across several pressure gradients, was a pertinent candidate. This conceptual framework implies four phases (Figure 44):
(1) *Inclusion test in the cluster of reference.* Verification if tested stations meet reference conditions.
(2) *Trajectory analysis.* Calculation of the distance metric of each ecological state, within each trajectory, with respect to the reference centroid. Data visualization. Checking links with variables (*e.g.* species).
(3) *Coupling with additional metrics.* Relation between biotic index value and the distance from the reference centroid.
(4) *Synthesis of Ecological Quality Status*. Synthetic symbols used to represent ecological status.

This conceptual framework was tested with the Glenan archipelago data set used by Labrune et al. (2021) for the GPBI index. The inclusion test helps to identify which stations currently meet reference conditions. Interestingly, 6 reference stations where sub-grouped together within the reference clusters, while others where sub-grouped with potentially affected or potentially not affected stations (Figure 45 A). Two main clusters of stations which do not meet the reference conditions were identified with the HCA. This diversity of affected patterns was also highlighted by the trajectory diagram to reference (Figure 45 B). GPBI values and the distance to the centroid of reference were significantly correlated [-0.93, p<0.0001 ;Figure 45 B].

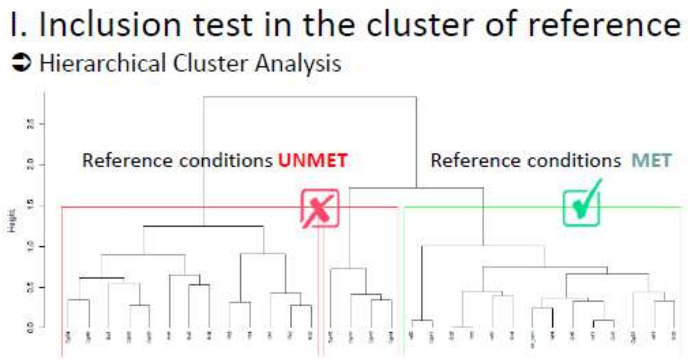
The simulated and Glenan archipelago applications bring interesting insights into the ecological status quality reporting, among with:

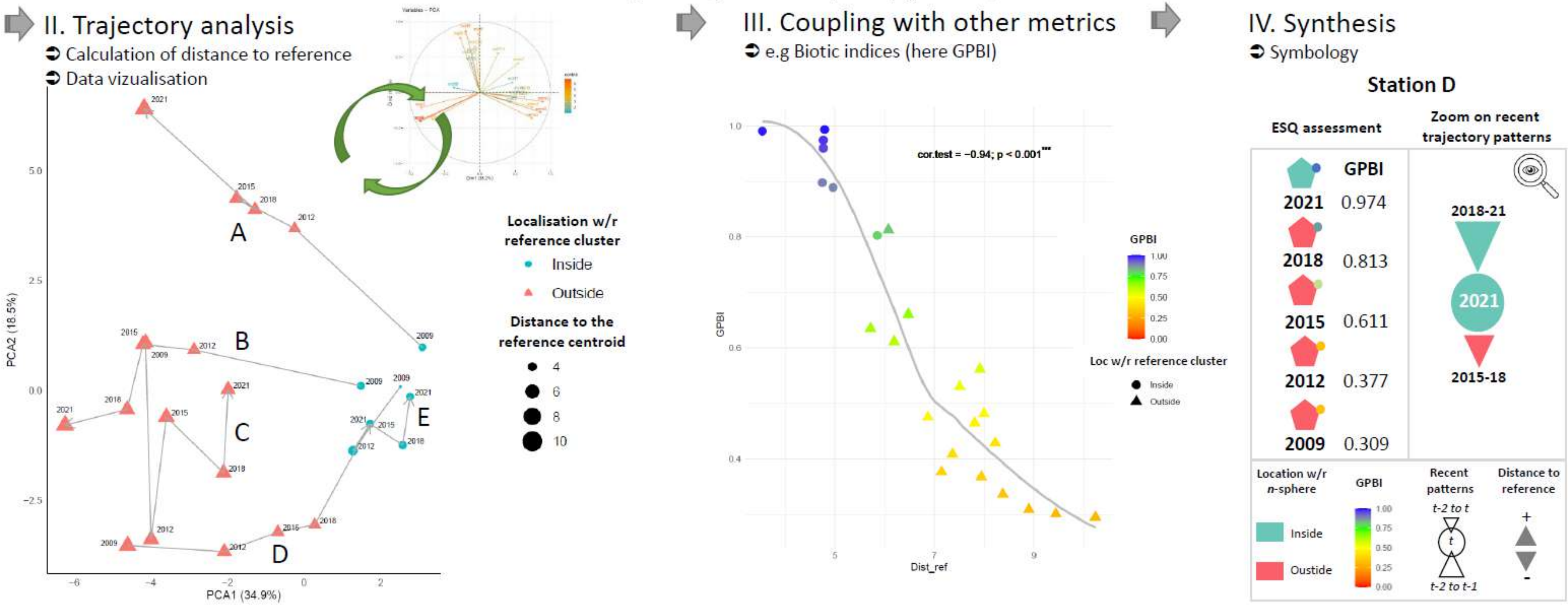
(1) the data-driven repeatable and objective determination of habitat meeting reference conditions, which notably allows discussing reference conditions, based on reference clusters properties;
(2) the complementarity between trajectory analysis and additional metrics, which could help to identify accurately different patterns of quality, relation to pressures, or in the definition of potential quality thresholds for habitats which unmeet reference conditions;
(3) the ability to synthetize and visualize ecological quality status for managers and stakeholders.

The complementarity of ETA and biotic indices claims for further development to secure the concept, explore potential applications, and draw the contour of this data-driven reference state framework. For instance, I used the Ward.D2 clustering method to present the concept, but several HAC methods exist and their ability to support ecological quality status assessment should be evaluated (Thrun and Stier, 2021; Xu and Tian, 2015). The major strength of this approach results in its potential ability to constitute a unique framework for the assessment of ecological quality status based on a variety of data sets including station*species matrices, and functional or any biotic and abiotic monitoring. Ideally, such approach should be tested and validated in different conservation contexts with complementary indices, and transcend the sub-disciplines of ecology.

Overall, I encourage trajectory distance- and direction-based metrics and associated recovering and departing patterns to be quantitatively and qualitatively compared at small and larger scales and to be tested with complementary approaches to report ecological status within European Directives (WFD, MSFD, DHFF), long-term observatories, and restoration ecology. Further works should explore the potentiality of this conceptual framework, including the synthetic proposed symbolism, and its ability to meet the needs and expectations of stakeholders, managers and scientists.

Figure 44: **Reporting ecological status quality of marine benthic habitats in four phases. Simulated data set:** PCA from a simulated Hellinger transformed sites*species matrix including reference samples. Simulation includes 5 sites used as a reference and 5 sites each surveyed in 2009, 2012, 2015, 2018, 2021 describing contrasted patterns of temporal change: A. Degradation mainly due to a decrease in abundance (e.g. sensitive species); B. Degradation due to a decrease and an increase of some species (e.g. sensitive and opportunistic species; C. Site that remained far from the reference state; D. Restoration; E. Site that remained close to the reference state. **Phase I: Inclusion test in the cluster of reference.** Verification if tested stations meet reference conditions. **Phase II: Trajectory analysis.** Calculation of distance metric of each ecological sate, within each trajectory, with respect to the reference centroid. Data vizualisation. Checking links with variables (e.g. species). Color of dots represent the inclusion (green) or the exclusion (red) of tested stations in the cluster of reference. Size of dots represents the distance to the reference centroid calculated for all tested stations in the multivariate space, and shape represents the position with respect to the cluster of reference (triangle: outside; circle: inside). **Phase III:** Calculation of a biotic indice. Relation between biotic indice and the distance from the reference centroid. **Phase IV:** Synthesis of Ecological Quality Status within symbols (e.g. station D).





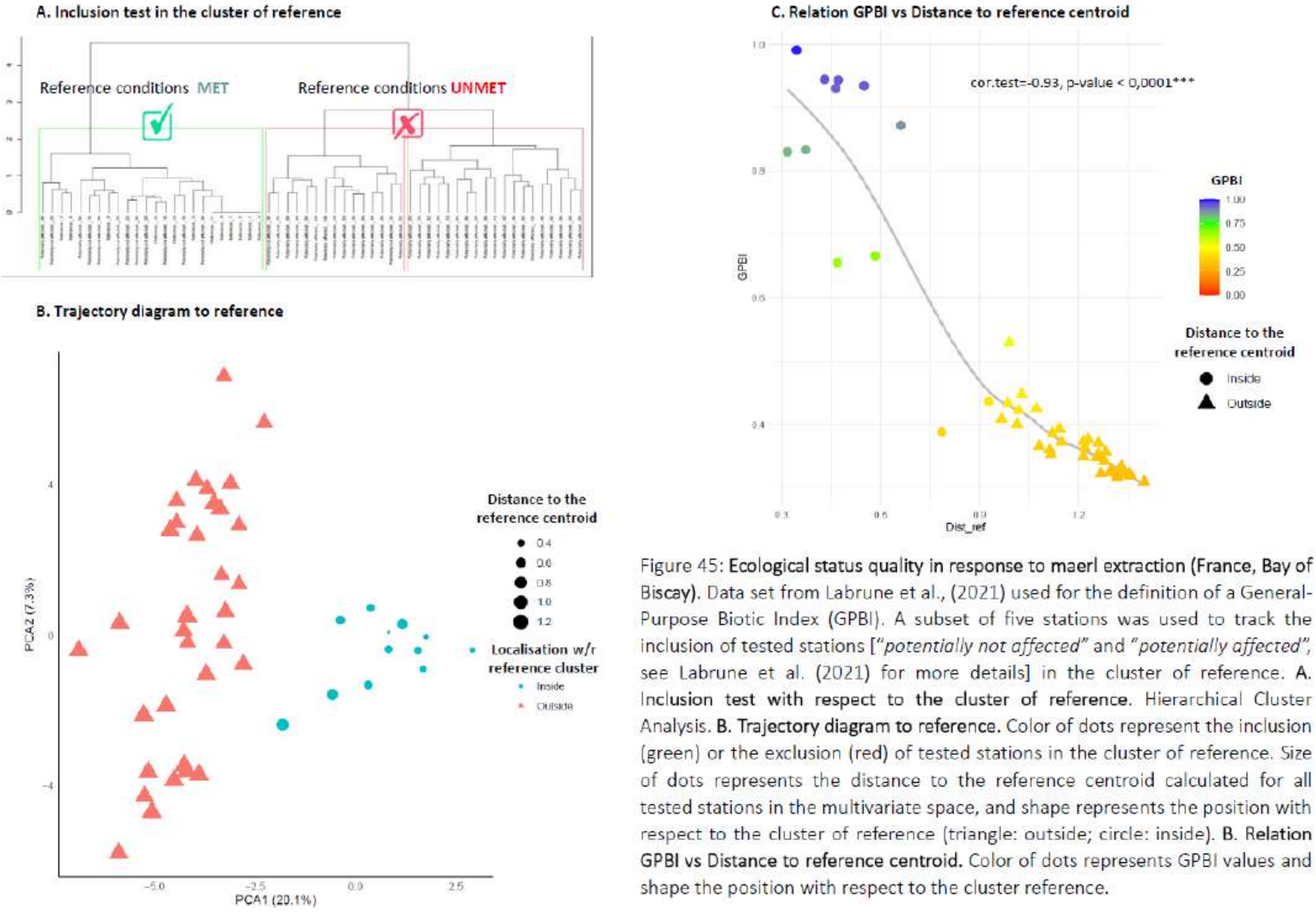


Figure 45: **Ecological status quality in response to maerl extraction (France, Bay of Biscay).** Data set from Labrune et al., (2021) used for the definition of a General-Purpose Biotic Index (GPBI). A subset of five stations was used to track the inclusion of tested stations [*"potentially not affected"* and *"potentially affected"*, see Labrune et al. (2021) for more details] in the cluster of reference. **A. Inclusion test with respect to the cluster of reference.** Hierarchical Cluster Analysis. **B. Trajectory diagram to reference.** Color of dots represent the inclusion (green) or the exclusion (red) of tested stations in the cluster of reference. Size of dots represents the distance to the reference centroid calculated for all tested stations in the multivariate space, and shape represents the position with respect to the cluster of reference (triangle: outside; circle: inside). **B. Relation GPBI vs Distance to reference centroid.** Color of dots represents GPBI values and shape the position with respect to the cluster reference.

4.4 | The crucial need for data at multiple spatial and temporal scales and the necessary challenge of reference states

Long-term records of biological data are valuable for documenting ecosystem changes and for differentiating natural changes from those caused by humans (Wolfe et al., 1987). Global changes and increasing anthropogenic impacts have reinforced the need for long-term monitoring and population dynamics analysis over the last century (Anderson et al., 2021). Even if the development of computer technologies for the accumulation, systematization, and analysis of data opens increasingly broader possibilities of dynamics analysis (Azovsky, 2019; Buckley et al., 2021a, 2021b; Dornelas et al., 2013; Yang, 2020), data remains the necessary basis of such approaches (Stuble et al., 2021). Overall, the potential and the interest of methods focusing on the analysis of ecological temporal dynamics, including ETA frameworks, often increases significantly with the size of the time series, urging for the initiation and the maintenance of long-term monitoring programs in a period of economic constraints that threaten long-term time series even for those that have been long-established (Beukema and Dekker, 2020).

There is virtually no appropriate benchmark data describing natural standards and alterations of most environmental systems concerned by cumulative impacts (Ellis et al., 2000). Like many estuarine and coastal areas, the bay of Saint-Brieuc has been exposed to strong human influence over the last decades. In the bay, the ecological state identified in 1987 and considered as the initial state, was defined under a pressure context already well established [notably nutrient enrichment, macroalgae proliferation, mussel farming, fishing activities, (Figure 43)]. The absence of a pristine reference state constitutes a strong limitation in the analysis of long-term trends (Hardman-Mountford et al., 2005; Rubal et al., 2014; Veiga et al., 2017). Furthermore, my intertidal and subtidal studies suffers from the absence of long-term accurate measurements of environmental factors and anthropogenic pressures, which would allow disentangling natural *vs* anthropogenic changes. Such weakness may be common in natural and/or protected areas where managers have historically prioritized the monitoring of biodiversity, potentially gathering information about pressures whenever available.

This study confirms the value of historical data for marine and coastal management, as well as the importance of maintaining consistent protocols, as underlined by Callaway (2016). Overall, the characteristics of the bay of Saint-Brieuc, and the complementary methods and scales used to analyse the datasets contributed to the research frameworks focused on the definition of changes and impact assessments at spatial and temporal scales in marine ecosystems. However, it also pointed the limitations of sampling strategies that imply only long-term networks. In intertidal habitat, the patterns of changes described were based only on three sampling occasions, which limits the understanding of processes occurring between each surveys, and potentially overshadowing important intermediate changes (*e.g.* occasional dominance by very large numbers from very few species as observed for *D. vittatus*). As suggested by Bacouillard et al. (2020), the coupling of different spatial and temporal scales in sampling strategy [few stations with high frequency sampling (Hewitt et al., 2016) *vs* low frequency larger sampling networks (Kröncke et al., 2011)] could help tracking changes between long-term networks. Bacouillard et al. (2020) propose in the bay of Seine 60 stations sampled every five years to assess long-term changes in the beta diversity (*i.e.* assemblage distributions) and five stations sampled at least once a year to analyse the heterogeneity in the responses of local community to multiple stressors. Such interests of coupling different spatial and temporal scales by the use of two complementary data sets (38 stations in 1987 and 2019, and one station from 2005 to 2019) have been demonstrated in this study. The 15 years time series suggested that changes observed in the subtidal benthic community over the last 30 years occurred probably from 2015. It claims for the local development of an ambitious monitoring strategy in the bay of Saint-Brieuc based on a network of 80 stations (42 + 38 in intertidal and subtidal area respectively) sampled every 10 years coupled with fewer stations sampled once a year in each assemblage and coupled with a monitoring of potential pressures and factors influencing benthic communities.

Assessing current ecological state with respect to reference conditions constitutes a fundamental principle underpinning the conservation, management and restoration of species and habitats. However, choosing 'which state' or 'which baseline' are questions that challenge conservation practitioners (McNellie et al., 2020). In many fields of ecology, long-term monitoring data sets are consequently increasingly compared to reference data sets that should describe benchmarks to be achieved and represent objective conservation targets (Bioret et al., 2009). Such approaches have notably been favoured by the reporting requirements as part of intergovernmental engagements (see section 4.3). It is recognised that historical states are rare and remain often criticisable, as they have potentially been defined in ecosystems under levels of pressure already well established. Even if it is still a complex task, it led conservation practitioners to look alternatively for reference conditions in unaffected, or less affected habitats. For instance, McNellie et al. (2020) propose the complementary concept of contemporary reference states that focuses on current ecological patterns and the definition of reference in areas with higher biodiversity values.

Data-driven reference state proposed in section 4.3 and in some biotic indices implies sampling design requirement underpinning long-term monitoring. Such assumptions have been recently summarised by Labrune et al. (2021):

(1) reference stations should be defined within a same or at least a similar ecological entity;

(2) a set of reference stations is preferable that one station as it allows for the definition of a reference state that integrate variability;

(3) even if they do not represent an optimum, historical data may represent an alternative in the absence of reference stations;

(4) shifting-baselines claims for a synchronous monitoring of both potential reference and tested stations over longer time periods to disentangle natural from anthropogenic drivers.

Such requirements implies that stakeholders:

(1) display a real financial ambition to favour researches and monitoring focusing on reference states allowing for instance sampling design specifically devoted to this task;

(2) provide regulations that allow ecosystems to exhibit healthier states. The use of the MPAs network or management project that may be lead to the potential exclusion of some factors of disturbances (*e.g.* wind farms in marine habitat) must be optimised, and such aim should contribute to their definition in the future.

Hopefully, such assumptions will also be considered in the designation of strong protection area as part of the national strategy of protected area (Comité Français de l’UICN, 2021).

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This thesis is by far among the most beautiful social and intellectual experiences in my personal and professional life. A lot of work has been done during these last three years, and before, to build the ResTroph Baie de Saint-Brieuc research program. There have been some difficult moments, sometimes confounding the light at the other end of the tunnel with an oncoming semi-trailer! In every new difficulties, the caring and competent people involved in the thesis, and in my personal environment, was an essential ingredient to keep confident and willing to surpass myself. Ok, my name is written on the thesis front page, but this work is the fruit of an amazing collective effort (Figure 46) by great people! I assume the size of this section, because one should never forget to say "thank you" properly. Each acknowledgment, comment or wink should be considered regardless of its order of appearance. Sorry in advance, if one does not recognise him/herself in this section despite the care I have taken in it. Do not hesitate, just tell me and I would modify the section.

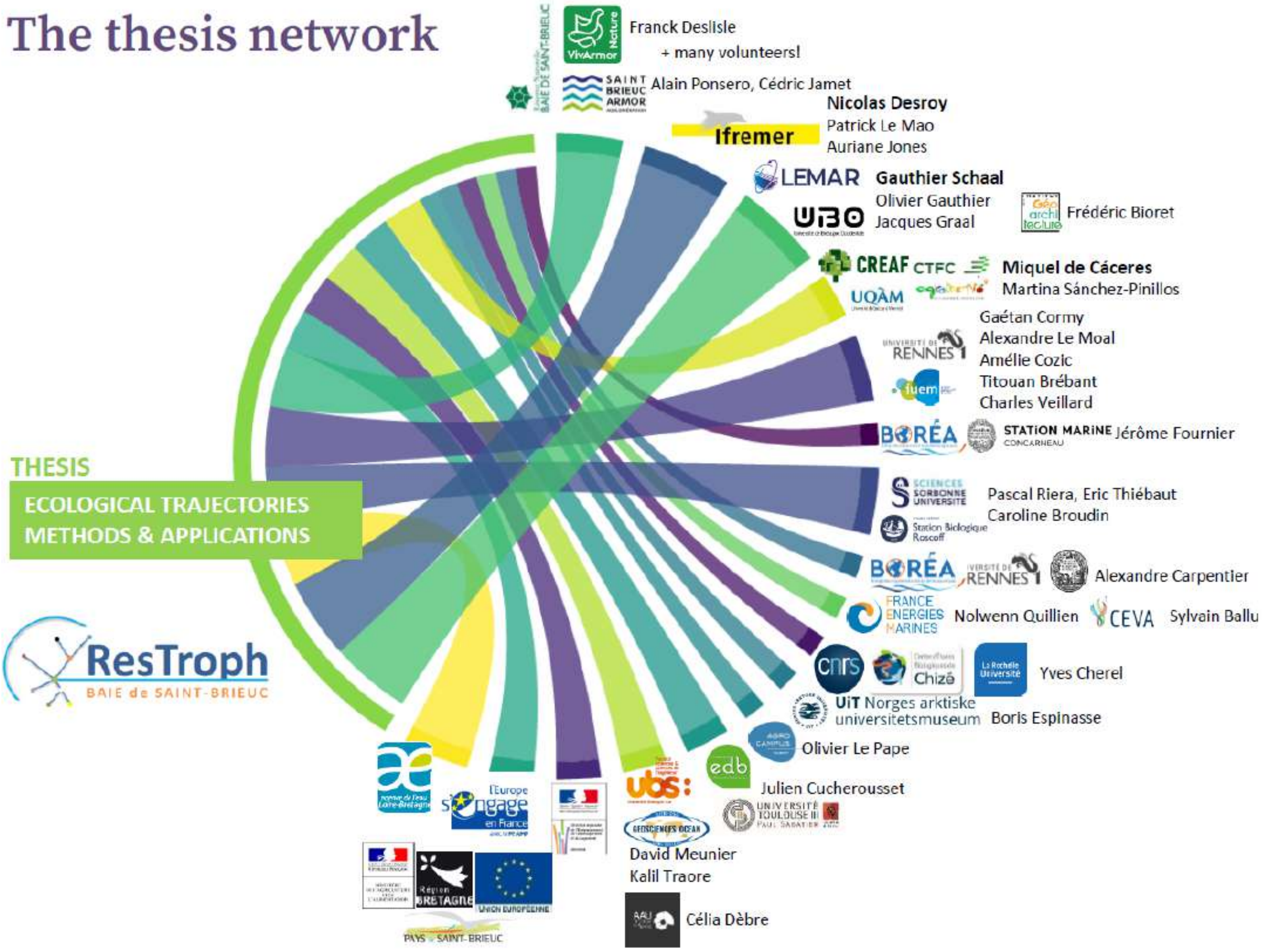

Figure 46: The thesis network has increased during the project and constitutes one of its main strengths

I want to thank, Didier and Jérémy, and Hervé and Franck, respectively and successively Presidents and Directors of VivArmor Nature, my employer. Even if it was not an obvious decision to take at the beginning of the project, thank you for having allowed me to realize the thesis as part of my job and the ResTroph research program. Didier, I know this resonates special for you and echoes your personal story. Jeremy you left before the final harvesting but I know you have kept interest in the project. Hervé, you believe in my work, and I know you will be determinant in the work that is awaiting, for sharing the updated knowledge and trying to improve the conservation of the bay. Franck, thanks for driving me into the financial and administrative coordination of ResTroph, your trust, your enthusiasm and your video editing skills. Overall, thanks to all the administrators and the team: we are sailing on a marvellous boat!

No money, no project, but, the relation with ResTroph funders is much more than pecuniary. From the beginning, teams involved at Agence de l'Eau Loire Bretagne, Direction Régionale de l'Environnement, de l'Aménagement et du Logement de Bretagne, le Pays de Saint-Brieuc (instruction supporting), Région Bretagne, Europe (Fonds FEAMP) trust in making the thesis a central part of the ResTroph program. Later, they maintained their trust, even when the work went temporarily far from local ecological questions to come back better in the bay. Behind these organisms' names, there are passionate people, notably, Hubert, Régis, Anne-Lise, Yannick and Justine. Thank you for your involvement in the project, your trust, and the interesting conversations about the link between science and management. Be proud of the funded work, your contribution was important.

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I had also the pleasure to count a third SUPERvisor in the team since 2020. Miquel, it was also a privilege to work at your side. I have just reread the first mail (of the list!) I have sent to you on the 15th of april 2020, and the answer you quickly made to me. A little backtracking: taking the best of the first COVID lockdown, I was wondering about the patterns of change in the bay of Saint-Brieuc looking for recovering and departing patterns, and spatial patterns in the magnitude of changes. The concept of, later named, net changes, net change ratio, angles ω and α, trajectory map, and roses were developed during this phase using trigonometry in the first two dimensions of multivariate ordinations. I was aware of the interest of such "homemade" approach, but also of its limitations, which mainly lied in the fact that additional dimensions were not considered. When Olivier Gauthier told me about you and the CTA framework (such an advice!), I immediately understood the strong potential of CTA and its ability to overcome the difficulties encountered. From that moment, you have played a central part in the thesis. I also particularly appreciate your special shot: generalization spirit. Miquel, me gustaría agradecerle que se haya interesado por mi trabajo, aunque sus comienzos hayan sido a menudo torpes. Me tendiste la mano para que pudiéramos trabajar juntos en el análisis de las trayectorias ecológicas, con nuestras respectivas competencias, sin juzgarme. Nunca lo olvidaré. Gracias especialmente por tu forma amable de señalar las cosas que hay que mejorar, por todas las nuevas habilidades que me has ayudado a adquirir, por tu capacidad de respuesta y, sobre todo, por abrirme las puertas del Community Trajectory Analysis framework.

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In our disciplines in ecology, Science begins on the field! I would like to thank all the people involves in field sampling. In the intertidal between the 19 and 22 of February 2019, under a bright sun: Alain, Annaig, Audrey, Cédric, Chloé, Daniel, Didier, Domnique, Elouan, Florence, Gauthier, Hervé, Jean-Pierre, Jessica, Justine, Leonie, Maëlan, Marc, Marie-France, Michel, Nicolas, Nicole, Patrick, Philippe. I thanks all of the Pommerit BTS GPN students, who came in the bay to sample *Arenicola marina* densities by counting worm casts. Also a huge thank you to the Thalia's crew: Arnaud, Franck, Régis, Alban, Antoine, Fabrice, François, Dominique and Christophe, for the two campaigns in March and September 2019.

Pascal, your involvement in the thesis followed a strong linear progression! Counting you at my side, especially during the last year for the SITA paper, food web analysis and the redaction of the manuscript was very important for me. Special thanks for you pedagogy and all the knowledge about food web analysis you shared with me.

Patrick, I was so happy that you could participate to the first phases of my thesis, and to board with you on the Thalia. I cannot limit my acknowledgements to the thesis, you have been so inspiring for me since I integrated the nature reserve team in 2009. The nature reserve can count on a great president for its scientific council and it is always a privilege to decide the menu together! Three great memories: tasting "Langouilles" with Daniel during a salt marsh fishing session, your enthusiasm when you where among the first with whom I shared the concepts of trajectory maps and roses, and of course this moment of sharing and gastronomy whit Daniel on a beautiful summer day at home in June 2021!

Fred and Jérôme, even if it has not been possible to achieve a concrete collaboration as part of the thesis, we had the occasion to discuss the potentiality of trajectory analyses in landscape phytosociology, restoration ecology, and sedimentary analysis. Fred, you gave me my first professional experiences, travelling through Corsica, Baleares and Brittany. You taught me the passion of hard working with pragmatic aims, and not to be afraid when tackling new areas of work. In this sense, you gave me some formidable tools to consider the thesis with confidence and serenity. Thanks for all of that! Jérôme, since we first met and from our first collaborations at the nature reserve, you were among people who makes me feel as a colleague, as a "real" scientific, whatever my educational path or my manager status, with no judgment. I often eared you saying "There is no little research". That is (f……) true! I also remember sharing with you my desire to realize a thesis, long before the ResTroph research program, and you said me that it was a good idea (but with a true subject!), and were ok to help and guide me in this adventure. Even if I am sometime nostalgic of past collaborations, I currently know that if I ask you, you will respond present, and that’s no small thing!

Olivier (Gauthier), I remember your interest when I did present to you my first attempt in the analysis of ecological changes in the bay through trajectory maps and roses. Among other advices, you immediately made the link with the CTA framework and it allows me integrating my thesis in greater dimensions, and saving a lot of time. Huge thanks for that. I am aware that your time is limited and that your integration in the ResTroph team was not planned. I hope we will find more time to collaborate in the future.

Olivier (Le Pape), I remember your critical look when I did present to you my first attempts in the analysis of ecological changes in the bay through trajectory maps and roses. Obviously, it did not look like it does today. Thank you for having pointed out the limitations of the approach. It has been important for its improvement. Our collaboration in the ResTroph program about the fish community just begins, and I am confident in the fact that it will lead to interesting works.

Alexandre (Carpentier), you have been invested in the second part of the thesis concerning SITA and food web analysis. Your are part of these researchers with whom managers could work without feeling judged, in a common aim of knowledge updating, understanding of ecological processes and management perspectives. Since you have integrated the scientific council of the nature reserve, it has been a pleasure to work with you in a caring environment, and I must confess that I am eager in the perspective to work together on the analysis of the fish community. Be ready, we will start in the end of December / early January!

Anick and Hervé, you were the external researcher of my thesis comity. Thanks to have accepted this task. I have appreciated your involvement very much in each of the three sessions! A particular thanks for the kind kicks, facing the amount of work, the diversity of track explored, and the need to make some choices. Sincere thanks for that!

I had the pleasure to work with a variety and a diversity of researchers during these three years, who have contribute to make this thesis an amazing training in the strict sense. It was unexpected initially, and I even did not know some of them before March 2021. Their contributions in my works were determinant, placed under the sign of SHARING in its noblest sense. Martina, has respondido con mucho entusiasmo a mi invitación en el artículo de ampliación de la CTA. Ha puesto sus conocimientos de análisis de trayectorias y su conjunto de datos sobre las respuestas de los bosques canadienses a los brotes de insectos al servicio de este proyecto. Muchas gracias, espero que sigamos en contacto para futuras colaboraciones. Aurianne, I have asked you in emergency for an english polish on a paper. You have accepted and you did more, questioning the work. Thanks! Eric and Caroline, thanks to bring the station R data set in the subtidal analysis. It was determinant for the proper understanding of the taxonomic and functional dynamics of this area. Eric, I thank you more particularly for you reactivity and the time you put on each of my request, not only on the subtidal article, but until the end for the perspectives of this thesis. Thank you for that, your advices, and for always finding kind and proper manner to highlight what is not working or should be improved. Julien, Yves, Boris, Nolwenn and Jacques you were on board for the SITA article. It was a pleasure to work with you on this project. Playing with your amazing data sets using the SITA framework brings interesting insights. It have been a marvelous travelling recreation. Be aware that your datasets also inspired the framework in return. Julien, thanks for your trust, the orientation and the validation of the approach and for your answer and advices always in time. We told you with Gauthier that it will be a flash paper, but you have not taken the measure of it immediately! Do you? Yves, it has been special and unexpected to work on fur seal whiskers raw data! No doubt that your reactivity and your accurate reviews of the article have contributed to its fast acceptance. The offer for a private visit of the nature reserve is still on the table! Boris, I have found the pacific data sets surfing on the net. My first thought was that it has been perfectly created for what we were planning for it. I remember my feeling when I discovered it: We need this one! You said ok to board in the adventure in something like three hours, unbelievable. The pacific data sets was perfect to illustrate the isoscape trajectory map concept, and has inspired the trajectory heat map one. Thanks for this collaboration and eager for the next one! Nolwenn and Jacques thanks for sharing the green tides data set, a subject that all the more resonate several time in the manuscript, not only in the SITA article. May be we can do more, if you think so do not hesitate. Nolwenn, as I have already told to you, your manuscript has inspired me a lot and stayed a long time on my desk from the time I have started thinking about the final redaction. Thank you for that!

The SITA framework was also an opportunity for a conference presentation at ISOECOL 2021. Margaux, as part of the conference staff, you supported our presentation proposal with a great enthusiasm! Many thanks for that. A bit sad about the inevitable online format of the conference, I have decided to make it an advantage and to take the best of the video opportunity. In this task, I thanks all the landscape and naturalist film-makers, which shared their image with us to make a beautiful presentation: Yannick, Ian, Marie and Fabien, Francine and Eric, Anne Cécile and Thierry. Special thanks to you Yannick: sharing this coffee break discussing on life, and observing as happy you were helping me and sharing your videos was a very great moment. Franck, thanks again for you help for editing the video.

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Servane, I was aware than discussing about fishing pressure was a very sensible topic and that it is, for the moment, not possible to access long-term raw data. Despite this, our exchanges have always been constructive and I want to thank you for that.

Alexandre (Robert) and Aurélien, I would like to thank you for your interest in my work and the perspectives you are sharing in its potential ability for the reporting of ecological quality status as part of the MSFD. I think there is a gap to bridge, and it will be a pleasure to work on that with you in order to contribute to the pragmatic ecological quality status reporting. Thanks again, be ready, we will start working on that from January 2022.

Maud, it was important for me to share my work with managers and colleagues of the nature reserves from Brittany. You have significantly favoured its diffusion in the Réseau des gestionnaires d'espaces naturels Bretons as part of the Agence Bretonne de la Biodiversité. Thank you for that, and for your encouragements.

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Celia, I am eager to work on that with you in 2022!

Other students currently work in the bay of Saint-Brieuc in complementary topics: Agathe, Marion, and Arianne in human and social science and Kalil in marine geophysics and coastal geomorphology. Thanks for our exchanges. I am convinced that further crossings of our approaches may bring interesting insights for the future of the Bay.
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Reviewer 2, you have generally very bad press in social media and your are often associated with strong comments strongly questioning works and claiming for deep restructuring, when not simply rejecting! Note that I have been so happy to read your enthusiasm and your comment about the SITA framework. Many thanks for that, it was the best review ever!

Gilles, there is no much poetry in this thesis while the bay is full of it! No doubt that we will have time to discuss on it properly. You taught me your true love for the bay, which makes you hurt deep in you heart when the bay is injured. Thank you for that my friend, and also for your childlike eyes.

Anne-Sophie, it is a bit improbable to find you here! Thank you for your graphic advice.

I also thanks my parents, my sister, Tony, Mathilde and Alizé, for their love and their support. Dad and mum you have always trusted in me during my educational pathway. It have largely contributed to what I have been able to do here. After thinking for a long time that I was a forest ranger, your find an easy way to describe my job in the bay of Saint-Brieuc. Sorry, things may have just gotten a little more complicated, but we can work on that!

Michel, my fantastic adoptive grandfather, from where you are looking at me, I know you are proud of me. My job and my love for nature is just the perfect continuity of your sweet woodland education that have encompassed so much. Thanks for all you gave to me, and for being still at my side at many occasions.

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Extending community trajectory analysis: New metrics and representation

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ABSTRACT

Ecological research focuses on the spatio-temporal patterns of ecosystems and communities. The recently proposed framework of Community Trajectory Analysis considers community dynamics as trajectories in a chosen space of community resemblance and utilizes geometrical properties of trajectories to compare and analyse temporal changes. Here, we extend the initial framework, which focused on consecutive trajectory segments, by considering additional metrics with respect to initial or baseline states. Addressing questions about community dynamics and more generally temporal and spatial ecological variability requires synthetic and efficient modes of representation. Hence, we propose a set of innovative maps, charts and trajectory roses to represent trajectory properties and complement the panel of traditional modes of representation used in community ecology. We use four case studies to highlight the complementarity and the ability of the new metrics and innovative figures to illustrate ecological trajectories and to facilitate their interpretation. Finally, we encourage ecologists skilled in multivariate analysis to integrate CTA into their toolbox in order to quantitatively evaluate spatio-temporal changes.

1. Introduction

Ecology aims to identify processes underlying the distribution and abundance of organisms, along with those that determine how organisms modify their abiotic environment (Kendall, 2015). Two paradigms are widely accepted amongst ecologists: (1) biological assemblages are amongst the best response variable to estimate the impact of changes in natural ecosystems and (2) temporal changes in community assemblages indicate that some processes have been at work to generate them (Legendre and Gauthier, 2014). Temporal changes in biological assemblages are the sum of local colonisation and extinction events, as well as changes in the biomass and relative abundance of taxa within and amongst samples (Buckley et al., 2018). Quantifying and forecasting temporal changes in biodiversity and ecological shifts due to both natural and anthropogenic drivers is therefore a central issue in ecology (Dornelas et al., 2013). This requires repeatedly sampling target communities over time and, often, studying their evolution compared to an initial state and/or a chosen baseline (goal defined as an ecological state to be achieved (Bioret et al., 2009)). To this aim, consecutive ecological states are defined by a set of environmental or biological parameters used as descriptors of the ecosystem existing on a given location, at a given time (chemical and physical parameters, absolute or relative abundance of population species, specific richness, pollution level…). In a period of dramatic increase of anthropogenic impacts, such approaches are particularly relevant for studying natural variability, and have potential implications in management and ecological restoration or in the development of ecological indicators.

The development of community ecology has historically been influenced by static depictions of inherently dynamic processes which led to many important insights about the structure of communities (Yang, 2020). Analytical and representation methods of biodiversity changes over time constitute an essential and important domain of innovation

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(Cimon and Cusson, 2018; Magurran et al., 2019) to study dynamics of natural systems since the beginning of community ecology (Elton, 1927). Accordingly, Yang (2020) suggests specific and complementary ways to continue building towards a more temporally explicit framework for community ecology, notably, by increasing the representation of temporal changes and developing specific and general insights into event -or factor- driven dynamics. In this way, complementary metrics are needed to document community and environmental changes (Cimon and Cusson, 2018). While the availability of long-term, large-scale, and high-resolution data is the most limiting factor to study temporal patterns in biodiversity (Dornelas et al., 2013), the development of methodological approaches to analyse, synthesize, and ultimately represent the dynamics of ecological systems is also an essential issue.

Until now, most analytical and representation frameworks have been based on the comparison of synchronous observations across sites and between repeated surveys (M. De Cáceres et al., 2019). One common approach is to analyse independently the changes observed between two surveys and to repeat this step as many times as necessary to cover the corresponding study period. However, this type of procedure quickly becomes inefficient as the number of samples increases. A potential solution to deal with long-term data sets could be to discard intermediate surveys and to focus only on starting and ending time points of a study period. However, this may hide crucial changes occurring during intermediate periods (i.e. transitional states) and, hence its usefulness to study the dynamics of ecological systems may be limited.

Multivariate analyses have been widely adopted for many decades in ecology, embracing all forms of statistical analyses applied to data in which more than one character are observed per individual (Kendall, 1958). Several multivariate statistical frameworks focus on testing hypotheses of community dynamics (Buckley et al., 2018). Consequently, multivariate frameworks still constitute the primary approach to analyse ecological datasets and an important source of methodological innovations. A common approach is the calculation of dissimilarity indices, which allows differences between a pair of ecological states to be summarized in a single metric. Since community data tables can represent both temporal and spatial variation of ecological states, the resulting symmetric dissimilarity matrices can contain spatial, temporal or spatio-temporal information. Then, the use of ecological trajectories in a multivariate space defined by the calculation of a dissimilarity index between all pairs of observations allows to representing the dynamics of a system. Ordination methods are therefore often complemented with trajectory analyses, in which changes over time or as a response to natural or anthropogenic pressures are represented by a set of vectors linking consecutive ecological states. These approaches have been previously applied to a wide variety of ecological systems, including plant assemblages (Austin, 1977; Fukami et al., 2005), bird assemblages (Hudson and Bouwman, 2007; Sica et al., 2018; Haig et al., 2019), and aquatic (Matthews et al., 2013; Mathers et al., 2016; Boit and Spencer, 2019; David et al., 2020) or marine ecosystems (Dauvin and Ibanez, 1987; Smith et al., 2010; Legendre and Salvat, 2015; Cimon and Cusson, 2018). In this context, geometric properties of trajectories, defined in the space of an ordination diagram, constitute relevant parameters to study the dynamics of ecological systems, including intermediate transitional states. The geometric study of community trajectories has sometimes been defined by two or three axes of an ordination space (Boit and Spencer, 2019; Matthews et al., 2013) but this has the drawback of discarding the information contained in additional dimensions. In order to generalize this approach, M. De Cáceres et al. (2019) considered community dynamics as trajectories in a chosen space of community resemblance, with no limit in the number of dimensions included. In the Community Trajectory Analysis (CTA) framework, trajectories are considered as objects composed of trajectory segments to be analysed and compared using their metrics based on their geometry in a multivariate space.

In 2D multivariate ordinations, accounting for fine-scale variability hinders readability especially when the number of sites and/or surveys is high, even if different line formats and colours are used to facilitate the identification of different trajectories. A common approach to represent the amount of change across space between two surveys (t_1 and t_2) is to produce a single map (i.e. a plot on geographical axes) in which, for instance, the symbol size is proportional to the distance between states (x_1 and x_2 for each sampling unit) (Bacouillard et al., 2020; Kröncke et al., 2011). However, with this method, the addition of one more survey involves the production of two more maps to represent changes between t_2 and t_3 states and the overall change between t_1 and t_3 after the last survey. For three ecological surveys, this method is still doable, but it fails to represent simultaneously all ecological trajectory segments and, more importantly, information about ecological directions. Although mapping diversity or similarity indices are fused in many ecological studies (Granger et al., 2015), mapping temporal changes through symbols representing trajectory metrics, rather than the dissimilarity between consecutive surveys, has not yet been sufficiently explored in our opinion. Considering the direction of ecosystem dynamics, circular statistics (analysis of directions ranging from 0 to 360°(Batschelet, 1981)), which are commonly used in behavioural ecology, appear as promising alternatives to quantitatively represent the direction of dynamics of ecological systems, and to complement traditional modes of representation. In this perspective, circular statistics may offer significant insights to represent trajectory properties, that are not evident from qualitative comparisons of ordination diagrams, as suggested for food webs by Schmidt et al. (2007).

In this paper, we propose an extension of the CTA framework to represent temporal changes between more than two temporal surveys with respect to a chosen baseline state. As initially defined in M. De Cáceres et al. (2019), CTA was focused on the study of ecological states corresponding to consecutive surveys. A complementary overarching question being to know how ecological states change with respect to an initial state and/or to a baseline, an alternative way to analyse trajectories can be developped, considering these fixed ecological states as central in the analysis. As CTA allows calculating lengths, angles between trajectory segments and directionality of trajectories, it is likely to be a complementary framework to approaches comparing data to initial state based on distances or distance sequences (Bacouillard et al., 2020; Bagchi et al., 2017; Legendre, 2019; Legendre and Salvat, 2015), differences in cluster classification (Kröncke et al., 2011) or shifts along multivariate axes (McLean et al., 2019).

The main contributions of this article concern: (1) the extension of CTA with new metrics that describe community trajectories with respect to a chosen state and new ways of defining angles, (2) the synthetic representation of trajectories through three innovative figure concepts: (a) map of changes between ecological states including information about recovering and departing dynamics with respect to a baseline or initial state, (b) a chart of trajectories from initial state to represent trajectory paths and overall changes, (c) trajectory rose to summarise, in a circular framework, the direction and length of ecological trajectories. Four case studies are then developed to illustrate the use of our proposed metrics and representation tools. Finally, their potential applications and limitations are discussed.

2. Methods

The methods detailed in the following subsections are based on trigonometrical properties of trajectories in n-dimensional spaces and their representation in innovative synthetic figures.

2.1. Characterizing ecological trajectories

2.1.1. CTA framework

We follow here the terminology of De Cáceres et al. (2019), for describing and comparing community trajectories in a multidimensional space. Given a target community whose dynamics are surveyed, let o_1,

o_2, …, o_n be an ordered set of n observations ($n > 1$) and t_1, t_2, …, t_n the corresponding set of ordered survey times (i.e. $t_1 < t_2 < \ldots < t_n$) (Fig. 1, A). For all i in {1, 2, …, n}, x_i contains the coordinates, or ecological state, corresponding to o_i in a multidimensional space Ω. The geometry of the trajectory T is formalized using a set of $n - 1$ directed segments $\{s_1, \ldots, s_{n\text{-}1}\}$, where $s_i = \{x_i, x_{i+1}\}$ is a segment with endpoints (community states) x_i and x_{i+1} (Fig. 1, A).

The multivariate space Ω supporting CTA is defined by the choice of dissimilarity coefficients (e.g. Bray-Curtis), which is used to evaluate resemblance between pairs of community observations (Legendre and De Cáceres, 2013; M. De Cáceres et al., 2019). Note that users can choose the scale of CTA by setting the scale at which communities are defined. For example, community trajectories may be studied at the site level, or at larger scales (e.g. landscape or regional level) if community data are aggregated across sites.

2.1.2. *Trajectory metrics*

Original CTA metrics relevant for this paper are first introduced (Section 2.1.2.1) and new contributions are detailed from Section 2.1.2.2.

2.1.2.1. Original CTA metrics. The *trajectory segment length* is the distance between two consecutive ecological states (De Cáceres et al., 2019). The greater the length of a trajectory segment, the greater the distance between ecological states is. The length of a segment s_i is given by the distance between its two endpoints in space Ω (Fig. 1, A): $L(s_i)=d$

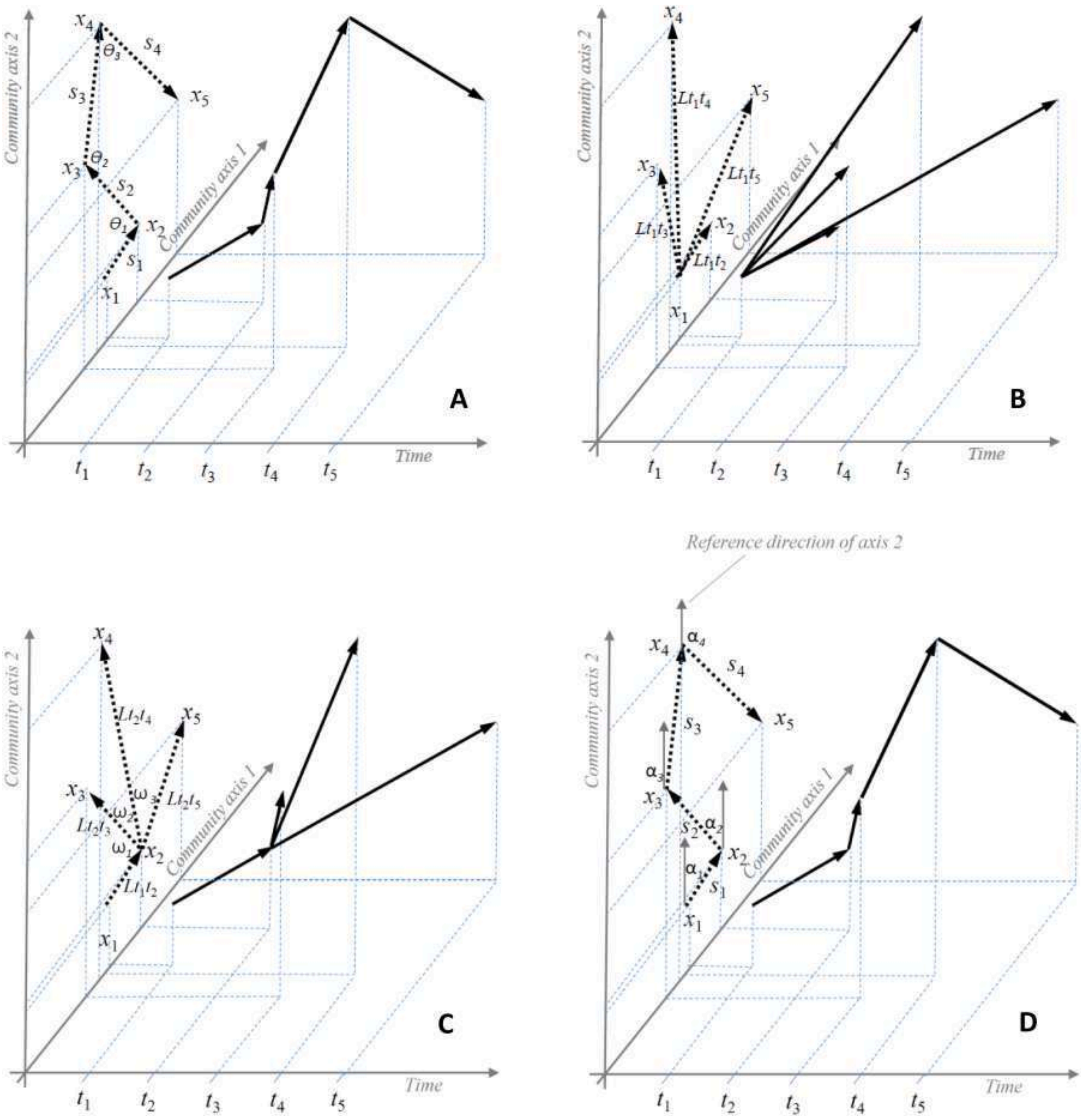

Fig. 1. Example of an ecological state trajectory T from five observations (o_1, …, o_5) at five ordered points in time (t_1, …, t_5). Ecological state observations are represented using a corresponding set of states (x_1, …, x_5) in a multidimensional space (two principal axes are shown only). The trajectory is represented on the plane formed by community axes and in a three dimensional plot including the time axis (continuous arrows). The trajectory can be also formalized in terms of four directed consecutive segments (s_1, …, s_4) in the same space (A). x_i represents positions (coordinates) and s_i are segments, so that the sum of consecutive segment lengths is the total length of the trajectory pathway. One can also consider vectors with respect to the initial state (B,C) with four vectors departing from x_1 (x_1x_2, …, x_1-x_5). Lengths Lt1ti measure the net change between t_1 and t_i (B). Several spherical angles ($\measuredangle$) can be considered, with different interpretation: $\measuredangle\ \Theta\ (x_i, x_j, x_k)$ is calculated between consecutive segments and defined as the change in direction of vector x_j-x_k with respect to vector x_i-x_j in this plane (A); $\measuredangle\ \omega\ (x_1, x_i, x_j)$ is calculated with respect to the initial state and defined as the change in direction of vector x_1-x_i with respect to vector x_i-x_j in this plane(C); $\measuredangle\ \alpha$ is calculated between each trajectory segment and a chosen direction (here axis 2) in a 2D multivariate space (D).

(x_i,x_{i+1}). The *trajectory path length* (De Cáceres et al., 2019) is the total length of all site trajectory segments over surveys of a study period. This metric contributes to informing about the overall temporal variation of the state of a site within a study period:

$$L(T) = \sum_{i=1}^{n-1} L(si) = \sum_{i=1}^{n-1} d(xi, xi+1)$$

Lengths of segments (or subtrajectories) are influenced by the time interval between surveys. Hence, lengths alone do not allow proper consideration of ecological dynamics (i.e. the speed of change). To this aim, a better alternative is to consider *trajectory speeds,* after dividing lengths by the time interval between observations $S(s_i) = L(s_i)/(t_{i+1}\text{-}t_i)$.

Another aspect of community dynamics is approached by the calculation of *angles* (De Cáceres et al., 2019). Let {x_i, x_j, x_k} be a triplet of ecological states of a trajectory *T* that are ordered in time (i.e. where $t_i < t_j < t_k$). If the set of distances {$d(x_i, x_j)$, $d(x_i, x_k)$, $d(x_j, x_k)$} fulfills the triangle inequality, then angles can be measured on the Euclidean plane that contains these three states (Fig. 1, A). The angle $0 \leq \Theta\ (x_i, x_j, x_k) \leq 180°$ is defined as the change in direction of vector x_j -x_k with respect to vector x_i - x_j in this plane. The trajectory is linear when $\Theta_i = 0°$ If $\Theta_i = 180°$, trajectory is still linear but opposite in sense.

Finally, the overall *directionality* of trajectories provides information about the consistency with which the site is following the same direction and, therefore, the stability of the drivers of ecological dynamics that condition ecological states. The directionality statistic (De Cáceres et al., 2019) of a trajectory is measured using the following:

$$DIR(T) = \frac{\sum Wijk^* \left(\frac{180-\theta ijk}{180}\right)}{\sum Wijk}$$

where $\Theta_{ijk} = \Theta(x_i, x_j, x_k)$, $w_{ijk} = d(x_i, x_j) + d(x_j, x_k)$ and summation is over all *r* time-ordered triplets. *DIR(T)* is bounded between 0 and 1 where the maximum value corresponds to a straight trajectory. This metric is useful to distinguish between communities subjected to stabilizing (non-directional) selection from those influenced by directional or disruptive selections (Lamothe et al., 2019; Matthews et al., 2013).

2.1.2.2. *Trajectory analysis with respect to an initial state.*

Net change (Lt_1-t_j) - Let x_1 be an initial (or baseline) state. The *net change* is defined for any pair of states {x_1, x_j} as the length (i.e. distance) $Lt_1\text{-}t_j = d(x_1, x_j)$ between x_1 and x_j (Fig. 1, B). When calculated at the scale of an overall study period between x_1 and $x_{n\ survey}$, this metric evaluates the difference between the community at the end of the study period and its initial state (*overall net trajectory change*).

Net change ratio (NCR) – The net change ratio is defined as the ratio between the overall net trajectory change and the trajectory path length: *NCR* = $Lt_1\text{-}t_{n\ survey}$ / *L(T)*. NCR informs about the straightness of recovering or departing processes with respect to the initial state.

A high NCR indicates that a great part of the trajectory path contributes to net changes and illustrate a relative stability of drivers of ecological dynamics. Inversely, a low NCR coupled with high segment lengths illustrates instability of drivers of ecological dynamics and highlights that a small part of the trajectory path contributes to net changes. In this sense, NCR and DIR(T) are complementary metrics. High DIR(T) would be equal to High NCR but, a low DIR(T) may not be equal to low NCR depending on segment lengths.

Recovering or Departing Trajectory (RDT) - Let us now consider a {x_1, x_j, x_k} triplet where the first element corresponds to the baseline state ($t_1 < t_j < t_k$). The net change of the {x_1, x_j} pair, $Lt_1\text{-}t_j = d(x_1, x_j)$, and the net change of the {x_1, x_k} pair, $Lt_1\text{-}t_k = d(x_1, x_k)$, can be used to qualify the

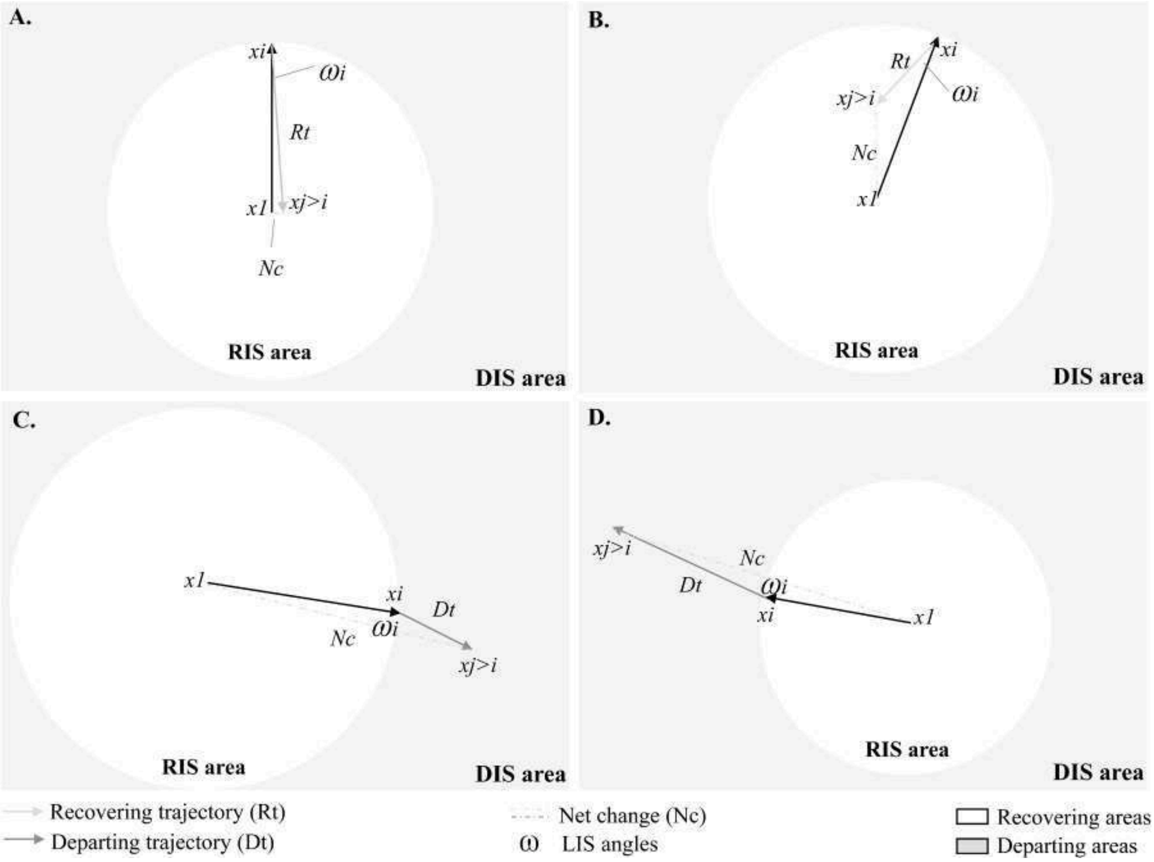

Fig. 2. Different *scenarii* (A, B, C and D) of lengths and ∡ ω induce recovering (*Rt*) or departing (*Dt*) trajectories from x_i. In a 2D multivariate space, the recovering area (RIS, white) is conceptually defined by a circle with centre x_1 and diameter 2 Lt_1-t_i, the rest of the space being considered as the departing area (DIS, grey). Angles (LIS) and lengths both contribute to net changes. Only two dimensions are shown. In a n-dimensional space, RIS area become an hyper-sphere.

dynamics with respect to the initial state as *recovering* (i.e. return to the initial state) or *departing* (i.e. increasing distance from the initial state). Let us define *RDT* (*Recovering or Departing Trajectory*) metric as the difference between these two distances: $RDT= d(x_1, x_j) - d(x_1, x_k)$. $RDT > 0$ indicates a closer ecological state in x_k than in x_j and, consequently, implies a recovering towards the initial state (*RIS*) x_1 between x_j and x_k (Fig. 2). Inversely, $RDT<0$ indicates a farther ecological state in x_k than in x_j and consequently implies a departure from the initial state (*DIS*) between x_j and x_k. *RDT* could help to determine the effectiveness of management on the ecological state of a community with respect to a baseline state defined as an objective to be achieved or inversely the impact of a natural or anthropogenic event. Additionally, in a context of disturbances in which x_1, x_j, and x_k represent pre-disturbance, disturbed, and post-disturbance states, respectively, *RDT* can be used as a measure of the ecosystem resilience.

2.1.2.3. Linearity of changes with respect to an initial state. *Linearity with respect to the initial state* (ω) - We propose to calculate the angle ω (x_1, x_j, x_k) between trajectory vectors {x_1, x_j} and {x_j, x_k} in a 0–180° system considering 0° as the same direction of the first vector (Fig. 1, C). Angles allow assessing the *linearity of changes with respect to an initial state* (*LIS*) according to a vector of reference [i.e. first segment or subtrajectory (aggregation of segments) of an ecological trajectory] in the Euclidean space. When space Ω is 2D, ω (as well as Θ) can be reported in a 0–360° system, if desired (see examples in Fig. 10 and 13).

The direction (angles) within a trajectory constitutes an important component of the ecological variability, as different directions do not make the same ecological sense, even if the lengths (or speeds) of these trajectories are equivalent. There is a correspondence between ω_i angles and RDT: Indeed, if angle $\omega_i < 90°$ or $\omega_i > 270°$ the trajectory departs from the x_1 initial state (i.e. $RDT < 0$) regardless of trajectory length. On the contrary, if $90° < \omega_i < 270°$ the trajectory recovers (*RIS* area; $RDT > 0$) or departs (*DIS* area; $RDT < 0$) depending on both angle and length values (Fig. 2).

2.1.2.4. Directions with respect to the plane formed by two axes. If users decide that the variance is sufficiently explained by the first two axes of an ordination, it becomes relevant to consider all trajectory segment directions with respect to the interpretation of axes, normally done using the loadings of original variables or their degree of correlation with additional variables.

Segment directions in 2D ordination (α) - We propose to assess angles α (x_i, x_j, *axis 2*) considering the second axis of the ordination diagram as the North (0°) (Fig. 1, D). α allows comparing segment direction with respect to the influence of the variables used to interpret the two ordination axes.

2.1.2.5. Testing and comparing trajectory directions. Circular data need special treatment in data analysis: an angle of 355° is much similar to an angle of 5° than it is to an angle of 330°, hence a simple arithmetic mean for example can be quite misleading (Landler et al., 2018). In order to analyse the uniformity of directions, Landler et al. (2018) recommended using the Rayleigh test when unimodal departure from uniformity is expected, and the Hermans-Rasson test (HR) for multimodal departures (Landler et al., 2019). Such tests allows verifying if there is a unimodal bias in the distribution of angles directions, i.e. if the direction of vector x_j-x_k changes with respect to vector x_i-x_j are evenly distributed (null hypothesis) or concentrated around one or more particular directions. One should prioritize the Rayleigh or the HR tests- depending the type of distribution of direction and following Landler et al. (2019) recommendations. The Watson-William's two test is used to test the homogeneity (null hypothesis) or the significance of difference of segment direction between different factors.

2.1.3. Software

To facilitate conducting the extension of the CTA framework, function options and new functions have been developed to calculate metrics considering x_1 as a constant baseline over time. This new set of CTA tools has been integrated into a new version (v.1.7.9) of the package 'vegclust' (De Cáceres et al., 2010) available on CRAN and GitHub repositories.

2.2. Representing the variability of ecological states and trajectories

2.2.1. Mapping trajectory dynamics with respect to an initial state

Here we suggest the use of maps to represent site scale dynamics through geometrical properties of trajectories in synthetic figures accounting for temporal variability at the sampling unit scale.

In order to avoid multiple distance maps between every pair of surveys, we propose the use of a single map to represent all at once for each site of a study area: (1) net change between x_1 and $x_{n\text{-}survey}$, (2) segment length (or subtrajectory length, *Sb*) $S_{i>1}$, and $S_{j>i}$, and (3) *RIS* or *DIS* segment or subtrajectory lengths between x_i and $x_{n\text{-}survey}$.

Symbols proposed in our synthetic map to represent net change and intermediate segments or subtrajectories (defined arbitrarily if n-surveys>3) are detailed in Fig. 3. Net changes are represented through a circular symbol proportional to the length to vector x_1-$x_{j>i}$. On both sides, a bottom triangle symbol represents the x_1-$x_{i>1}$ vector and a top triangle the $x_{i>1}$-$x_{j>i}$ vector. For both triangles, the size is proportional to the length of respective vectors, while the orientation and colour of the top triangle illustrate the direction (recovering or departing) of the second vector with respect to the initial or baseline state. When more than three ecological states are used, directionality of subtrajectories can be represented with colors in both triangles (Fig. 4).

In this map, circles representing net changes are drawn on the geographical coordinates of sampling locations, while the bottom and top triangles are placed on the map by subtracting or adding an arbitrary value to the Y coordinate.

It may be relevant to define subtrajectories according to a critical event, which influence ecological states [e.g. new pressures, management activities, disturbance (fire, storm, volcanic eruption, oil spill…)] or to a period considered as a baseline in order to help to better understand the shape of trajectories in terms of lengths and angles before and after perturbation. In this case, one should adapt the temporal period represented in the bottom triangle. Inversely, without *a priori* knowledge about such event, the occurrence of saltatory and non-directional trajectories (Lamothe et al., 2019; Matthews et al., 2013), which vary with the overall shape of the trajectory path could help to identify key periods in the history of an ecosystem regarding environmental or other contextual parameters.

2.2.2. Adding CTA metrics to ordination diagrams

Trajectories are traditionally represented on 2D or 3D ordination diagrams using arrows for segments. Here, we propose to complete this kind of chart by adding information about trajectory metrics such as net changes. Data point symbols represent the coordinates of each ecological state according to the axes of the ordination diagram and lines represent segments between transitional ecological states. The novelty lies in representing the distance to the initial state (i.e. first state of the time series) and time by the dot size and colour, respectively. If a single trajectory is represented and one wants to better illustrate the evolution of net changes over time, the trajectory can be centred around the initial state by subtracting the coordinates of the state corresponding to the initial state (x_1) from the coordinates of all ecological states.

2.2.3. Trajectory rose diagrams

We propose to use a Trajectory Rose (TR) to represent the distribution of directions in the multivariate space Ω, as it is traditionally done in meteorology to represent wind directions and speeds (Azorin-Molina et al., 2017; Cieszyńska and Stramska, 2018) or in currentology (Dalbosco et al., 2020; Dufresne et al., 2014). The TR consists of a circular

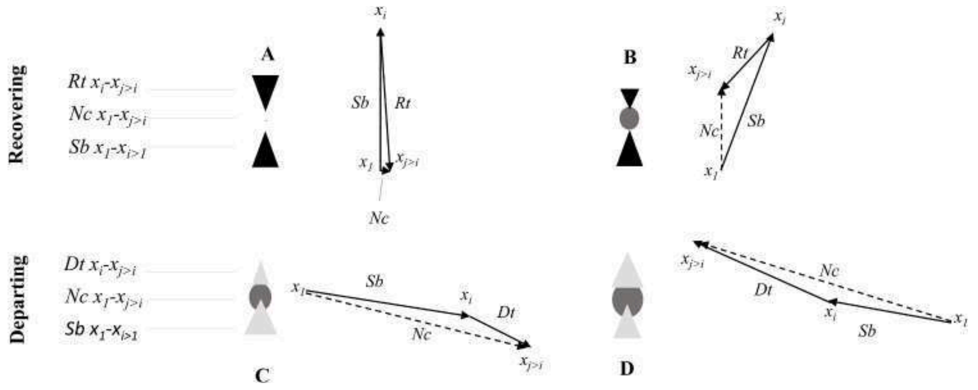

Fig. 3. Symbols used to represent site ecological net change between ecological state x_1 and $x_{j>i}$ (circle) and segment or subtrajectories for *Sb* $x_1x_{i>1}$ and $Rx_ix_{j>i}$ *or Dt* $x_ix_{j>i}$ (triangle): the size of the symbols corresponds to the length of segments. Recovering segment or subtrajectories (*Rt* $x_ix_{j>i}$) are represented with black triangles in A and B whereas departing (*Dt* $x_ix_{j>i}$) appears in grey ones (C and D). Trajectory *scenarii* come from Fig. 2.

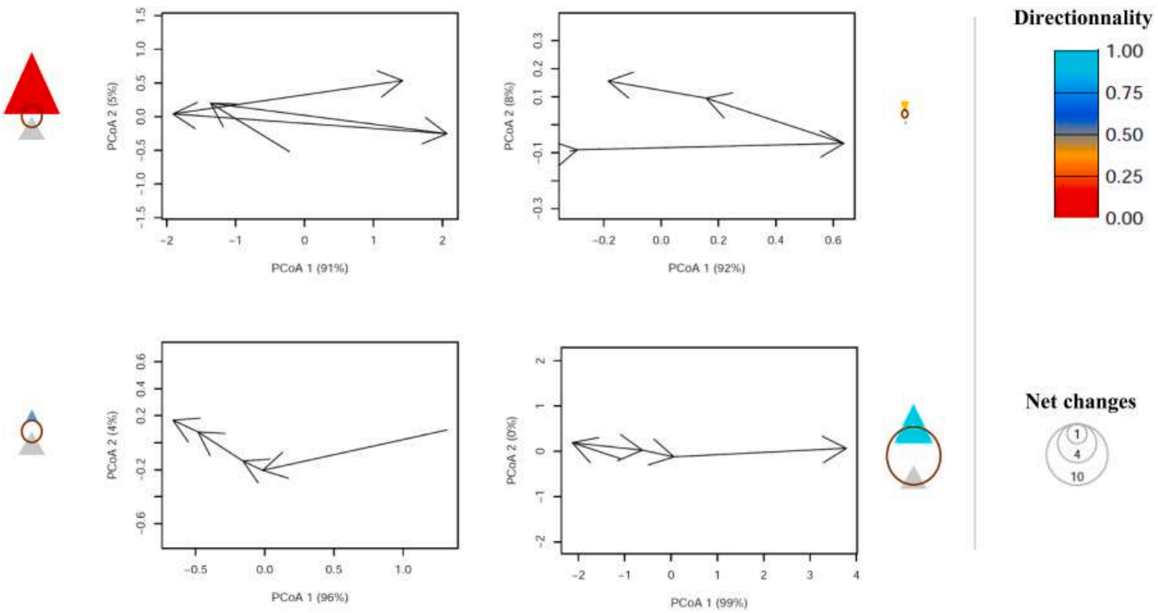

Fig. 4. Examples of RIS, DIS illustrating temporal ecological variability. The size of brown circles is proportional to the net change between x_1 and x_5. Grey bottom triangles represent the first segment between x_1 and x_2 used as a reference, and the top triangle represents the mean length of the following segments (x_3 to x_5) respectively orientated and coloured according to RIS/DIS trajectory and directionality.

bar plot of angles ranging from 0Â° to 360Â°. The barplot structure of TR allows representing factors in different bar sections. Depending on the aim of the analysis, users can choose to represent Θ, ω or α angles in a TR.

2.2.3.1. *Distribution of* Θ, *ω values.*

The baseline state TR provides a synthetic visualisation of ecological trends at the scale of a study area according to directional changes (0–360°) of one vector with respect to the previous one for each consecutive triplet over time. Users can choose to represent distributions of Θ, or ω, angles in order to analyse changes of direction of each triplet or the direction of each segment with respect to the previous or the first segment of the trajectory, respectively.

Angles Θ_i between segments x_i-$x_{j>i}$ and $x_{j>i}$-$x_{k>j}$ are defined between 0° and 180° when considering all multivariate dimensions, or can be reported in a 0–360° system if calculated from 2D coordinates. Angles ω_i between segments x_1-$x_{i>1}$ and $x_{i>1}$-$x_{j>i}$ are also reported in a 0–360° system when calculated on 2D coordinates. At this step of the procedure, the user must consider whether the variance explained by the two first components is high enough to evaluate angles in a 0–360° system.

A value of 0° indicates a straight DIS segment with no change of direction with respect to x_1-$x_{i>1}$ vector. The distribution of angles is represented in barplots whose size indicates the number of segments following a given direction: *RIS* on the bottom part ($90° < \omega_{RIS} < 270°$) and *DIS* in both parts depending on the length of the second segment of each triplet. Lengths of vector $\{x_j, x_k\}$ are aggregated on the top of each bar section and coloured according to distance, in order to underline if direction trends occur in short or long trajectories.

2.2.3.2. *Distribution of α values.*

α angles are calculated considering the second axis of the ordination diagram as the North (0°) and represented in a TR in order to illustrate distribution of segment direction in a 2D Euclidean space. It allows the characterization of the nature of change by comparing segment direction with respect to the interpretation of ordination axes. Variables names aiding the interpretation of directions can be positioned in the periphery of the TR (see Fig. 10).

3. Ecological applications

Four ecological applications were chosen to illustrate the proposed CTA metrics and modes of representation in different ecological systems.

3.1. *Ecological application 1 – Temporal variability of waterbird communities in a marine protected area*

The national nature reserve of Saint-Brieuc (Brittany, France) is a marine protected area designed in 1998 to protect wintering birds. Anatidae populations are monitored each winter as part of the International Waterbird Census (IWC). CTA has been performed on the nine most abundant species for which a census has been performed during 21 wintering, from 2000 to 2020 (Supplementary data - Appendix A). Anatidae monitoring has been carried out each year in January and encompassed the overall presumed functional area (i.e. intertidal feeding ground). Lengths, angles, and directionality were calculated (Supplementary data - Appendix B). The temporal variability of the bird community was illustrated with an ordination diagram centred on the initial survey and representing time and net change using symbol colour and size, as suggested in SubSection 2.2.2. For the trajectory rose, a bar plot of ϴ angles of each consecutive triplet ranging from 0° to 360° was produced (range of 15° for each bar) and this chart was transformed in a rose with the function coord_polar() of the package ggplot2 (Wickham, 2016).

Lengths of trajectory segments ranged from 2.03 to 6.16 but were quite stable over time (3.46 ± 1.06, total trajectory path= 69.14). At the end of the study period, distance to the initial state (5.79) was slightly higher than the mean value of net change (4.96 ± 1.28). Fig. 5 shows the ordination diagram representing the temporal variability of the community with respect to the initial state during the 21 years of sampling. The first axis explained twice as much variance (39%) as the second axis (20%). Different species have influenced the anatidae community (Supplementary data – Appendix A). Three species mainly contribute to the first axis and are characterized by a clear decrease in numbers: *Branta bernicla, Mareca penelope,* and to a lesser extent *Mareca strepera*. Other species characterised by stable abundances or drastic interannual variations were mostly expressed on the second axis. The first axis highlights the temporal pattern of the community which is confirmed by the clustering of the most recent sampling occasions on the positive side of the first axis (Fig. 5).

The dominance of $90< \Theta <270$ (84.2%) and RIS and DIS alternation (Figs. 5 and 6, Supplementary data – Appendix A) suggest an ecological turnover in the species involved in ecological change. This results in a strong spring effect around the first state of each consecutive survey, which explains the very small NCR between 2000 and 2020 (8.35%) and low directionality (0.375). In absence of straight departing (0°) and recovering (180°) clear dominance, trajectory trends step by step to a different ecological state from 2000 to 2020.

The anatidae community mainly varied depending on the decline of two of the most numerous species *B. bernicla* and *Mareca penelope*. Other influencing species are not consistent over time which resulted in a clear spring effect around the initial state. CTA results confirmed conclusions of (Sturbois and Ponsero, 2019) and bring new insights concerning the way that ecological variability could be expressed through trajectory properties of bird communities within a given site.

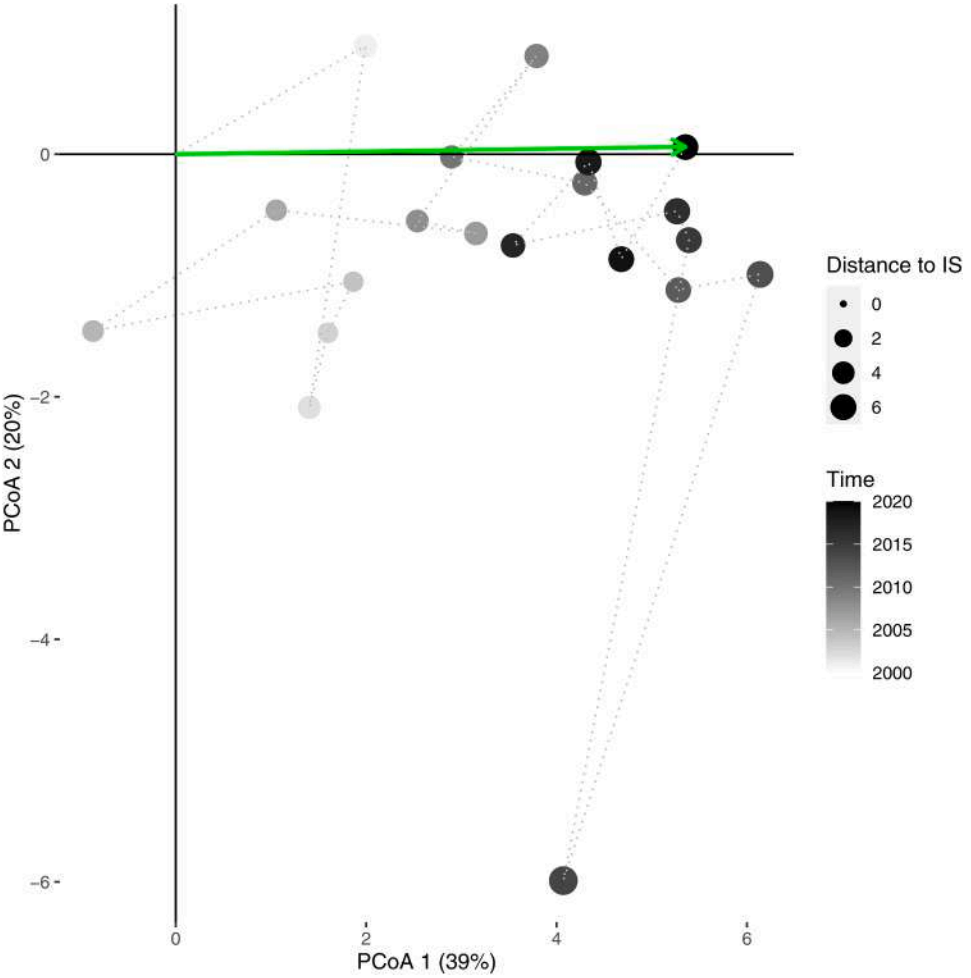

Fig. 5. Anatidae community state relative to the initial state chart between 1999 and 2020. The origin of the chart represents the initial state characterized in 1999, points represent intermediate ecological states [size=length of each state to initial state, colour= light grey (2000) to black (2020)] and lines represents segments between transitional state. The green arrow represents the net change between 2000 and 2020.

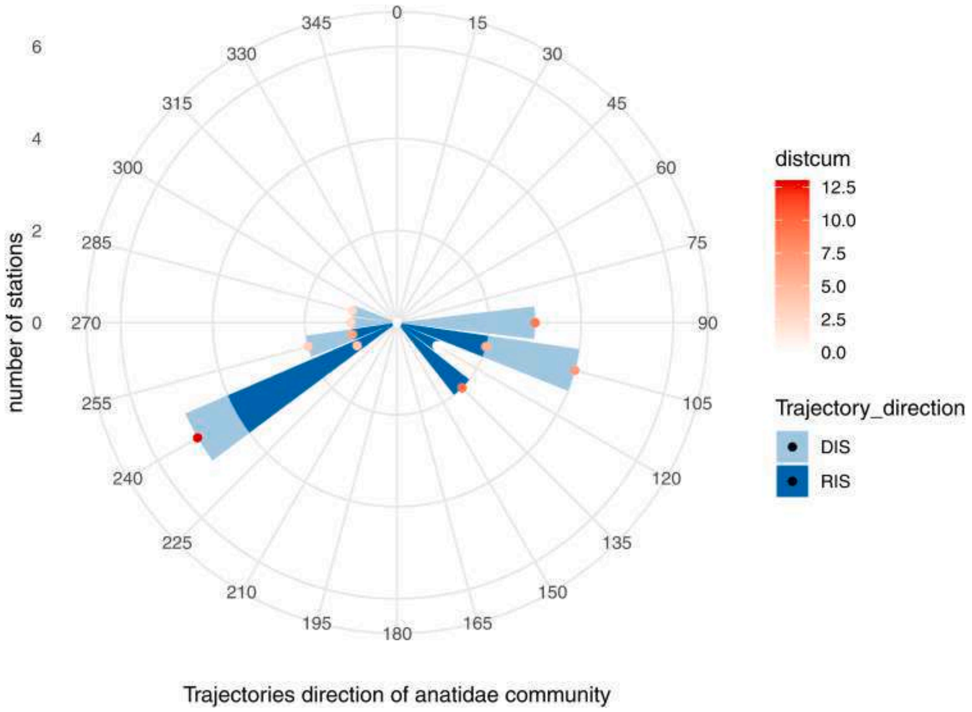

Fig. 6. ϴ trajectory rose for anatidae communities. Bars represent the number of segments concerned by each range (15°) of direction (RIS: dark blue; DIS: light blue). The length of the second segment of each triplet is represented with point at the head of each bar and coloured according to lengths values. Direction 0° represents a straight departing in the same direction as the first segment of each triplet. Direction 180° represents the direction of the return to the initial state (first ecological state of each triplet).

3.2. Ecological application 2- Spatio-temporal changes of benthic communities in a modified system controlled for a tidal power station

The spatio-temporal variability of benthic communities was studied in the Rance estuary (Brittany, France), a modified system whose main physical characteristics are controlled by the functioning of a tidal power station (Desroy and Retière, 2004). The construction of the facility began in 1963 and was completed in 1966. Before the building of

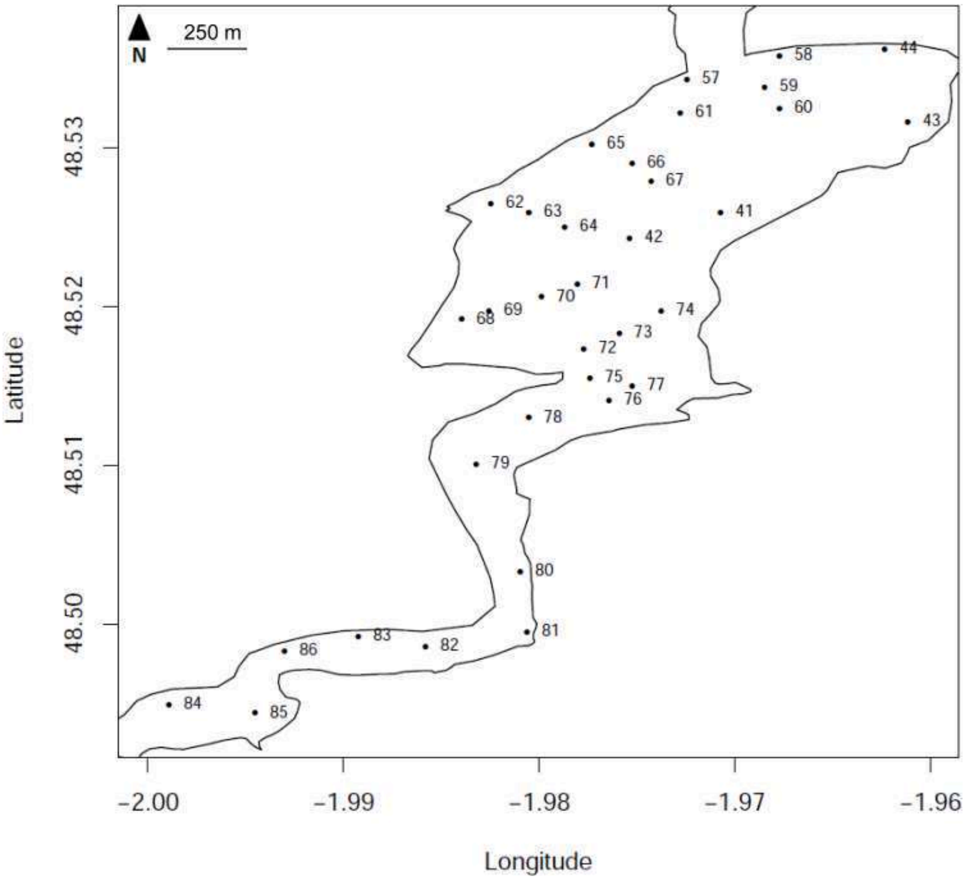

Fig. 7. Localisation of stations sampled in 1976, 1995 and 2010 in the upstream Rance, Brittany, France.

this infrastructure, the Rance was a ria with sectors differentiated by saline stratification whereas the system is now clearly separated into two main entities: the marine reservoir and the upstream estuary (brackish water). The construction step led to the formation of a hypohaline basin, inducing immediate strong mortality events for benthic macrofauna, and a period of instability (1967–1975). The control of the physical characteristics of the system has affected sediment dynamics, and deeply modified benthic habitats (Bonnot-Courtois, 1997; Bonnot-Courtois and Lafond, 1991; Retière, 1979).

Soft bottom benthic communities were sampled at 34 stations in 1976, 1995 and 2010 in the upstream estuary in order to analyse the ecological variability associated with the recovery process and sedimentary changes [Fig. 7, (Desroy and Retière, 2004)]. Temporal Beta-diversity Index [TBI (Legendre, 2019)] was run in order to verify if species gains or losses were responsible for net changes at the scale of both consecutive periods. A Hellinger transformation was performed on the overall data set prior to multivariate analysis (PCA) and coordinates of sites on the ordination diagram for the three surveys were used as inputs for community trajectory analysis (Supplementary data - Appendix C). A trajectory map was produced in order to synthetize trajectories of benthic communities on each site through the three surveys. After data aggregation depending on the station location (upstream vs down-stream), a second CTA analysis was performed in order to verify if local changes resulted in larger scale variations.

The species richness dramatically decreased from 149 species in 1976 to 54 and 73 species in 1995 and 2010, respectively. 27 species were common to the three surveys. A high variability of faunal composition was observed since 14 species appeared and 70 disappeared between 1976 and 1995 vs 38 new species and 19 less between 1995 and 2010. At the scale of the overall monitoring period, 34 new species were observed between 1976 and 2010 and 71 species disappeared. TBI index (0.46) confirms that species losses dominated species gains between 1976 and 1995 (losses for 18 stations and gains for 16 stations). Inversely gains dominated losses (0.60) for the 1995–2010 period (losses for 10 stations vs gains for 24 stations).

According to the cumulative trajectory path length of all sites, the first period was characterized by a higher ecological variability 539.69 (15.87 ± 7.70) than the second 469.92 (13.82 ± 5.14). Considering trajectory path length at the station scale, seven stations (59, 66, 63, 67, 57, 61, 58) represented 32.48% (327.96) of the whole trajectory path and segment lengths were more important during the second period for 13 stations (31,71%). Two main spatial trajectory patterns were identified (Fig. 8). Eight stations mainly located in the upstream part (south) of the study area were characterized by lower net (19.67 ± 3.84) and consecutive changes (9.07± 2.30). Inversely, higher changes characterized other stations mainly located in the downstream part (north), both at the scale of the overall study period (37.60 ± 13.98) and consecutive ones (16.41 ± 6.43). This increasing change along the upstream/downstream gradient is confirmed by significant correlations between latitude and net changes (0.40; p-value = 0.01944) and trajectory path lengths (0.45; p-value = 0.00685). RDT was positive for 12 sites and negative for 22, showing an overall departure dynamic from the initial state for 64.71% of sites, mainly located in the northern part of the study area (Fig. 8). Lower NCR values indicate significant direction changes between 1976 and 1995 and 1995–2010 trajectory segments (Supplementary data - Appendix C). It implies that changes are induced by different species groups between both periods. Differences in the magnitude of changes revealed at local scales areas also result in

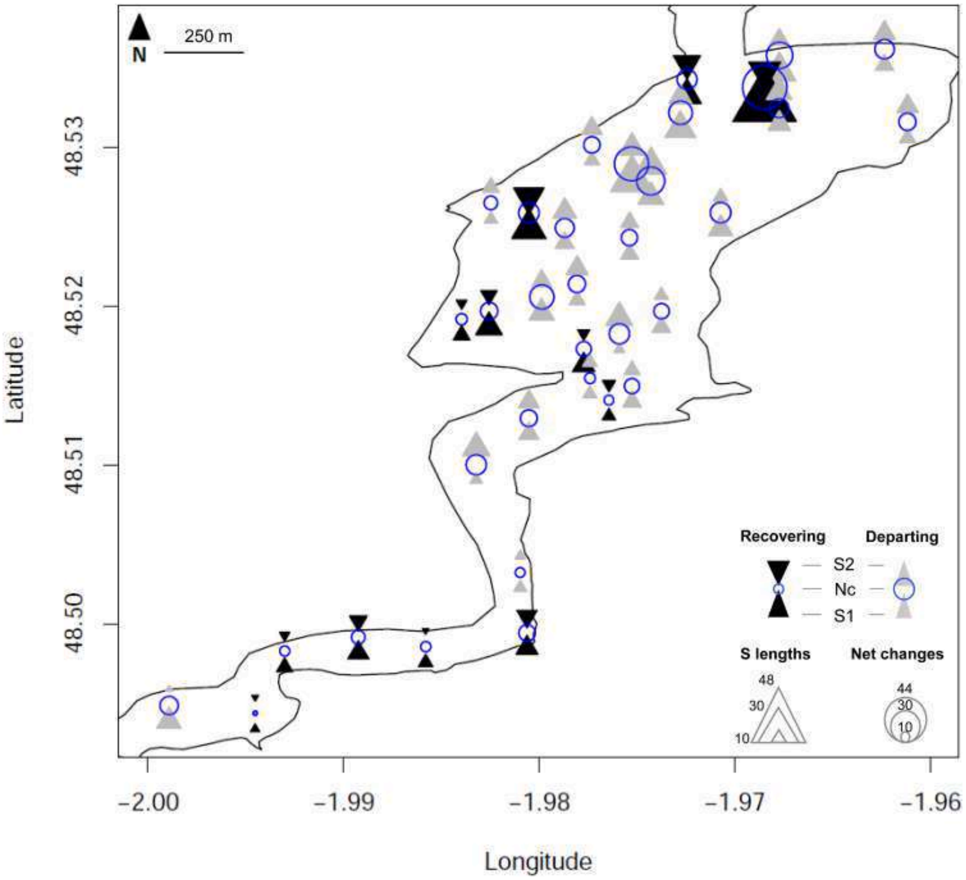

Fig. 8. Benthic community trajectory map. Net changes (Nc) are represented with blue circles between 1976 and 2010. Bottom triangles represent S1 (1976 to 1995) and top ones S2 (1995 to 2010). The size of the symbols corresponds to lengths. For triangles, colors are used to distinguish recovering (black) from departing trajectories (grey).

contrasted overall trends (Net change) at the larger scale of upstream (23.59) and downstream (49.77) communities.

The community described in 1976 was already undergoing a recovery process, which explains species losses and gains in the following surveys. According to the trajectory length of both periods and departing trajectories occurring in 64.71% of the stations, benthic communities are not yet stabilized in the study area. This seems particularly true for downstream stations which suffered most changes. In this area, regular changes in environmental conditions according to the estuary functioning influenced by the power station would probably not lead to a stabilization of benthic communities except if some species characterized by high dynamics induce long term changes of sediment facies (e.g. invasive species such as *Crepidula fornicata* and *Ruditapes philippinarum)*. Future surveys will help to verify these hypotheses. Inversely, upstream stations are more stable probably due to environmental factors (influence of fresh water) which limit the variability of communities through a drastic selection of species.

3.3. Ecological application 3 – Temporal sedimentary variability in a marine intertidal area

Sediment facies were studied at 42 sites in the intertidal area of the bay of Saint-Brieuc in 1987 (Gros and Hamon, 1988), 2001 (Bonnot--Courtois and Dreau, 2002) and 2019 (Sturbois et al., unpublished data). At these dates, one sample of sediment was collected with a handcorer (5 cm diameter, depth of 5 cm) on each site and subsequently analysed for grain size distribution in the laboratory. Statistical analyses were performed with the package G2sd (Fournier et al., 2014). Sedimentary data from the three periods were combined in the same dataset subjected to CTA analysis (Supplementary data - Appendix D and E). Two TR were then produced in order to illustrate the distribution of α angles for both periods with respect to sedimentary variables localised at the periphery of TR according to their position in the variable factor map (PCA). Finally, HR and Watson-William's tests were performed to test the homogeneity of angles distribution and the difference of segment direction between periods, respectively.

The first two dimensions of the PCA explained 81.8% of the variance so consideration of trajectory and segment properties with respect to these components is allowable. Trajectory path was lower for the period 1987–2001 (72.17; 1.72±1.55) than for the period 2001–2019 (99.67; 2.37±1.96) which indicated more sedimentary variability in the second period. However the sedimentary dynamics (i.e. speed of changes) was quantitatively quite similar for the two periods (1987–2001:5.16 vs 2001–2019: 5.53). During the first period, 7 stations contributed to 46.38% of the trajectory path, whereas 12 stations were responsible for 59.20% of changes between 2001 and 2019 (Fig. 9, Supplementary data - Appendix D and E). This reveals that few sites are characterized by a high sedimentary variability (length >3) while changes in most stations were more moderate. The TR qualitatively represents the pattern of the segments direction according to sedimentary variables (Fig. 10). During the first period, segment direction mainly occurred in the bottom part of the rose (HR test: $T = 11.07$, p-value=0.004) according to different sand variables from very fine to fine whereas for the segments of the second period it occurred in the top part of the rose (HR test: $T = 13.77$, p-value=0.002) according to very fine sand, mud and coarse sediment variables (Watson test: $T = 0.896$; p-value<0.001). These results are consistent with the conclusions of Sturbois et al. (unpublished data) who showed that thirty years sedimentary changes in the intertidal part of the bay of Saint-Brieuc resulted in: (1) an overall slight sloughing revealed by the increase in the contribution of very fine sediment classes over the study period, (2) a high variability at few stations contrasting with moderate changes in the rest of the study area. This ecological application confirmed that angles and lengths are relevant trajectory properties to qualitatively and quantitatively describe trajectory patterns according to period or other factors such as habitat, management or pressure.

3.4. Ecological application 4 – Response of boreal forests to insect outbreaks

The spruce budworm (*Choristoneura fumiferana* Clem.) is considered amongst the most severe defoliating insects of boreal and sub-boreal forests of eastern North America (Blais, 1957). Every 30 to 40 years, its populations synchronously reaches outbreak levels over large spatial scales, generating dramatic ecological and economic impacts due to important mortality events in areas dominated by balsam fir (*Abies balsamea* L.) and spruce (*Picea* spp.). Whereas balsam fir usually presents higher levels of defoliation and mortality rates than spruce species of northern latitudes, a recent study (Sánchez-Pinillos et al., 2019) found a higher resilience of forests dominated by balsam fir than by black spruce (*P. mariana* Mill.). On the contrary, black spruce forests proved to be highly resistant to the insect attack but collapsed under long and severe outbreaks. We used a subset of plots affected by spruce budworm outbreaks and selected by Sánchez-Pinillos et al. (2019) from Quebec's Forest Inventory (Ministère des Ressources Naturelles, 2013) to assess forest responses to insect outbreaks with respect to individual pathways. In particular, we compared the dynamics of 74 mixed communities co-dominated by balsam fir and white birch (*Betula papyrifera* Marsh.) and 74 stands dominated by black spruce (Fig. 11). Forest plots were characterised with species abundance and size classes for the most common species. CTA metrics (Supplementary data - Appendix F) were used to characterize forest responses to the perturbation and a trajectory map was used to illustrate spatial patterns of trajectories according to the three types of responses to the outbreak (Sánchez-Pinillos et al.,

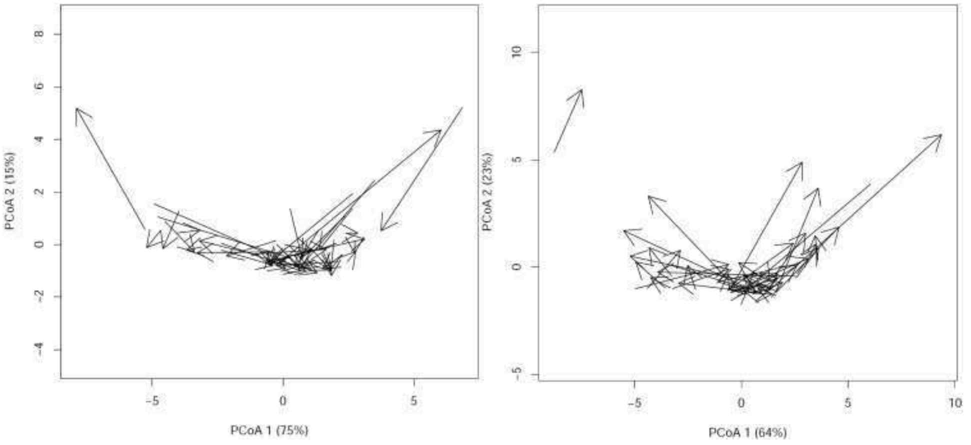

Fig. 9. Sedimentary trajectory segments. Arrows represents respectively 1987–2001 (left) and 2001–2019 (right) trajectory segments.

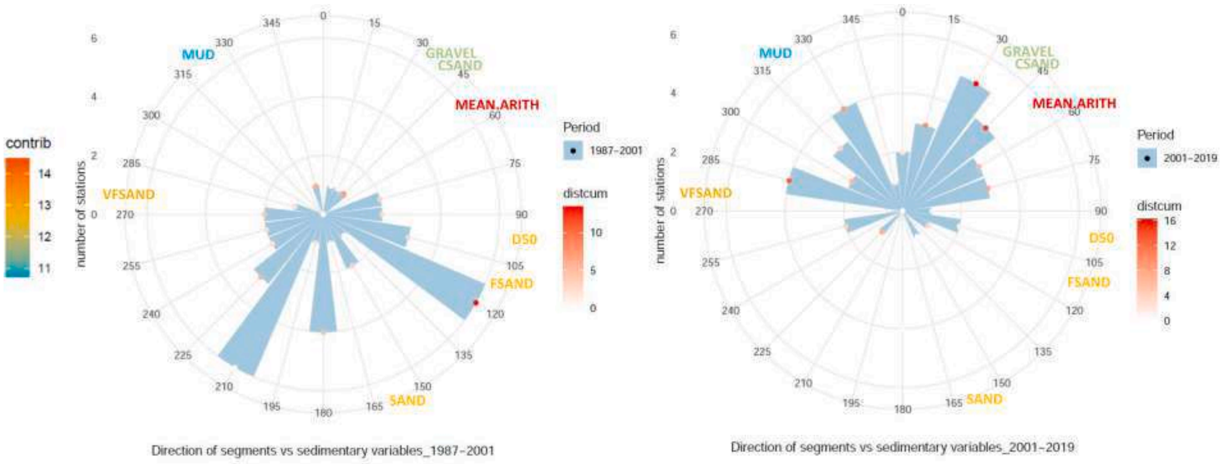

Fig. 10. α trajectory roses for both periods (1987–2001 and 2001–2019) with respect to the two first components of the PCA (81.8% of the variance). Bars represent the number of stations concerned by each range (15°) of direction. Cumulative segment lengths are represented with point at the head of each bar and coloured according to length values. Sedimentary variables occurred in the periphery of the TR faithfully to the PCA ordination diagram and are coloured depending on their contribution to the two first component.

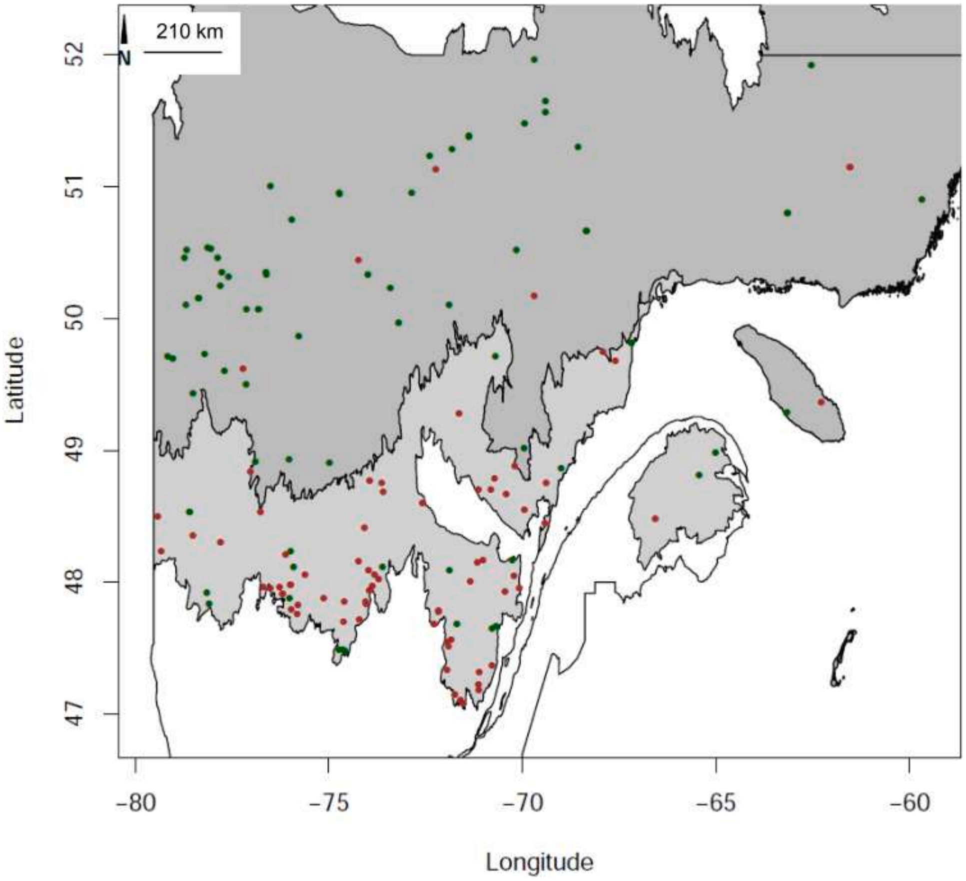

Fig. 11. Forest plots sampled in Quebec, Canada. Boreal zone dominated by Basalm fir - White birch appears in dark grey whereas zone dominated by Black spruce – Moss appears in light grey. Coloured dotes indicates the type of forest on each station before the outbreak (pre-disturbance state): *ABBA-BEPA* in red and *PIMAhigh* in green.

2019). We finally used a TR of ω distribution to illustrate differential responses according to the type of forest.

The changes of mixed fir-birch forests was reflected through longer trajectory paths (64.73) and lower net change (42.17) than the homologous in black spruce forests (47.70 and 59.95, respectively). However, both forests showed similar trajectory patterns, with longer distances between the pre-disturbance and disturbed states (sum $S_{1,\text{fir-birch}} = 37.95$; sum $S_{1,\text{spruce}} = 39.12$) than between the disturbed and post-disturbance states (sum $S_{2,\text{fir}} = 26.77$; sum $S_{2,\text{spruce}} = 20.83$).

The trajectory map (Fig. 12) underlines the different responses of forests to the outbreak: (1) resistant plots were mainly characterized by departing dynamics and low segment length and net change, (2) resilient

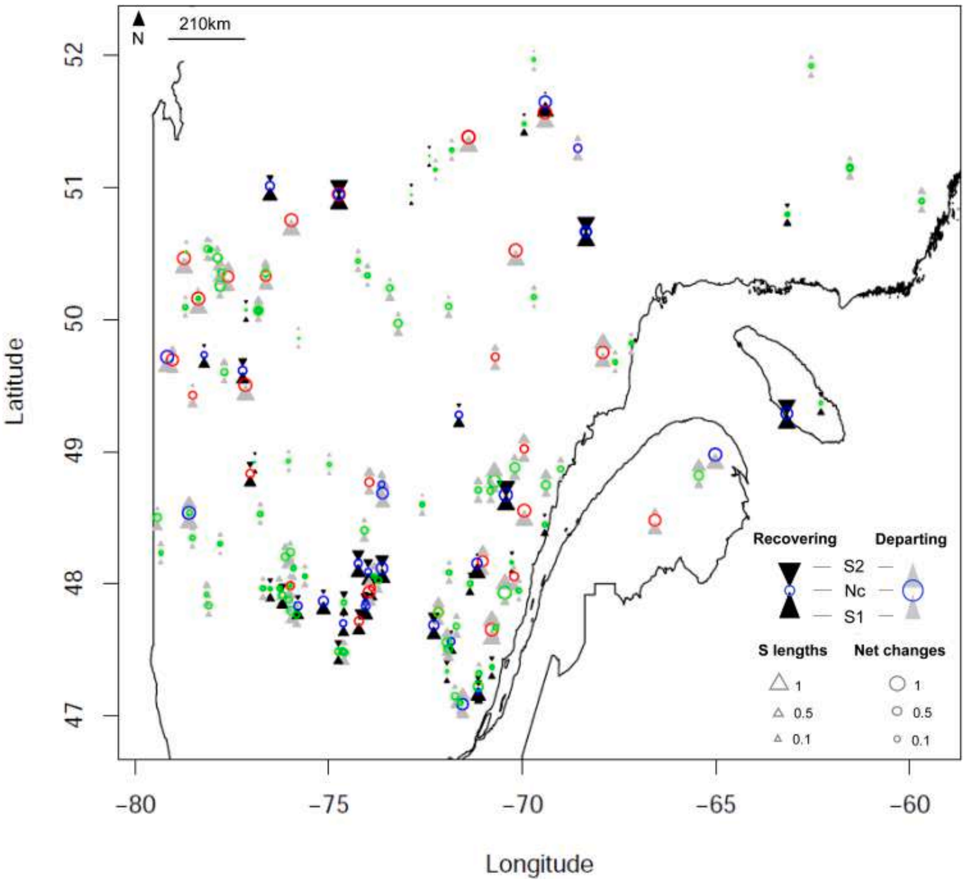

Fig. 12. Map of forest trajectories in response to insect outbreak. Net changes are represented by circles coloured according to forest responses to outbreak [resistant (green), resilient (blue) and changed (red)]. Bottom triangles represent S1 (pre-disturbance to disturbed state) and top ones S2 (disturbed to final state). Colours of triangles are used to distinguish recovering (black) from diverging trajectories (grey). The size of the symbols corresponds to lengths.

plots mainly occurred through recovering dynamics, high segment lengths, and moderate net change and, (3) changed plots were defined by departing dynamics and high segments lengths and net changes. In agreement with Sánchez-Pinillos et al. (2019), a higher percentage of recovering trajectories was found at southern latitudes, where balsam fir co-dominates the stands with white birch. Thus 42% of the plots classified as fir-white mixed forests showed recovering trajectories in comparison to the 30.1% of black spruce stands. On the contrary, shorter trajectories were found above latitude 49°, reflecting the greater resistance of black spruce to the spruce budworm attack. It is important to note that, whereas we represented forest dynamics of all forest types in the same map, one could be interested in assessing the spatial differences in the responses of a given forest community. In such a case, a potential alternative could be to generate independent maps or different symbols or colours for each forest type.

TR diagrams of ω distribution showed a clear rupture in trajectory

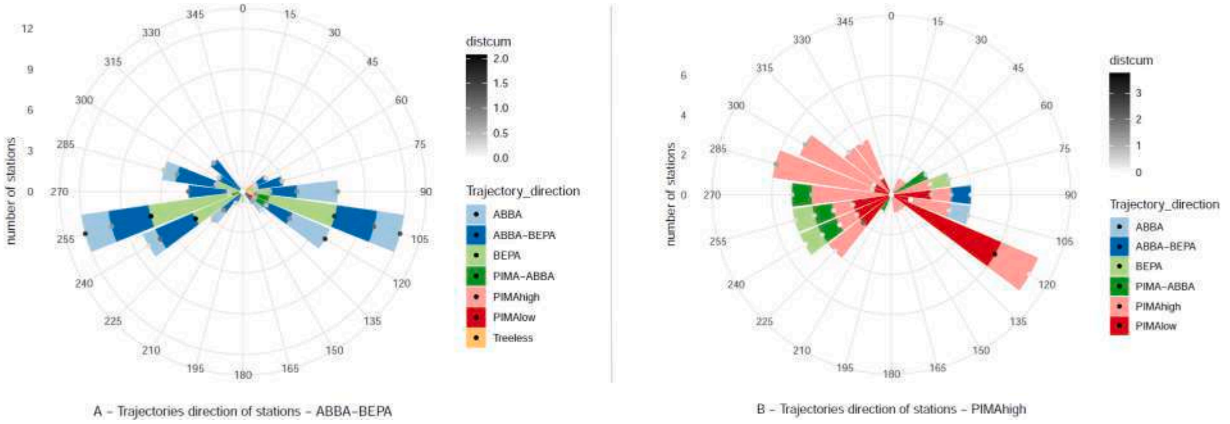

Fig. 13. ω trajectory roses for forest plot characterised as ABBA-BEPA (A) or PIMAhigh (B) at the pre-disturbance state. Bars represent the number of segments concerned by each range (15°) of direction with coloured sections according to the type of forest defined at the final state. Cumulative lengths of the second segments (disturbed to final state) of each triplet are represented with point at the head of each bar and coloured according to lengths values (white to black). Direction 0° represents a straight departing in the same direction as the first segment of each triplet. Direction 180° represents the direction of the return to the initial state (first ecological state of each triplet).

direction between disturbed and final state for both forest typologies. Many plots did not show changes in forest classification. It is important to note that dissimilarities between forest surveys were calculated by considering different size classes for the most common species in boreal forests (*P. mariana, P. glauca, A. balsamea,* and *B. papyrifera*). The TR analyses, therefore, illustrated the changes in forest structure resulting from the death of the most vulnerable trees. Thus, most black spruce forests remained with the same composition after the outbreak or changed toward forests with a lower basal area represented by a different forest typology (Fig. 13-B, *PIMAhigh*). In the case of mixed forests of balsam fir and white birch (Fig. 13-A, *ABBA-BEPA*), our results showed different successional stages including the dominance of white birch colonizing gaps, a transient stage of mixed fir-birch stands, and a last successional stage dominated by balsam fir.

4. Discussion

The CTA framework represents a valuable approach to assess ecological dynamics based on the geometric analysis of trajectories defined in a multidimensional space of community resemblance: geometric properties of trajectories, projection of a community state onto a trajectory, convergence/divergence and geometric resemblance between a pair of trajectories, spatial variation in community dynamics (De Cáceres et al., 2019).

Here, we went further in the definition of geometric properties of trajectories by complementing the available metrics and proposing synthetic methods of applied representation that facilitate the interpretation of ecosystem dynamics over time. For that, we integrated new tools (options, and new functions) into the original version of the CTA framework (available in package 'vegclust' on CRAN and GitHub repositories).

4.1. Extending CTA metrics

The proposed extension makes the CTA framework more complete in order to address a larger panel of ecological questions, especially in applied ecology. The new metrics can be useful, for instance, when monitoring ecosystem responses to disturbances, or in the context of ecosystem restoration, by focusing CTA on geometric properties with respect to baseline ecological states. Net changes, new angles and the RDT metrics, along with recovering and departing characterisation of trajectories, allow addressing these issues, as shown in the case studies section.

The extension includes a new set of functions, based on the two first axes of the dissimilarity space in which trajectories were originally defined. This facilitates the use of CTA to users aiming to restrict analyses to a 2D Cartesian space or to study trajectories in a biplot including only two variables. As the first two axes often explain a part of the total variance, the user must be cautious with the interpretation of the angles used in trajectory roses, particularly when the two first axes explain a small proportion of total variance. When most variance proportion is captured, we consider that these metrics can be compared to variables in multivariate spaces in order to provide ecological meaning to the direction. When using Θ and ω angles in TR, CTA returns angles between trajectory segments regarding 2D point coordinates of the third survey of each triplet with respect to the previous segment. The variance explained by the first two axis remains also important here to evaluate the relevance of angles transformations even if the coordinates of the third point in the 2D space are only used to flip the 0–180 angles in positive or negative. Consequently, this step does not influence the accuracy of angle calculations considering all components. As each triplet forms its own plane it is not possible to provide an ecological meaning related to the environmental variables, but we consider that this step of the procedure still contributes to efficiently illustrating the degree of ecological variability.

As shown in the second case study, CTA allows the comparison of cumulative (departing) or buffering (recovering) local trajectory patterns with changes at higher community levels in the multivariate space. Measuring changes at these two scales, local vs assemblage or community, help to determine if small scale changes result in larger scale variations. It helps for the potential detection of 1. station dispersion occurring without significant centroïd variations at community scale, or 2. cyclic community variability contrasting with constant departing trajectories in other community.

Further CTA extensions could be envisaged, beyond the one presented here. To complete the qualitative characterisation of recovering and departing trajectories, an interesting potential extension of CTA may concern the routine definition of trajectory shape with respect to the occurrence of saltatory and non-directional trajectories (Lamothe et al., 2019; Matthews et al., 2013). Another perspective of CTA extension could concern the integration of figures codes (Supplementary data - Appendix G) in graphical functions in order to produce trajectory maps, charts, and roses.

4.2. Representing trajectory properties

We presented and illustrated set of innovative figures to represent trajectory properties, offering an interesting alternative to traditional representations used in community ecology and other fields where temporal series are naturally multivariate.

4.2.1. Maps of trajectory properties

Mapping trajectory properties allows the illustration of spatio-temporal patterns taking into account all the variability contained in multivariate analysis. Information about net change and dynamics occurring within the whole study period at a site level is consequently efficiently synthesized and sites characterized by stability or high ecological variability are easily identifiable. The forest application (Section 3.4) highlighted the ability of trajectory maps to illustrate the potential link between CTA metrics and other indices. In this article, we used lengths, trajectory path and net change as inputs to map RIS and DIS dynamics. We encourage also users to represent other CTA metrics (e.g. overall trajectory length or speed, directionality or NCR) or the behaviour over time of diversity indices or any other ecological variables coming from other analytical frameworks.

4.2.2. Adding CTA metrics to ordination diagrams

An ordination diagram centred on the initial state of a trajectory allows highlighting both the whole shape of the trajectory (i.e. lengths and angles) and the distance to the baseline state (i.e. the net change) at each survey of the study period. In ecological application 3.1, net changes include all n-dimensional components, but coordinates of data points and lines originate from 2D representation of trajectories. If the first two multivariate axes do not explain a sufficient part of the variance, the representation of the distance to the initial state should not be optimal for trajectory path which is the best fit with other components. If one should prioritize between the representations of distances to initial states for the relative trajectory directions, a good approach would be to centre trajectories considered individually. In this way, each trajectory path could express itself on the 2D graph with its maximal variability. When the first two axes of multivariate analyses explain the main part of the variance, the first option fulfills correctly both the distance and relative direction considerations.

In case of ecological cycles, the net changes, as well as directionality, are two good metrics to illustrate distancing trajectories following by recovering patterns. The relative to initial state chart proposed in Section 2.2.2 and Fig. 5, or a simple 2D graph representing net changes according to time could be useful to represent alternative distancing and recovering trajectories inherent to ecological cycle. However, long time series are needed to be able to describe ecological cycles.

4.2.3. Using trajectory roses and circular statistics together with CTA

The trajectory rose concept offers an innovative way to represent angles and lengths at the scale of a study area with the possibility to explain metrics by explanatory variables using the bar sections of the TR (RIS or DIS trajectories, period, habitat, pressure, management…). Doing this, the TR allows visualization of direction trend changes with corresponding lengths and offers a synthetic way to illustrate ecological variability in response to natural or anthropogenic factors. The different variants of the TR diagrams, related to different types of angles, are useful in representing the distribution of temporal changes in the direction of community or ecosystem dynamics and circular statistics allows testing and comparing these patterns. Used together, CTA metrics and circular statistics are helpful to quantitatively analyse trajectories and compare directions, since they provide important insights into elements of community or ecosystem dynamics that are not evident from qualitative descriptions of multivariate ordination diagrams.

4.3. Applications and limitations of the proposed framework

Multivariate ecological methods are descriptive by nature. Despite CTA allows more precise measurement and illustration of ecological changes, it suffers the same limitations. Consequently, users should complete CTA outputs by a strong specific examination of datasets (i.e. species or other variables) in order to improve the ecological meaning of observed changes, as done in the four ecological applications of this paper, or by complementing CTA with additional analyses providing statistical background on community changes. Otherwise, conclusions provide an incomplete picture and can mislead the description of ecological states (Cimon and Cusson, 2018) with potential misdirecting conservation actions or overstating conservation progress.

Note that ordination spaces are specifically constructed for each given data set. Therefore, any data transformation on the raw data or sampling decision is likely to affect trajectories, and subsequently, all metrics to be calculated. We alert future users and urge them to test for this effect before any overall transformations, change in sampling design and/or suppression of rare species in a community data set. Furthermore, when choosing a dissimilarity coefficient, users should check the properties the coefficient has, to determine whether they are suitable for the objectives of the study (Legendre and De Cáceres, 2013) and implications in CTA performing.

Users should also be aware of the importance of the definition of the first state of a time series. If a sampling program starts in the middle of a disturbing event it will not be possible to measure the overall ecological response to disturbance because sampling design prevents the definition of a predisturbance state. This “missing part” of the ecological trajectory depends on sampling starting according to disturbing events and the type of disturbance. In applications characterized by cyclic variability, the ecological cycle will be underlined whatever the first survey used to identify the first ecological state of the time series. However, the position of this first state within the ecological cycle would only be identified regarding future surveys.

Despite the CTA framework has no limit on the number of components considered in metric calculations, some of new applications (reporting angles Θ, ω in a 0–360° system, angle α calculation) refer to the first two components. In this context, performing CTA analysis imposes a careful interpretation of the multivariate space in order to assess the consequences of such environment reduction. Consequently, users have to assume and decide if the variance explained is sufficient to calculate these CTA metrics.

4.4. CTA as a useful multivariate toolbox

Whereas the extended CTA framework and the associated modes of representation constitute potential management and decision-making tools, we urge users interested in sharing our synthetic tools with managers or stakeholders that interpretation must be done carefully with a hand of experienced multivariate ecologists and necessarily coupled with a precise data examination. In restoration or perturbation contexts, lengths, net change, and RDT metrics allow a real-time measurement (i.e. after each survey) of ecological dynamics in response to management interventions or potential disturbances, and a quantitative assessment of the degree of success in achieving conservation objectives or the impact of natural or anthropogenic changes on environmental conditions. In this perspective, consideration of angles is complementary to length-based approaches and allows, for instance, the identification of changes in variables responsible for ecological changes (as in TR based on Θ angles), as well as the interpretation of the nature of these changes (TR based on α angles).

Our extended CTA framework and our new representation tools can easily be applied to other input data and fields in ecology (e.g. abundance, biomass, biometry, functional traits, food web) and beyond, as it is illustrated in the four case studies. This framework provides useful tools in order to (1) assess the achievement of restoration goal (recovering after perturbation), (2) highlight ecosystem modifications (departing to the initial state), (3) highlight different ecosystem responses regarding chosen factors (RDT and angles), and (4) to potentially contribute to the documentation and the representation of long-term monitoring observatories.

In conclusion, the CTA metrics and the extension provide a valuable toolbox for trained ecologists (aware of multivariate applications and limitations), to analyse ecological variability and trajectories with respect to a baseline state. The case studies highlighted the complementarity and the ability of our figure concepts to illustrate spatio-temporal trends of different fields in ecology and to modestly contribute to the facilitation of their interpretation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

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Article II

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ARTICLE

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Stable Isotope Trajectory Analysis (SITA): A new approach to quantify and visualize dynamics in stable isotope studies

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Abstract

Ecologists working with stable isotopes have to deal with complex datasets including temporal and spatial replication, which makes the analysis and the representation of patterns of change challenging, especially at high resolution. Due to the lack of a commonly accepted conceptual framework in stable isotope ecology, the analysis and the graphical representation of stable isotope spatial and temporal dynamics of stable isotope value at the organism or community scale remained in the past often descriptive and qualitative, impeding the quantitative detection of relevant functional patterns. The recent community trajectory analysis (CTA) framework provides more explicit perspectives for the analysis and the visualization of ecological trajectories. Building on CTA, we developed the Stable Isotope Trajectory Analysis (SITA) framework, to analyze the geometric properties of stable isotope trajectories on n-dimensional ($n \geq 2$) spaces of analysis defined analogously to the traditional multivariate spaces (Ω) used in community ecology. This approach provides new perspectives into the quantitative analysis of spatio-temporal trajectories in stable isotope spaces (Ω_δ) and derived structural and functional dynamics

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(Ω_γ space). SITA allows the calculation of a set of trajectory metrics, based on either trajectory distances or directions, and new graphical representation solutions, both easily performable in an R environment. Here, we illustrate the use of our approach by reanalyzing previously published datasets from marine, terrestrial, and freshwater ecosystems. We highlight the insights provided by this new analytic framework at the individual, population, community, and ecosystems levels, and discuss applications, limitations, and development potential.

KEYWORDS
changes, composition, dynamics, food web, functioning, spatial, stable isotope, structure, temporal, trajectories

INTRODUCTION

Stable isotope analysis has emerged as one of the most popular approaches to assess the trophic ecology of organisms (Fry, 2008), fluxes of matter and energy within and between ecosystems (Peterson & Fry, 1987), and animal movements (Bouillon et al., 2011; Rubenstein & Hobson, 2019). The quantitative analysis of stable isotope data is based on a large variety of available analytical tools ranging from qualitative inferences using isotopic niche (Newsome et al., 2007) to complex Bayesian mixing models that can be used to characterize food web structure and trophic pathways at multiple levels of biological organization (Layman et al., 2012). Understanding and quantifying spatial and temporal changes is an overarching topic in stable isotope ecology but studies are, to date, largely qualitative, and the development of quantitative approaches is needed.

The quantitative analysis of stable isotope dynamics in response to ecological and environmental changes, notably those induced by human activities, has been explored through the comparative analysis of temporal trajectories in a two-dimensional (usually δ^{13}C and δ^{15}N) isotopic space (δ space). For instance, Schmidt et al. (2007) and Wantzen et al. (2002) quantified the direction and magnitude of temporal changes in food web structure based on the geometric properties of trajectories in the δ space. Schmidt et al. (2007) used specifically circular charts and statistics to represent and test direction shifts in the δ space. Turner et al. (2010) characterized attributes of path trajectories (size, direction, and shape) over data sets containing more than two temporal samples to provide a quantitative description of how stable isotope compositions change in response to spatial and temporal gradients, and tested their differences. Despite the fact that these works have provided substantial new perspectives notably for statistical and hypothesis testing, some limitations remain for the explicit quantitative description, analysis, and representation of the magnitude and the nature of changes in stable isotope composition.

In community ecology, several statistical frameworks have been proposed and used to test hypotheses on community dynamics (Buckley, Day, Lear, et al., 2021; De Cáceres et al., 2019). The dynamics of ecological communities has been traditionally represented on ordination diagrams in which changes over time are represented by a set of vectors linking consecutive ecological states (Austin, 1977; Hudson & Bouwman, 2007; Legendre & Salvat, 2015; Matthews et al., 2013). The geometric properties of trajectories, defined in the space of an ordination diagram, are considered as relevant parameters to quantify the dynamics of ecological systems. The potential of geometrically based methods was illustrated by De Cáceres et al. (2019) in the community trajectory analysis (CTA) framework. Compared with previous approaches based on ordination diagrams, De Cáceres et al. (2019) considered community dynamics as trajectories in a chosen space of community resemblance, with no limit in the number of dimensions included. In CTA, trajectories are defined as objects composed of consecutive segments to be analyzed and compared using distance- and direction-based metrics in the chosen multivariate space. Extending the initial framework, Sturbois, De Cáceres, et al. (2021) developed new CTA metrics and synthetic representation approaches, such as trajectory roses, and the inclusion of trajectory metrics in maps or ordination diagram.

By analogy to community ecology, the term and the concept of trajectory have been informally used in stable isotope ecology to characterize dynamics and represent them in spaces of analysis (either δ space, p-space sensu, Newsome et al., 2007; or spaces based on community-wide indices, e.g., Rigolet et al., 2015). The analysis and representation of stable isotope trajectories or contrasted patterns requires the use of quantitative geometric properties in 2D δ spaces often complemented by vectors in stable isotope scatter plots and/or circular representation (Agostinho et al., 2021; Black & Armbruster, 2021; Cucherousset et al., 2013; Schmidt et al., 2007). However, scientists are increasingly faced with multivariate datasets (i.e., >2 dimensions) in stable isotope ecology in response to the potential use of (1) other isotopes to complement δ^{13}C and δ^{15}N (e.g., ^{34}S ([Connolly et al., 2004], δD [Doucett et al., 2007]) and (2) numerous structural and functional community-wide metrics or indices (Cucherousset & Villéger, 2015; Layman et al., 2007). While the availability of long-term, large-scale, and high-resolution data is one of the most limiting factors to study temporal patterns in stable isotope ecology, the development of methods to analyze, synthesize, and ultimately represent the dynamics of ecological systems still remains an essential issue to complete current approaches by more quantitative and formal explicit frameworks.

Building on CTA, we aim to provide a framework for the temporal analysis of stable isotope data at different levels of biological organization, from individuals to ecosystems to derive structural and functional trajectories in a new approach referred to as Stable Isotope Trajectory Analysis (SITA). We (1) provide a general definition of the trajectory concept applied in stable isotope ecology, adapted from CTA framework to stable isotope analysis, (2) present the package *ecotraj* designed for ecological trajectory analyses and here used specifically for SITA, and (3) illustrate potential applications of SITA using field, experimental or modeled data that include four main topics in stable isotope ecology: (i) individual and (ii) population levels, (iii) structural and functional trajectories of entire food webs, and (iv) modeling of stable isotope dynamics at high spatio-temporal resolutions.

TRAJECTORY CONCEPTS

Trajectory concept in stable isotope ecology

Founding works

Wantzen et al. (2002) and Schmidt et al. (2007) were the first to study directions and distances in δ spaces. Building on these works and the Adams and Collyer (2009) approach, Turner et al. (2010) provided a more explicit use of the concept of trajectory by the definition of trajectory attributes (size, direction, and shape). Despite the fact that Layman et al. (2012) recommended these geometrically based approaches in conjunction with area based in bivariate or multivariate isotopic space, to our knowledge, their use has currently been limited to bivariate spaces (e.g., δ^{13}C-δ^{15}N biplots).

Conceptual definition

A trajectory in stable isotope ecology can be defined as a path in a chosen space of analysis, (Ω_δ or Ω_γ, depending whether the space is based on raw stable isotope data, or on derived indices, respectively), composed of one or different consecutive segments, resulting from repeated observations of a same sampling unit (individuals, populations, stations, food web, etc.). Observed temporal patterns can be characterized by distances and directions in Ω and used to define the nature (i.e., ecological meaning) and magnitude (i.e., importance) of temporal changes. The overall trajectory concept in stable isotope ecology can be adapted to different ecological questions, as illustrated in Section *Applications of SITA*.

Characterizing stable isotope trajectories

Formal definition of trajectory in stable isotope ecology

We follow here the CTA notation used by De Cáceres et al. (2019) to describe and compare trajectories in a multidimensional space of community composition. Given a target sample (individual, population, entire food web, station) whose dynamics is surveyed, let $o_1, o_2, \ldots, o_n$ be an ordered set of n observations ($n > 1$) and $t_1, t_2, \ldots, t_n$ the corresponding set of ordered survey times (i.e., $t_1 < t_2 < \ldots < t_n$). For all i in $\{1, 2, \ldots, n\}$, x_i contains the coordinates corresponding to o_i in a multidimensional space Ω. The geometry of the trajectory T is formalized using a set of $n - 1$ directed segments $\{s_1, \ldots, s_{n-1}\}$, where $s_i = \{x_i, x_{i+1}\}$ is a segment with endpoints (community states) x_i and x_{i+1}.

Definition of spaces supporting SITA

As for CTA, SITA requires the definition of Ω defined by the resemblance between pairs of observations, measured using a dissimilarity coefficient d. SITA is based on dissimilarity values contained in a distance matrix $\Delta = [d]$ (De Cáceres et al., 2019).

The trajectory concept in stable isotope ecology may be addressed in terms of stable isotope composition or food web structure and functioning involving similar attributes (i.e., trajectory metrics) but different data inputs and space of analysis.

Stable isotope Ω_δ space

Ω_δ is defined with stable isotope values of different elements. Coordinates in this space of analysis correspond to raw stable isotope data. Despite δ^{13}C and δ^{15}N being the most commonly used in a bidimensional context, other elements that are ecologically meaningful may also be considered for defining the Ω_δ space (e.g., hydrogen δD, sulfur δ^{34}S, or oxygen δ^{18}O). Coordinates in Ω_δ are used to compute the resemblance between ecological states using d, where we suggest the adoption of the Euclidean distance, as it is commonly used in stable isotope ecology (Ben-David et al., 1997; Kline Jr. et al., 1993; Schmidt et al., 2007; Turner et al., 2010; Wantzen et al., 2002; Whitledge & Rabeni, 1997).

Structural and functional Ω_γ space

Looking for patterns in stable isotope ecology often leads to the calculation of community-wide metrics or any structural or functional indices based on raw stable isotope data (Cucherousset & Villéger, 2015; Layman et al., 2007; Rigolet et al., 2015). Ω_γ is defined with any indices derived from raw stable isotope data, used as ecological proxies, such as to characterize food web structure, and allow a comparison within and among systems.

Trajectory metrics

Metrics detailed in Section Trajectory metrics, here adapted for a stable isotope purpose in Ω_δ and Ω_γ, are part of the CTA framework (see De Cáceres et al. [2019] and Sturbois, De Cáceres, et al. [2021] for equations and more details). Note that additional metrics, not used here, are defined in these articles.

Distance-based metrics

Segment length (S). The trajectory segment length is the distance between two consecutive surveys (i.e., measurements). The length of a segment is given by the distance between its two endpoints. The greater the length of a trajectory segment, the greater is the distance between states. This metric is particularly relevant to analyze the magnitude and the variability of trophic trajectories and allows the distinction between gradual and abrupt changes.

Trajectory path length (L(T)). The trajectory path length is the sum of segment lengths for a given sampling unit. This metric informs about the overall temporal change.

Net change (NC). The net change is defined as the length between a pair of states, which includes a chosen baseline state (i.e., initial or reference state). When calculated at the scale of an overall study period or at the end level of a gradient, this metric evaluates the difference between the initial and the final state, that is, the overall net trajectory change.

Net Change Ratio (NCR). The net change ratio is defined as the ratio between the overall net trajectory change and the trajectory path length. A high *NCR* indicates that a great part of the trajectory path contributes to net changes and illustrates a relative consistency in the drivers of ecological dynamics. Inversely, a low NCR illustrates the versatility of these drivers and highlights that a small part of the trajectory path contributes to net changes.

Recovering or Departing Trajectory (RDT). Let us consider a triplet of states composed of baseline, intermediate, and final states. The dynamics with respect to the baseline state can be defined as recovering (i.e., return to the initial state) or departing (i.e., increasing distance from the initial state) by subtracting $\mathrm{NC}_{\text{baseline to intermediate}}$ to $\mathrm{NC}_{\text{intermediate to final}}$. $RDT > 0$ indicates a closer position at final state than intermediate state and consequently implies a recovering toward the initial state (RIS). Inversely, $RDT < 0$ indicates a farther ecological state at final than intermediate state and consequently implies a departure from the initial state (DIS).

Direction-based metrics

Angle Θ. Θ is the angle between two consecutive segments ordered in time measured on the Euclidean plane that contains the three states. The angle $0° < \Theta < 180°$ is defined as the change of direction in this plane. The trajectory is linear when $\Theta = 0°$. If $\Theta = 180°$, the trajectory is still linear but opposite in sense.

Angle ω. Instead of considering consecutive segments, angle ω allows the assessment of the linearity of changes with respect to a chosen reference segment (e.g., first segment) of an ecological trajectory.

When space Ω is 2D, ω (as well as Θ) can be reported in a 0–360° system, if needed.

Angle α. When space Ω_δ and Ω_γ is 2D, it becomes also relevant to consider trajectory segment directions with respect to the interpretation of the axes defining the space. Angle α is measured considering the second axis of the 2D diagram as the North (0°). α allows the comparison of segment direction with respect to the influence of the variables used to interpret the two axes. When Ω is an ordination space, users may calculate α if they decide that the variance is sufficiently explained by the first two axes of the ordination and can refer to the loadings of original variables or their degree of correlation with additional variables. In an Ω_δ space, α angles are a convenient way to express dynamics with respect to single isotope variability.

Directionality (DIR). The overall directionality of trajectories provides information about the consistency with which a sample follows the same direction and, therefore, the stability of ecological drivers that condition the stable isotope trajectory. DIR is bounded between 0 and 1 where the maximum value corresponds to a straight trajectory (see equation 3 in De Cáceres et al., 2019).

Geometric resemblance between trajectories

De Cáceres et al. (2019) developed a geometrically based approach to trajectory resemblance that included the shape, size, direction, and position of trajectories with respect to the resemblance between all observations (state) belonging to a same trajectory. The approach defines resemblance between pairs of segments or overall trajectories and allows the centering trajectories to exclude differences in position, while keeping the other components of trajectory resemblance. Different distance are proposed and discussed to compute dissimilarity calculation depending of users interests (De Cáceres et al., 2019).

Representing trajectories in stable isotope ecology

The representation concepts provided here are valid for the representation of trajectories in both Ω_δ and Ω_γ spaces.

Trajectory diagrams

Temporal dynamics in stable isotope ecology are sometimes represented in 1D or 2D δ space by segment or arrows between consecutive surveys (Agostinho et al., 2021; Guzzo et al., 2011). Here, we propose a trajectory diagram (TD) concept to customize ordination diagrams by adding notably SITA metrics. Trajectory segments are normally represented by segments between surveys to form the trajectory path whose last segment is ended by an arrow. If one wants to go further in the representation of trajectory net changes, (1) net changes may be represented at each transitional state by the data point size and (2) the overall net change may be represented by a dotted line or arrow between the initial and final state of a time series. We recommend also the generalization of density curves in the periphery of trajectory diagrams, as is sometimes done to compare different food webs (Zapata-Hernández et al., 2021).

Trajectory rose diagram

Schmidt et al. (2007) first introduced the use of direction and distance in their arrow diagrams. Building on this approach, we propose a complementary use of the trajectory rose (TR) diagrams proposed by Sturbois, De Cáceres, et al. (2021) to represent stable isotope dynamics in a circular way. The TR diagram consists of a circular bar plot of angles ranging from 0° to 360°. The barplot structure of TR allows the presence of representing factors in different bar sections. Depending on the aim of the analysis, users can choose to represent the distribution of Θ, ω or α angles. Bars sizes represent the number of segments concerned by each range of direction (e.g., 15°) and cumulative segment length may be represented by a point at the head of each bar and colored according to length values (Sturbois et al., 2021). In $\delta^{13}C/\delta^{15}N$ Ω_δ space, angle α illustrates different stable isotope (SI) trajectory patterns according to increase and/or decrease in $\delta^{13}C$ and $\delta^{15}N$ values (0–90°: $+\delta^{13}C$ and $+\delta^{15}N$; 90–180°: $+\delta^{13}C$ and $-\delta^{15}N$; 180–270°: $-\delta^{13}C$ and $-\delta^{15}N$; 270–360°: $-\delta^{13}C$ and $+\delta^{15}N$). In Ω_γ space, directions distribution refers to structural and functional indices. Note that the TR diagram may be adapted if one wants to represent, with similar visually importance, both direction and distance (segment lengths or net changes instead of number of trajectory segments). In this case, the information of the TR becomes more similar to that of arrow diagrams (Schmidt et al., 2007).

Trajectory heat map

Stable isotope datasets with high temporal resolutions may require special representations as they can potentially saturate TD or TR diagrams.

Here, we propose the concept of a trajectory heat map (TH) to represent long-term SI dynamics. The heat map is a two-dimensional representation of data in which the changes in the distribution of a chosen trajectory metric over time are represented using cell colors (see Section *Spatio-temporal variability of $\delta^{13}C$ and $\delta^{15}N$ modeled isoscapes in the northeast Pacific*). TH allows the representation of the distribution of distance- and direction-based trajectory metrics.

If users aim to favor the representation of directions in TH, angles Θ, ω or α can be represented in a matrix of fixed cell size whose colors vary depending of the number of a given direction range occurring in a given period. As in the TR, we advise the use of any direction bin size (e.g., 15°) to provide a synthetic representation. The TH can be completed by peripheric bar plots to represent trajectory lengths involved in each direction range and period (see Section *Spatio-temporal variability of $\delta^{13}C$ and $\delta^{15}N$ modeled isoscapes in the northeast Pacific*). In 2D Ω_δ space, angle α illustrates, for example, different SI trajectory patterns according to respective increase and/or decrease of the two SI values (see Section *Direction-based metrics*). TH therefore provides a relevant visual summary of complex data sets, highlighting the magnitude and the nature of SI dynamics (TH cells clustering, barplots). In the TH concept, users can easily choose to represent the distribution of segment lengths or any trajectory metrics with respect to time, depending on ecological questions.

Trajectory maps

Expanding Sturbois, De Cáceres, et al. (2021), we propose the use of trajectory metrics as trajectory map (TM) input for the representation of temporal patterns in sampling units on geographic coordinates. Two examples are included here to illustrate the potential of the TM concept.

Trajectory map from initial state

We suggest the adaptation of the TM concept proposed by Sturbois, De Cáceres, et al. (2021) to represent site scale dynamics in Ω_δ or Ω_γ through geometrical properties of trajectories in synthetic figures accounting for temporal variability at the spatial unit scale. The use of a single map is proposed to represent all at once for each site of a study area (see Section *Biological invasions and trophic structure dynamics of lake fish communities*): (1) net change between x_1 and $x_{\text{n-survey}}$, (2) segment length (or subtrajectory length) $S_{i>1}$, and $S_{j>i}$, and (3) RIS or DIS segment or subtrajectory lengths between x_i and $x_{\text{n-survey}}$. Net changes are represented through a circular symbol proportional to the length to vector x_1-$x_{j>i}$. On both sides, a bottom triangle symbol represents the x_1-$x_{i>1}$ vector and a top triangle the $x_{i>1}$-$x_{j>i}$ vector. For both triangles, the size is proportional to the length of respective vectors, while the orientation and color of the top triangle illustrate the direction (recovering or departing) of the second vector with respect to the initial or baseline state.

Isoscape trajectory map

The spatial distribution of SI in environmental materials can be predicted, using models of isotope-fractionating processes and data describing environmental conditions, and represented through isotopic landscape, called isoscapes (Bowen, 2010; West et al., 2008). We adapted the TM concept for isoscape datasets characterized by high spatial resolutions and a minimum of two temporal surveys or modeling. This particular concept of TM is inspired by wind/current map where the magnitude and the direction of wind/current are represented through multiple vector covering large areas. In the isoscape TM (ITM), the direction of arrows represents angle α in a 2D Ω_δ space (e.g., $\delta^{13}C/\delta^{15}N$), and size illustrates trajectory length (see Section *Spatio-temporal variability of $\delta^{13}C$ and $\delta^{15}N$ modeled isoscapes in the northeast Pacific*). The representation of trajectory length is improved by a color raster of spatially interpolated length values.

SOFTWARE AVAILABILITY

In 2019, De Cáceres and colleagues proposed the CTA framework and functions for the calculation of associated metrics. These functions were included in package *vegclust*. In 2021, Sturbois et al. extended the CTA framework with new metrics and figure concepts. New functions were added in package *vegclust*. The present article goes further in the adaptation of CTA, bridging a gap identified in the consideration of dynamics in SI ecology, and starting the exploration of trajectory analysis beyond the sites × species matrix. All these recent developments, and the fact that trajectory analysis can be applied to different spaces, claimed a new package specifically devoted to ecological trajectory analysis that would allow taxonomic, functional or SI trajectory analyses within the same tool through complementary space of analysis (Ω).

The package *ecotraj* (De Cáceres [2019], Sturbois, De Cáceres, et al. [2021]) assists ecologists in the analysis of temporal changes of ecosystems, defined as trajectories on a chosen multivariate space, by providing a set of trajectory metrics and visual representations. It includes functions to perform trajectory plots and to calculate the set of distance and direction-based metrics (length, directionality, angles, etc.) as well as metrics to relate pairs of trajectories (dissimilarity and convergence). Currently, Trajectory analysis (SITA as well as CTA) can be performed using the "ecotraj" functions available on CRAN and GitHub repositories (https://emf-creaf.github.io/ecotraj/index.html). R codes to create figures are also shared to facilitate the use and the customization of our trajectory chart concepts (Data S1) and a new vignette has been added in the documentation of the package.

APPLICATIONS OF SITA

Six ecological applications (EA) were chosen to illustrate the use of SITA metrics and representation concepts for stable isotope dynamics within different ecological systems and to answer various ecological questions (Figure 1): stable isotope trajectories at the (1) individual (EA1 and EA2) and (2) population (EA1, EA3 and EA4) levels, (3) structural and functional trajectories at the scale of entire food webs (EA4 and EA5), and (4) stable isotope dynamics at high spatio-temporal resolutions (EA6).

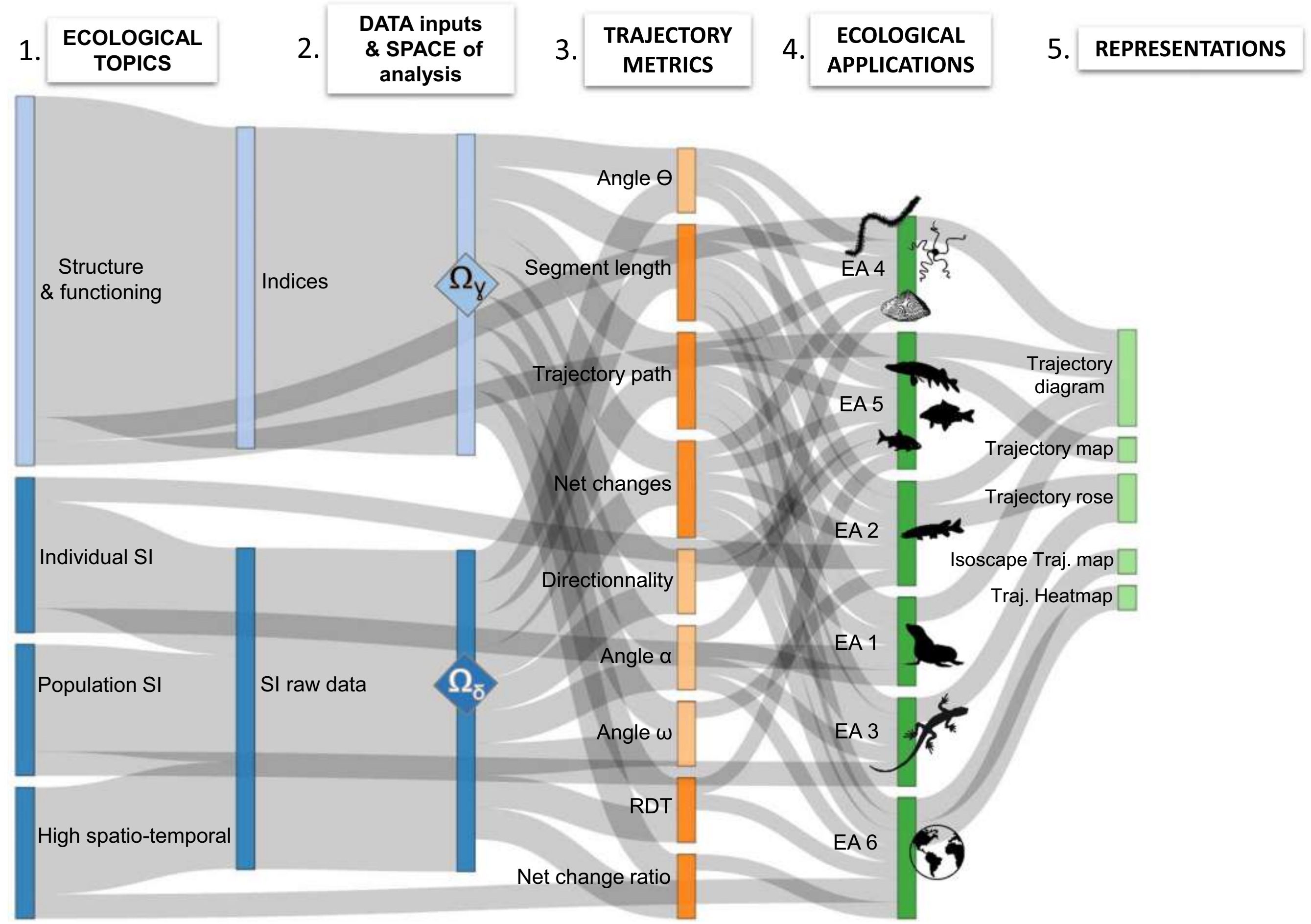

FIGURE 1 Levels of analysis and ecological questions drive input data used to define the space of analysis supporting SITA. While structural and functional analysis requires community-wide metrics or indices to define Ω_γ, raw stable isotope data are used for the definition of Ω_δ that supports stable isotope trajectories at different levels from individual to population, or for ecological questions that involve high stable isotope spatio-temporal resolutions. The SITA adaptability allows the calculation of distance- and direction-based trajectory metrics in both, Ω_δ and Ω_γ, and their visualization in different figures devoted to the representation of dynamics

Spatial and temporal resource partitioning in fur seals

Context

Many generalist populations are composed of individual specialists and individual specializations are increasingly recognized as an important component of many ecological and evolutionary processes (Bolnick et al., 2003), making crucial testing the consistency of individual specialization.

Methods

δ^{13}C and δ^{15}N values of metabolically inert tissues reflect diet at the time of their growth, and continuously growing tissues can be used as time-recorders of the movement and dietary history of individuals. Fur seals (the Antarctic fur seal *Arctocephalus gazella* [AFS] and sub-Antarctic fur seal *A. tropicalis* [SAFS]) whisker SI values yielded unique long-term information on individual behavior that integrated the spatial, trophic, and temporal dimensions of the ecological niche (Cherel et al., 2009; Kernaléguen et al., 2012). The foraging strategies of these two species of sympatric fur seals were examined in the 2001/2002 winter at Crozet, Amsterdam, and Kerguelen islands (Southern Indian Ocean) by measuring the SI compositions of serially sampled whiskers (see Kernaléguen et al., 2012, 2015 for SI preparation and analyses). The method consists of the analysis of consecutive whisker sections (3-mm long) starting from the proximal (facial) end, with the most recently synthesized tissue remaining under the skin. Only individuals ($n = 47$) with whiskers totaling at least 30 sections were selected, and only those 30 sections were considered here (Sturbois, Cucherousset, et al., 2021a), from t_1 (more recent values) to t_{30} (oldest values). SITA was performed to track individual specialization within and among four fur seal populations. Different metrics (segments lengths, trajectory

TABLE 1 Characteristics of fur seal trajectory clusters: number of individuals (*n*), stable isotopes (SI), distance-based metrics, number of individuals depending of species and genders (female *A. gazella* [FAFS], male *A. gazella* [MAFS], female *A. tropicalis* [FSAFS], male *A. tropicalis* [MSAFS]) and breeding sites (Crozet [Cro], Kerguelen [Ker], Amsterdam [Am]). Values are means ± SE. Data sets from Kernaléguen et al. (2012)

		Whisker SI values		**Distance-based SITA metrics**			***n*/species-genders**				***n*/breeding places**		
Clusters	***n***	**δ^{13}C ‰**	**δ^{15}N ‰**	**Trajectory path**	**Segment length**	**Net changes**	**FAFS**	**MAFS**	**FSAFS**	**MSAFS**	**Cro**	**Ker**	**Am**
1	2	−22.29 ± 0.17	9.77 ± 0.20	21.77 ± 6.14	1.50 ± 0.21	3.86 ± 0.51		2			2		
2	19	−17.54 ± 0.04	10.52 ± 0.02	14.59 ± 0.99	0.99 ± 0.03	1.79 ± 0.09	15	1	3		13	6	
3	6	−16.65 ± 0.07	11.93 ± 0.07	19.61 ± 1.01	1.33 ± 0.03	2.70 ± 0.11		2		4	6		
4	4	−18.96 ± 0.23	11.39 ± 0.14	35.22 ± 3.51	2.36 ± 0.12	6.53 ± 0.24		4			4		
5	6	−16.57 ± 0.03	10.79 ± 0.03	9.39 ± 0.80	0.64 ± 0.03	1.21 ± 0.09			5	1	6		
6	10	−15.42 ± 0.02	13.32 ± 0.04	12.54 ± 0.55	0.84 ± 0.02	1.59 ± 0.06			10				10
Total	**47**						**15**	**9**	**18**	**5**	**31**	**6**	**10**

path, net changes, angle α) were calculated in the 2D Ω_δ space (δ^{13}C/δ^{15}N) for each individual. Dissimilarities between individual trajectories were calculated (directed segment path dissimilarity; De Cáceres et al., 2019), and was used with the resulting symmetric matrix as input in a hierarchical cluster analysis (ward.D2 clustering method), to define different groups of similar individual trajectories. Segment length, trajectory path length, and whisker δ^{13}C/δ^{15}N values were summarized to illustrate the trophic variability for each trajectory cluster. Hermans–Rasson and Watson–William tests were performed to test the homogeneity of angle distribution among trajectory within each cluster and the difference of segment direction between clusters. SITA metrics were represented in trajectory diagrams and a trophic TR.

Results

SITA revealed contrasted stable isotope dynamics among species, sexes, and individuals. Hierarchical cluster analysis identified six main trajectory clusters, characterized by differences in SITA metrics and whisker δ^{13}C/δ^{15}N values (Table 1 and Figure 2). Clusters 1, 3, and 4 were exclusively composed of trajectories corresponding to males, from AFS only (clusters 1 and 4) or from both species (cluster 3). These clusters were characterized by the highest values in distance-based metrics, revealing wider foraging strategies (Table 1). Clusters 1 and 4 were characterized by lower δ^{13}C values contrasting with cluster 3. Cluster 2, characterized by a lower isotopic variability, grouped all of the 15 AFS females from Crozet and Kerguelen and included also one AFS male and three SAFS females. Individuals in cluster 5 (five females and one

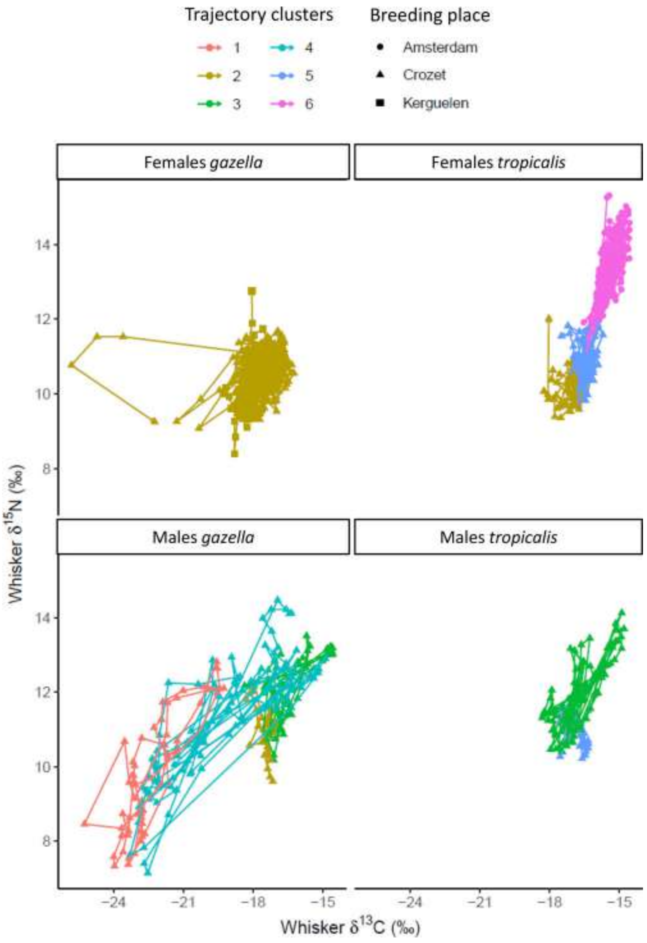

FIGURE 2 Individual fur seal trophic trajectories for males and females of *A. gazella* and *A. tropicalis*. Arrows connect all whiskers section stable isotope values from t_1 to t_{30} (i.e., most recent to oldest stable isotope values). Colors correspond to trajectory clusters and shapes to breeding sites. Data from Kernaléguen et al. (2012)

male SAFS from Crozet) exhibited the lowest isotopic variability. Cluster 6 was exclusively composed of SAFS females from Amsterdam, revealing a clear trophic segregation of females breeding there.

Different foraging strategies characterized by some overlaps, and partly influenced by breeding sites (Figure 2), were revealed for AFS males (distributed in four trajectory clusters) and SAFS females (three clusters). The time series of net changes (Figure 3, Table 1) revealed that each individual exhibited a more or less well defined trophic cycle whose amplitude and period depended on trajectory clusters. The distribution of trajectory segment directions (α angles) was heterogeneous for five of the six clusters (Herman–Rasson tests, $p > 0.05$) and some differences also existed among clusters (Figure 4).

Discussion

The estimated $\delta^{13}C$ values of the Polar Front and of the Subtropical Front for fur seal whiskers were approximately −19 and −16‰, respectively (Cherel et al., 2009). Accordingly, Kernaléguen et al. (2015, 2012) showed (1) a spatial foraging gradient from southern cold waters to northern and warmer areas for, in the order, AFS male, AFS female and SAFS male and female, (2) male benthic feeding strategy near breeding places, and (3) $\delta^{13}C$ and $\delta^{15}N$ oscillation patterns in most whiskers. Trajectory analysis results were congruent with those conclusions, but we went further showing that individual feeding strategies transcend pre-established categories such as species, genders, and breeding places, which was not primarily evident from analysis at the population level. This application confirms that SITA metrics and representations are relevant to track the shape and the magnitude of stable isotope trajectories in δ space, at different scales, from individual to population, and particularly to reveal subtle relevant functional patterns in spatio-temporal resource partitioning.

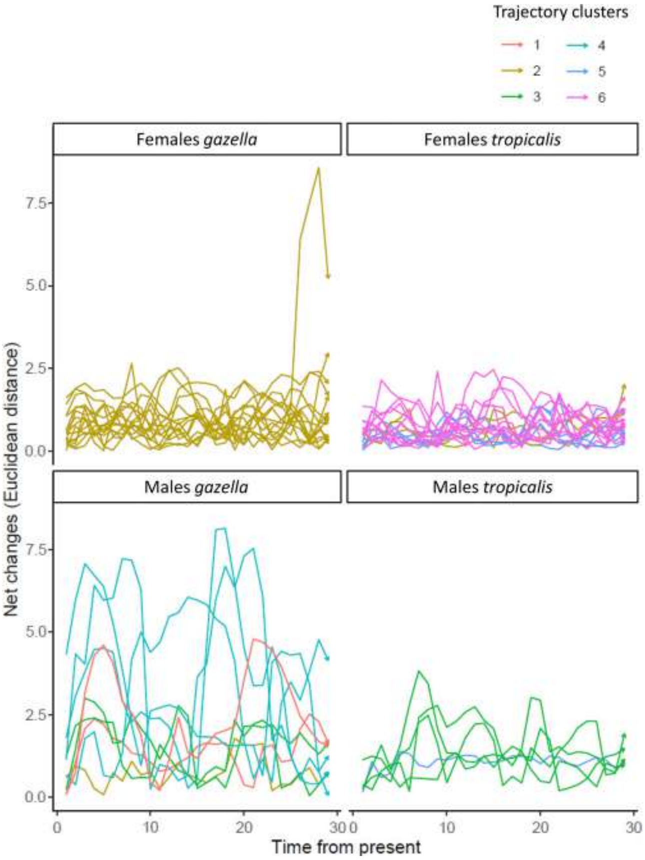

FIGURE 3 Fur seal individual trophic trajectories. Net change time series for males and females of both AFS and SAFS. Arrows connect all whiskers section stable isotope values from t_1 to t_{30} (i.e., most recent to oldest stable isotope values). Colors correspond to trajectory clusters. Data from Kernaléguen et al. (2012)

Ontogenic stable isotope trajectories of juvenile fish

Context

Intraspecific variability has strong ecological implications across levels of biological organization and can modulate the outcomes of individual life history. This is particularly true for movement along habitats, which is an ubiquitous phenomenon with important consequences on individuals.

Methods

Cucherousset et al. (2013) released 192 individually tagged, hatchery-raised, juvenile pike (*Esox lucius* L.) with variable body size and initial trophic position (fin $\delta^{13}C/\delta^{15}N$ values). Based on $\delta^{15}N$ values, individuals were classified into zooplanktivorous ($\delta^{15}N < 10‰$) and piscivorous ($\delta^{15}N > 10‰$), as cannibalism is commonly observed in this species. Individuals were released in a temporarily flooded grassland (FG) where pike eggs usually hatch in the Brière marsh (France) to identify the determinants of juvenile natal departure. The release site was connected through a unique point to an adjacent pond (AP) used as a nursery habitat. The pond strongly differs from the FG in many ecological features such as food availability (zooplankton and fish prey). Fish were continuously recaptured when migrating from the FG to the AP. Recaptured individuals ($n = 29$) were anesthetized, checked for tags, measured for fork length,

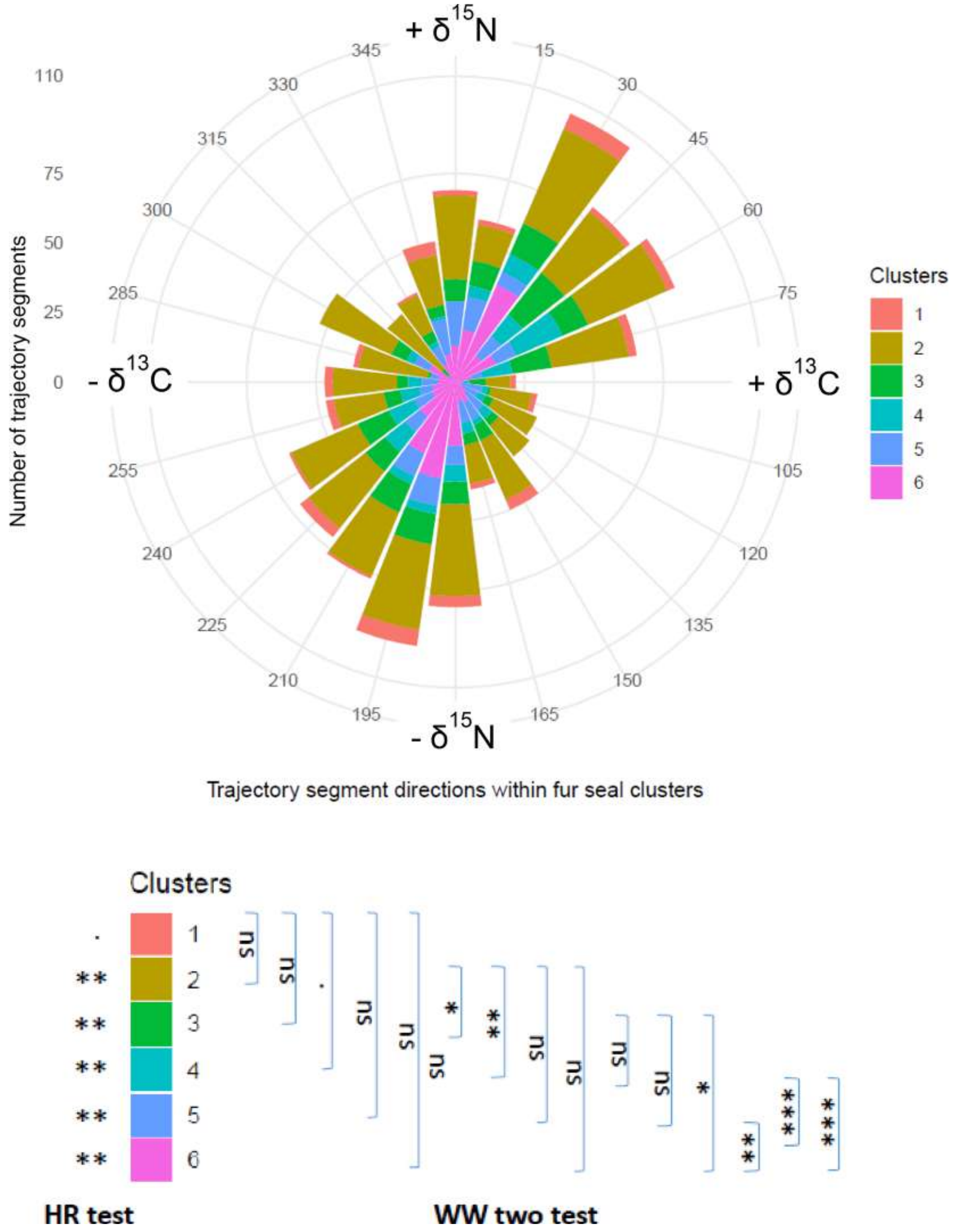

FIGURE 4 Angle α trajectory roses of fur seals trajectory cluster. Angle α was calculated in 2D Ω_δ space ($\delta^{13}C/\delta^{15}N$) and represented by range (15°) of direction. Bar size represents the number of trajectory segments (all individual within each trajectory clusters). Watson–William (WW) two test and Herman–Rasson (HR) test were used to test the difference between cluster and the uniformity of directions, respectively. (p-values: >0.05; * <0.05; ** < 0.01; < 0.001). Data from Kernaléguen et al. (2012)

fin-clipped to quantify changes in $\delta^{13}C$ and $\delta^{15}N$ values (Sturbois, Cucherousset, et al., 2021a), and released. Net changes and angle α were calculated in Ω_δ, and followed by hierarchical clustering of trajectories, as explained for the previous example.

Results

Overall, released individuals exhibited lower $\delta^{13}C$ (−2.49 ‰ ±0.82, mean ± SD) and $\delta^{15}N$ (−1.46 ‰ ± 0.89) when recaptured. The hierarchical cluster analysis

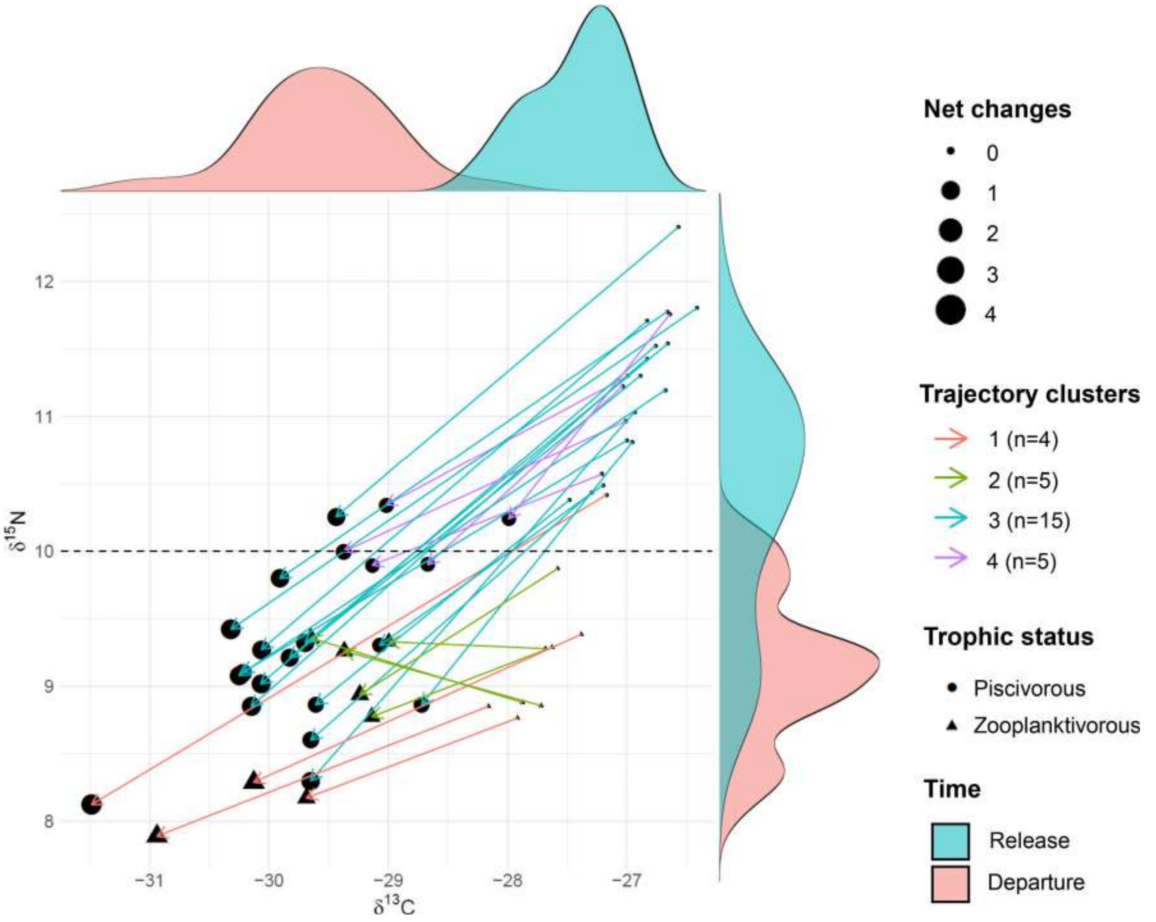

FIGURE 5 Trajectory diagram of pike released in a flooded grassland and recaptured when emigrating into an adjacent pond. Arrows represent the trajectory path for each pit-tagged individual. Colors correspond to trajectory clusters. Density curves at the periphery of the trajectory diagram represent the distribution of all samples according to $\delta^{13}C$ (*x*) and $\delta^{15}N$ (*y*), and capture (green = release; red = departure). The dashed line separates piscivorous from zooplanktivorous individuals (zooplanktivorous [$\delta^{15}N < 10$‰] vs. piscivorous [$\delta^{15}N > 10$‰]). Data from Cucherousset et al. (2013)

TABLE 2 Characteristics of pike trajectory clusters: number of individuals (*n*), residence time in flooded grassland (Res. time), size shift (mm), growth rate (mm day^{-1}), SI shift, SITA metrics, trophic status at release (zooplanktivorous [$\delta^{15}N < 10$] vs. piscivorous [$\delta^{15}N > 10$]). Values are means ± SE (±SD for total). Data sets from Cucherousset et al. (2013)

					SI shifts		SITA metrics		Trophic status	
Clusters	***n***	**Res. time**	**Size shift**	**Growth rate**	**$\delta^{13}C$ ‰**	**$\delta^{15}N$ ‰**	**Net changes**	**Angle α**	**Zplankt.**	**Pisciv.**
1	4	18.50 ± 0.87	35.25 ± 1.44	1.90 ± 0.38	−2.90 ± 0.20	−1.24 ± 0.14	3.16 ± 0.63	248.14 ± 2.17	3	1
2	5	18.20 ± 0.86	34.40 ± 0.71	1.90 ± 0.23	−1.58 ± 0.03	−0.10 ± 0.11	1.67 ± 0.10	266.57 ± 8.89	5	
3	15	13.67 ± 1.42	26.13 ± 4.78	1.91 ± 0.10	−2.90 ± 0.28	−2.10 ± 0.19	3.13 ± 0.26	233.92 ± 1.35		15
4	5	9.60 ± 1.21	18.20 ± 1.71	1.96 ± 0.18	−1.86 ± 0.17	−1.09 ± 0.15	2.63 ± 0.42	239.12 ± 5.53		5
Total	**29**	**14.41 ± 5.14**	**27.45 ± 10.06**	**1.92 ± 0.27**	**−2.49 ± 0.82**	**−1.46 ± 0.89**	**2.95 ± 1.02**	**242.41 ± 15.60**	**8**	**21**

performed on pike trajectory dissimilarities matrix between release at FG and departure to AP separated four main trajectory clusters (Figure 5 and Table 2). Clusters 1 and 2 grouped mostly zooplanktivorous individuals at release, characterized by late emigration to the pond (18.50 ± 0.87 and 18.20 ± 0.86 days, mean ± SE). Cluster 1 was characterized by higher net changes (3.16 ± 0.63) and more uniform direction (248.14° ± 2.17) than cluster 1 (1.67 ± 0.10; 266.57° ± 8.89). Clusters 3 and 4 grouped initially piscivorous individuals. High $\delta^{15}N$ values for most individuals at emigration suggested either that these individuals kept feeding at higher trophic levels than individuals from clusters 1 and 2, or a post-release period in the FG not long enough to reach the isotopic equilibrium. Difference in residence time (i.e., 13.67 ± 1.4 and 9.60 ± 1.2 for clusters 3 and 4 respectively) was responsible for the difference in δ^{15}N values between these two clusters (i.e., there was less time for hatchery SI values of cluster 3 to be diluted in FG stable isotope values). Among all clusters, the growth rate was very similar (1.92 ± 0.27 $\mathrm{mm \cdot day^{-1}}$).

Discussion

Results obtained using SITA confirm the initial findings and interpretation in Cucherousset et al. (2013) but also provided additional information. The cluster analysis of trajectory dissimilarity allowed an efficient discrimination of trajectory patterns. Although these patterns were briefly discussed in the initial study, we were able to define trajectory and SI properties in the four clusters, which clearly separated different ontogenic strategies among released individuals. Furthermore, the use of the TD offered a more complete representation of (1) trajectories properties at the population level (density curves), and (2) clusters and individuals levels (individual trajectory paths).

Trophic consequences of experimental warming on lizards

Context

Climate change is an important facet of ongoing environmental changes induced by human activities. While there is an increasing knowledge of how species will respond to climate changes in term of distribution, our ability to understand and predict changes in biotic interactions, such as predator–prey dynamics, is limited.

Methods

Bestion et al. (2019a) experimentally quantified the consequences of a 2°C warming on the trophic niche of a generalist lizard predator (*Zootoca vivipara*). Climate was manipulated in a 10 × 10 m enclosure with similar natural vegetation and invertebrate communities, and a wide variety of thermal microhabitats (dense vegetation, rocks and logs, ponds; see Bestion et al. [2019a] for more details). In June 2013, individuals belonging to two life stages (juveniles and adults) and from both sexes were allocated at similar density to 10 enclosures: five enclosures with a "present-day climate" and five enclosures with a "warm climate," that is, 2°C warmer on average. There was no difference in δ^{13}C and δ^{15}N values between treatments at the start of the experiment. In mid-September 2013, surviving lizards were recaptured and a tail tip was collected for SI analysis. Because SI values of trophic resources varied among enclosures, a baseline correction ($\delta^{13}C_{cor}$ and $\delta^{15}N_{cor}$) was performed to allow between-treatment comparisons (Bestion et al., 2019a, 2019b). Enclosures from the two treatments were paired in five blocks (A–E used as replicates), and used to characterize, respectively, the initial (present-day climate) and final (warmer climate) states of a one-segment trajectory for five paired lizard populations in response to warming. Because the analysis focused particularly on shifts rather than absolute SI values, we favored the representation of net change and angle α, calculated in Ω_δ, in TR.

Results

Some differences in the magnitude of trajectories were observed among pairs of enclosures (Figure 6). Block C was characterized by the highest net change (1.63 ± 0.19) for all individuals (adults and juveniles of both sexes), whereas shifts in SI values in response to warming were more limited in other blocks (A: 0.36 ± 0.15; B: 0.39 ± 0.36; D: 0.55 ± 0.44; E: 0.47 ± 0.21‰). Some differences were also observed within paired enclosures where net changes were contrasted between individuals. For instance, in block D, adult males displayed the highest response (1.12), whereas juvenile females displayed the lowest response (0.12). Differences were also observed in the direction of the trajectories (Figure 6). In block C, all individuals displayed similar directional changes (10.23 ± 3.88°) with trajectories mainly implying increase in $\delta^{15}N_{cor}$ values and limited $\delta^{13}C_{cor}$ shifts. The other blocks displayed more variable responses to warming. For example, individuals from block A exhibited different directions in Ω_δ, revealing different patterns of SI changes.

Discussion

Using conventional statistical analyses, Bestion et al. (2019a) concluded that lizards from warmer conditions had higher $\delta^{15}N_{cor}$ values, whereas nonsignificant changes in $\delta^{13}C_{cor}$ values were observed. By pairing enclosures for trajectory analysis, SITA results were in accordance with these findings, but they also highlighted the existence, in some cases, of other responses to warming, with approximately

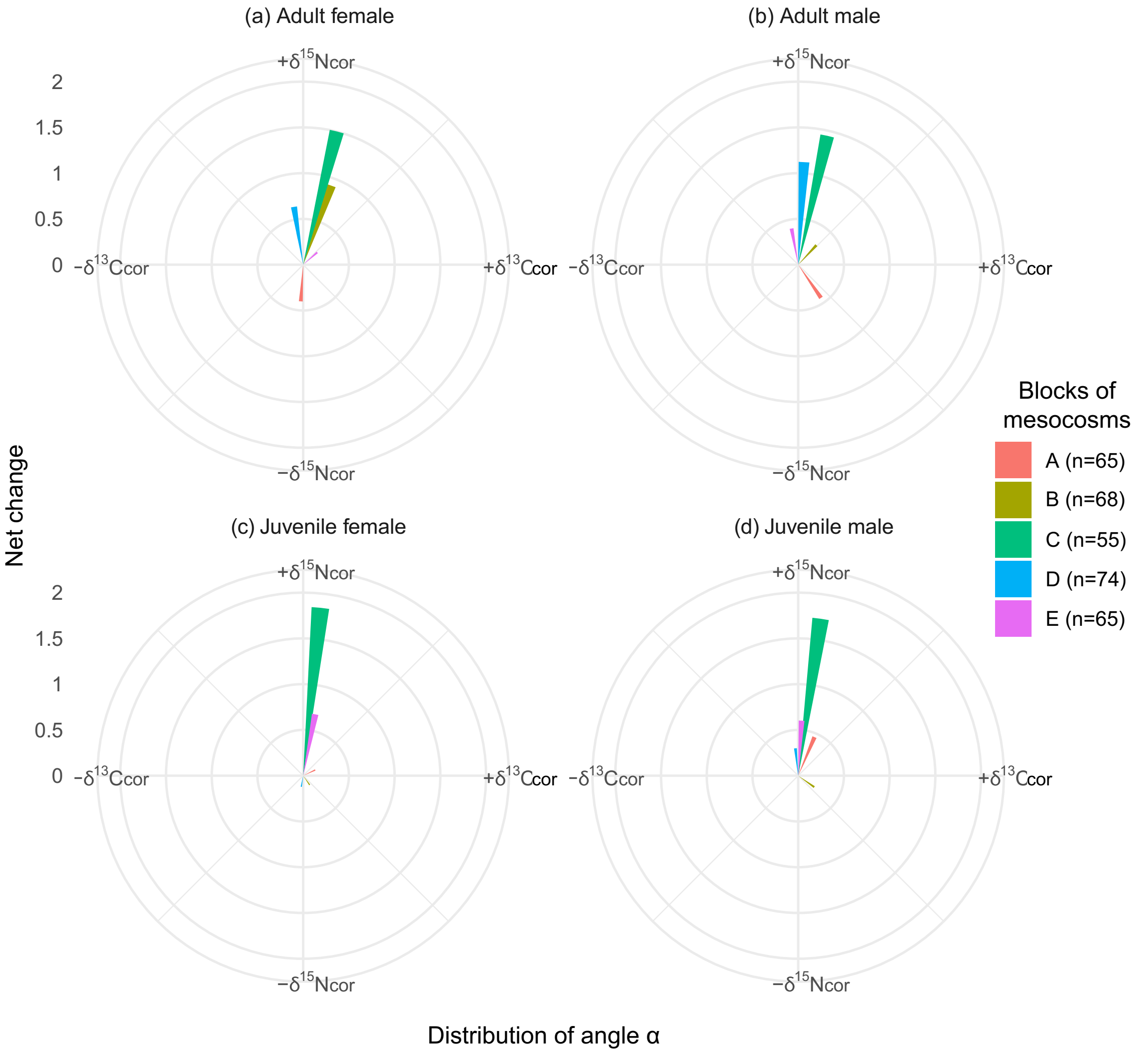

FIGURE 6 Angle α trajectory roses for each lizard life stage/sex categories within each block of enclosures (warming between present day and warm treatments). Angle α was calculated in 2D Ω_δ space ($\delta^{13}C_{cor}$ and $\delta^{15}N_{cor}$). Bar size represents the net change for each enclosure block (colors) and each life stage/sex (a: adult females; b: adult males; c: juvenile females; d: juvenile males). Data from Bestion et al. (2019b)

25% of all individuals (life stage, sex and blocks) displaying slight decreases in $\delta^{13}C_{cor}$ and $\delta^{15}N_{cor}$ values. These findings may reveal some additional context dependency in the response to warming observed at the individual level.

Contrasted trajectories in pristine and impacted sandy beaches undergoing green tide events

Context

Excess nutrient inputs is one of the most important human-induced pressures in freshwater and marine water bodies. The assessment of the consequences of the resulting eutrophication on ecosystems functioning is necessary to identify and describe disturbance pattern, especially in comparison with unperturbed habitat.

Methods

Quillien et al. (2016) studied changes in sandy beach (SB) food web structure and functioning in response to green algae proliferation during green tide (GT) events. Fieldwork was conducted seasonally in the bay of Douarnenez (Brittany, France) in May, July, September and November 2012 at two SB: one impacted by GT events and the other under pristine conditions (No_GT). Sampling and laboratory steps performed for community and SI analyses were described in Quillien et al. (2016). Trophic trajectories in pristine and impacted SB were analyzed both at the food web (1) and basal source/centroid/population (2) levels. At the food web level, functional diversity indices (Villéger et al., 2008) were calculated in the SI space (Sturbois, Cucherousset, et al., 2021a) as proposed by Cucherousset and Villéger (2015) and Rigolet et al. (2015): Isotopic functional richness (IFRic), evenness (IFEve) and divergence (IDFiv). Mean distance to nearest neighbor (MNN) and centroid (MDC) were also calculated. Patterns of biomass were assessed by weighting SI values of every species prior to indices calculations. A principal component analysis (PCA), followed by SITA was performed on trophic indices (Ω_γ) to analyze changes in food webs properties at pristine and impacted SB over time. Distance (segment length, net changes) and direction-based metrics (DIR, angle Θ) were calculated. SITA was complementarily performed in Ω_δ defined with $\delta^{13}C$ and $\delta^{15}N$ values (Sturbois, Cucherousset, et al., 2021a) for basal sources and food web centroids. Distance-based metrics were calculated and trajectories at the different levels were represented in trajectory diagrams.

Results: Structural and functional trajectories

The pristine SB was characterized by a lower structural and functional temporal variability (trajectory path = 6.09, mean segment length = 2.33 ± 0.48) than impacted SB (16.13, 5.38 ± 1.46) (Figure 7). Low DIR indicated non-straightforward trajectories for both sites (No_GT = 0.45 vs. GT = 0.33). Considering the first two Ω_γ dimensions, responsible for 92% of the total variance, the first trajectory segments (i.e., between May and July) were quite similar in direction for both sites (angle α: No_GT = 89.06° vs. GT = 69.07°) but different in magnitude (S1 length: No_GT = 2.29 vs. GT = 5.43), therefore highlighting similar trends of index values, except for IFDiv (Figure 7). For GT SB, S1 and S2 were followed by a directional rupture in Ω_γ ($\Theta_1 = 107.00°$; $\Theta_2 = 133.14°$) implying contrasted functional and structural shifts. At No_GT SB, S2 followed a more straightforward path, whereas S3 was characterized by an important direction change ($\Theta_1 = 34.03°$; $\Theta_2 = 138.90°$). At the scale of the overall study period, structural and functional variability was higher in SB harboring GT (NC = 4.74) than in pristine SB (NC = 3.30). Between May and November, pristine SB was characterized by positive shifts in IFRic, and MDC and MNN, and negative shifts in IF Eve and IFDiv. At GT SB, IFDiv and IFRic were characterized by a moderate increase, whereas MNN, IFEve, and MDC decreased. At the scale of each trajectory segment, No_GT SB was mainly characterized by shifts in IFRic values, whereas GT SB was typified by highest magnitudes of changes and contrasted shifts. Specifically, the decrease in MDC and MNN values occurring between July and September started to recover in November.

Sources/centroid-specific trajectories in the $\delta^{13}C$ and $\delta^{15}N$ space

Basal sources trajectories were longer, therefore highlighting a high variability in SI values (Figure 8). Whereas particulate organic matter (POM) in impacted and pristine beaches exhibited similar trajectory length (6.67 vs. 5.99), sedimentary organic matter (SOM) was characterized by a lower variability where GT occurred (3.66 vs. 6.05). *Ulva* spp. was characterized by the highest SI variability (8.56). Specifically, POM trajectories at both sites were similar in terms of nature, seemingly cyclic, but different in magnitude. SOM at both sites depicted more complex trajectories, with similar but not synchronized SI trends, notably in September and November (i.e., November SOM No_GT vs. September SOM GT, and inversely). Trajectories of centroids did not reflect the magnitude of basal sources dynamics in GT (trajectory path = 1.40, net change = 0.76) and No_GT SB (1.62, 0.53). Trajectories of basal sources and centroid highlighted a constant enrichment in ^{13}C, except for SOM in September, while $\delta^{15}N$ patterns were less obvious.

Discussion

Results were congruent with the conclusions of Quillien et al. (2016) that showed a simplification of food web structure and functioning in the SB where the GT tide occurred. The consideration of SI dynamics at basal sources and centroids levels helps to better understand structural and functional trajectories at both sites. The interest in SITA was due to the consideration of both sites through their own dynamics exhibited at different levels. Specifically, SITA pointed out (1) low differences and variability of food web centroids at both beaches, and (2) contrasted structural and functional trajectories depicting the initiation of two potential food web cycles, which differed in nature and magnitude.

Biological invasions and trophic structure dynamics of lake fish communities

Context

Community assembly can strongly impact the dynamics of biological diversity and the functioning of ecosystems

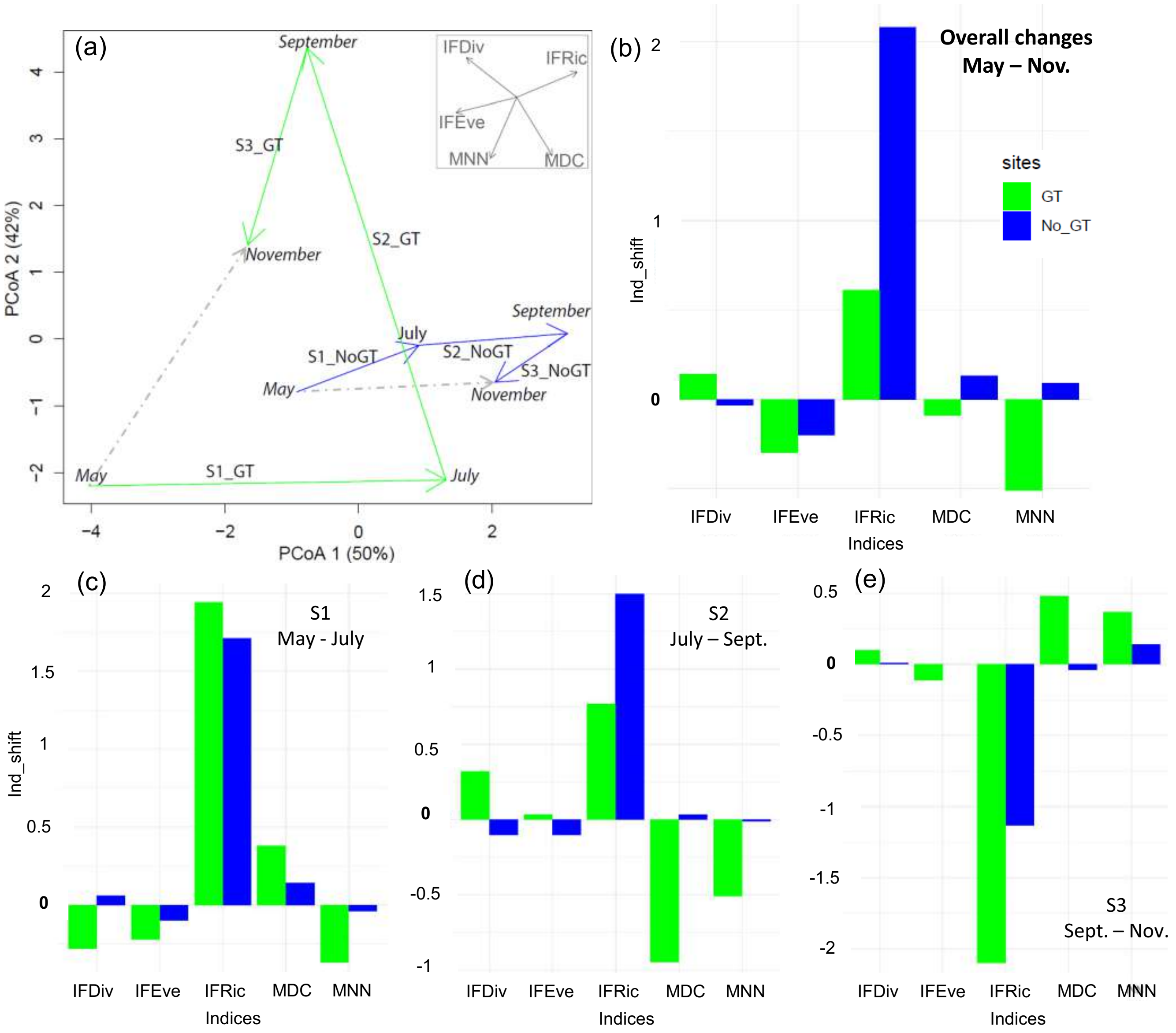

FIGURE 7 Structural and functional trajectories at impacted (green) and pristine (blue) beaches. (a) Trajectory diagram in Ω_{γ} space. Only two dimensions are shown, representing 92% of the total variance. Solid lines ending with an arrow represent segment lengths and dotted arrow net changes. (b–e) Bar plots represent the shift in value of five structural and functional indices: isotopic functional richness (IFRic), evenness (IFEve), divergence (IDFiv), and mean distance to nearest neighbor (MNN), and centroid (MDC). Bar plot panels show changes in indices values between May and November (b) and for all pairs of consecutives periods (c: May to July, d: July to September, e: September to November). Data from Quillien et al. (2016)

(Bannar-Martin et al., 2018). Environmental changes strongly affect the way species interact and how communities assemble and it is therefore important to assess how the trophic structure of communities will respond to these changes.

Methods

This question was investigated by quantifying the temporal dynamic of the trophic structure of fish communities in a network of gravel pit lakes displaying varying levels of biological invasions (Zhao et al., 2019). Fish were sampled in 2014, 2016, and 2018 using a standardized protocol (gill netting and electrofishing) in six gravel pit lakes located along the Garonne river (Figure 9) (Alp et al., 2016; Evangelista et al., 2017; Zhao et al., 2019). Fish were identified at the species level, counted, measured, and fin clips were collected for $\delta^{13}C$ and $\delta^{15}N$ analyses.

The overall data set (all lakes and sampling year pooled) included 19 species. Five species were present in more than 75% of all communities (18 lakes × years): two non-native species, namely pumpkinseed (*Lepomis*

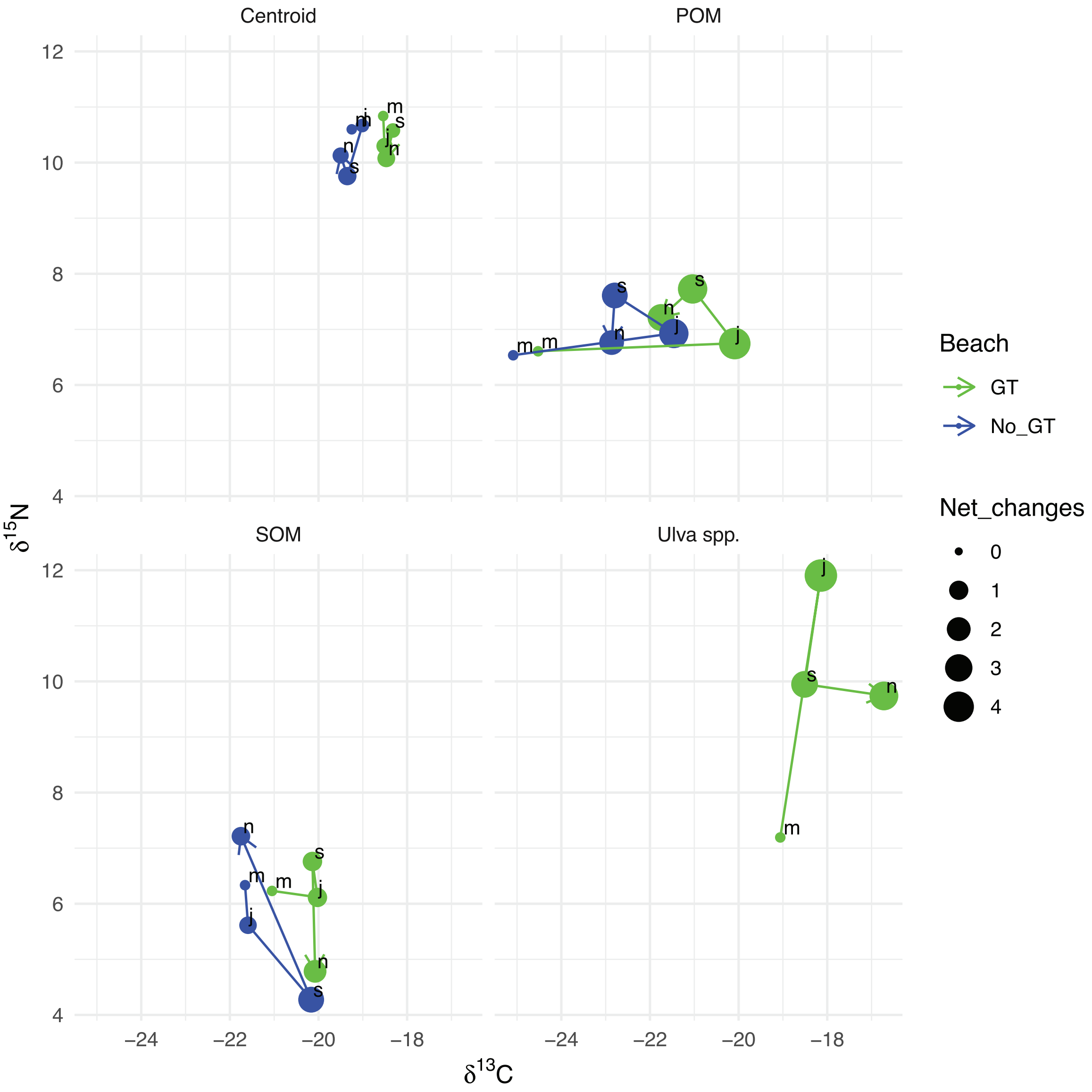

FIGURE 8 Trajectory diagram of food web centroids and basal sources at impacted and pristine beaches. Panels represent specific trajectories for food web centroid, particular organic matter (POM), sedimentary organic matter (SOM), and *Ulva* spp. Size of dots corresponds to net changes, arrows to trajectory path, and colors to beach (GT: green, No_GT: blue). Data from Quillien et al. (2016)

gibbosus) and black bullhead (*Ameiurus melas*) and three native species, namely roach (*Rutilus rutilus*), perch (*Perca fluviatilis*) and rudd (*Scardinius erythrophthalmus*). Rarer species such as *Oncorhynchus mykiss*, *Gymnocephalus cernua*, *Anguilla anguilla*, and others were sampled only for 1 year in one lake. Across all sites and all years, the most abundant species included two invasive species mosquitofish (*Gambusia affinis*) (22.98 ± 18.35%) and black bullhead (17.46 ± 16.37%) followed by the native roach (15.72 ± 14.55%).

The variability of frequency and relative abundance among lakes and years illustrated the strong community dynamics occurring in lakes. A trajectory analysis was performed to determine if changes in community composition were associated to changes in the SI structure of communities over time. Four SI structure indices (namely isotopic richness, δ^{13}C range, δ^{15}N range, isotopic evenness following Cucherousset & Villéger, 2015 and Layman et al., 2007) were calculated (Sturbois, Cucherousset, et al., 2021a) using abundance data and used in SITA for Ω_γ. Distance (segment length, net change, trajectory path, NCR, RDT) and direction-based (angle Θ, directionality) were calculated and are represented in TD and maps.

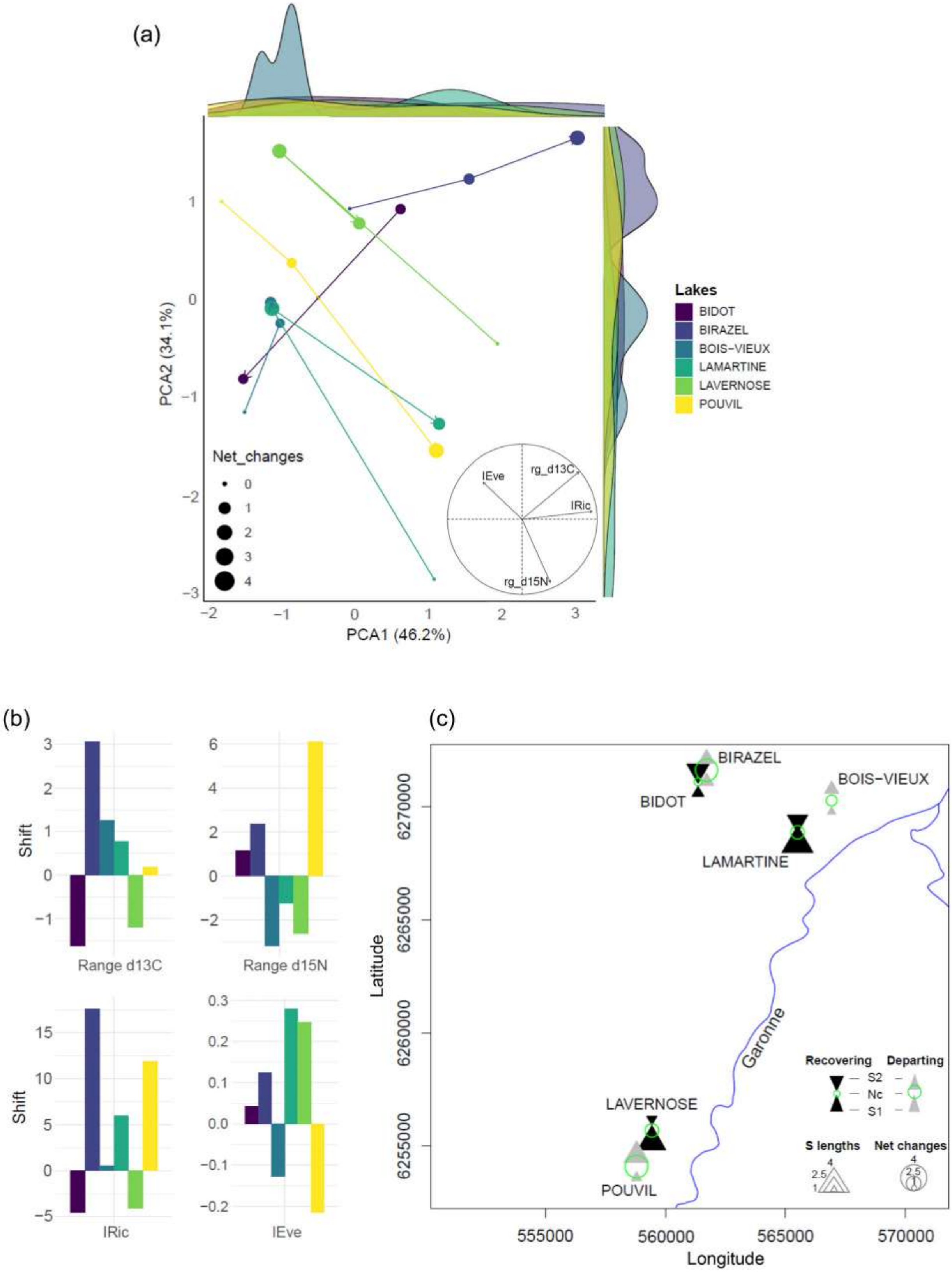

FIGURE 9 Structural trajectories of fish communities in six gravel pit lakes. (a) Trajectory diagram in Ω_γ space. Only two dimensions are displayed, representing 80.3% of the total variance. Bar plots represent the shift in the value of four structural indices: isotopic functional richness (IFRic), evenness (IFEve), and δ^{13}C and δ^{15}N ranges. (b) Bar plot panels show changes in indices values. (c) Structural trajectory map: net changes (Nc) are represented with green circles between 2014 and 2018. Bottom triangles represent S1 (2014 to 2016) and top ones S2 (2016 to 2018). The size of the symbols corresponds to segment lengths. For triangles, colors are used to distinguish recovering (black) from departing trajectories (gray)

Results

SITA highlighted a high level of variability between lakes. Lakes Lamartine (trajectory path: 6.70), Lavernose (4.95) and Bidot (4.45) were characterized by a recovering pattern (Figure 9a,c) between 2016 and 2018, as indicated by high angle Θ (146.05°, 164.09°, 172.41°), low DIR (0.19, 0.09, 0.04) and moderate NCR (0.35, 0.48, 0.31) values, respectively. The efficiency of the recovering pattern contributed to low net changes (2.37, 2.37, 1.38). In the opposite, lakes Pouvil (TP: 4.54), Birazel (3.94) and Bois-Vieux (2.90) were characterized by different trajectory patterns characterized by lower angle Θ (63.25°, 16.22°, 100.99°), and higher DIR (0.65, 0.91, 0.44) and NCR (0.88, 0.99, 0.66) values. Differences were also observed in the nature of the structural trajectories among lakes (Figure 9a,b). Specifically, the structural trajectory of Lake Bidot was mainly characterized by a decrease in the δ^{13}C range, contrasting with Lake Birazel trajectories that were mainly characterized by a strong increase in δ^{13}C range and isotopic richness, and a moderate increase in δ^{15}N range and isotopic evenness. We also found that the structural trajectories of Lake Pouvil were primarily characterized by a strong increase in δ^{15}N range and isotopic richness and a decrease in evenness.

Discussion

SITA approach provided a global and quantitative analysis to compare the magnitude and nature of structural change over time and across multiple lakes with different invasion levels. Coupling distance and direction-based metrics underlined the recovering and departing trajectories characterized by contrasting changes in isotopic indices. In some lakes, exhibiting departing trajectories, direction-based metrics underlined persistent changes through strong linear trajectories, while potential cyclic dynamics were suggested for recovering lakes over the study period. The TM constitutes a synthesis of distance-based metrics and an efficient way to compare the structural food web variability of all lakes. The SITA approach could therefore help to understand the patterns of trophic structure variability in disturbed ecosystems.

Spatio-temporal variability of δ^{13}C and δ^{15}N modeled isoscapes in the northeast Pacific

Context

Isoscapes are increasingly used to assess the relative trophic position of higher trophic levels, to provide information on the relative productivity of different regions, and they can also be used to track the migration of animals. Despite isoscapes providing a wide distribution of the variations of SI values, this tool is currently limited for the synthetic analysis of SI dynamics.

Methods

Espinasse et al. (2020) tested the application of isoscapes modeled from satellite data to the description of secondary production in the northeast Pacific. Several key parameters (sea surface temperature, sea level anomaly, and chlorophyll *a*) were used as inputs on a general additive model. The output model fits in a 0.25° × 0.25° spatial grid covering the region spanning from 46 to 62°N and from 195 to 235°E and supporting δ^{13}C and δ^{15}N isoscapes from 1998 to 2017 (Espinasse, 2020). We subset modeled δ^{13}C and δ^{15}N values of a 1° × 1° spatial grid from the original modeled dataset. Isoscapes modeled for 2013, 2015, and 2017 were selected as they were characterized by high SI dynamics and consequently constituted relevant inputs to test our ITM concept. Modeled SI values for which one of the parameter was missing were excluded. Mapping trajectory metrics requires that stations are synchronously surveyed. Consequently, stations where values were missing for one date within each pair of dates (2013–2015 and 2015–2017) were also excluded. The subset of stations supporting SITA was finally composed of 489 and 488 stations for the periods 2013–2015 and 2015–2017, respectively. Segment lengths (2013–2015 and 2015–2017), and angle α were calculated in the modeled 2D Ω_δ space (δ^{13}C/ δ^{15}N) for all stations and periods and used as input in a modeled ITM. RDT and overall NCR were also calculated to qualify departing or recovering patterns between 2015 and 2017 with respect to the δ^{13}C and δ^{15}N values modeled in 2013. Additionally, a long-term SITA was performed from 1998 to 2017, using directions and net changes calculated for all pairs of dates (1998–1999, … , 2016–2017) as input for a TH.

Results

Modeled ITM revealed contrasted dynamics between 2013–2015 and 2015–2017 (Figure 10). While differences in the nature of changes (i.e., direction) were highlighted in the ITM, the overall magnitudes of the dynamics were similar (total segment length = 638.90 between 2013 and 2015 vs. 620.41 between 2015 and 2017). A few areas concentrated an important part of the overall dynamics, especially in the southeast part and, to a lesser extent, in

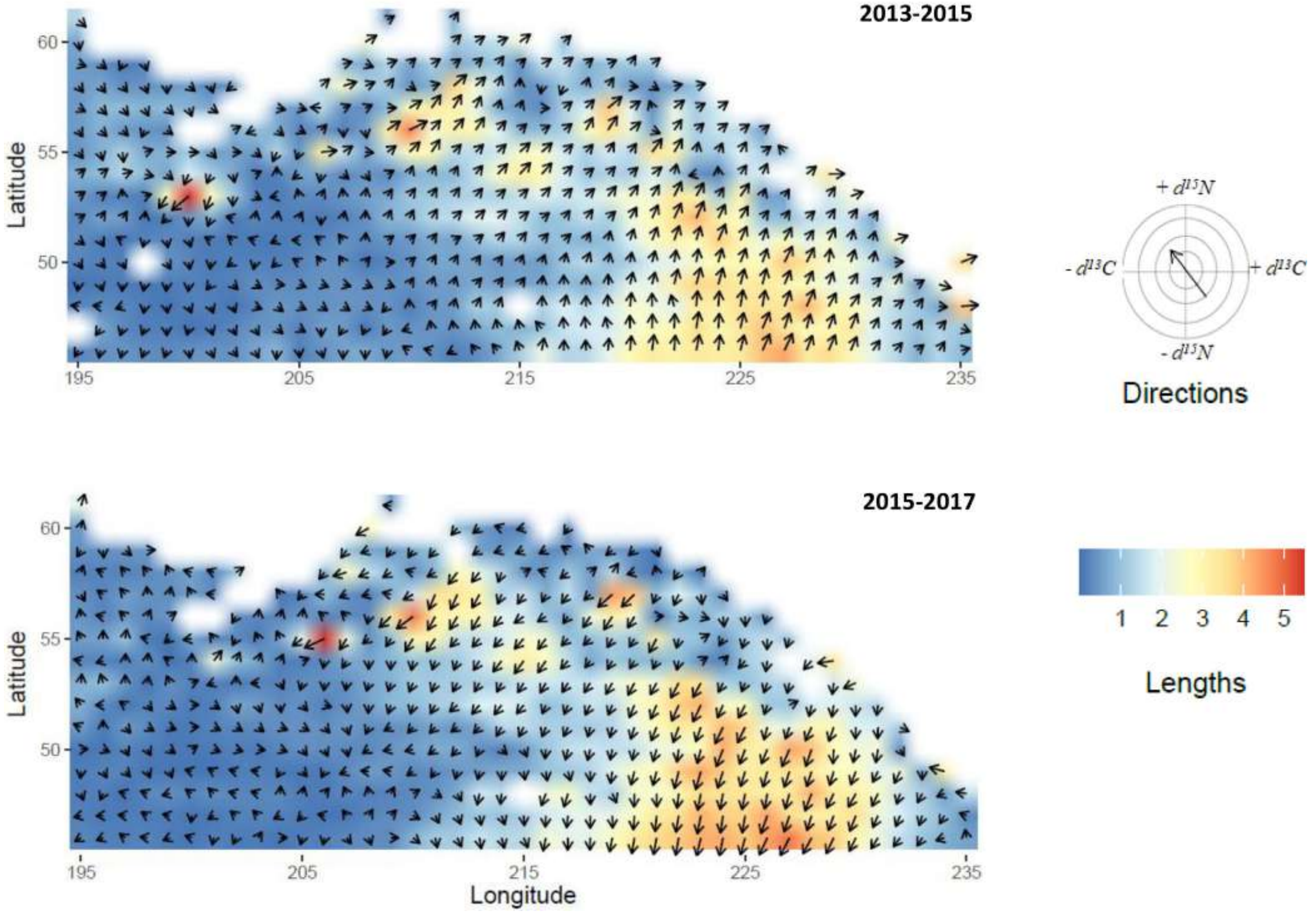

FIGURE 10 Isoscape trajectory maps in the northeast Pacific for the periods 2013–2015 and 2015–2017. SITA metrics were mapped to illustrate stable isotope spatio-temporal dynamics. Direction of arrows (angle α) illustrates direction in the modeled 2D Ω_δ space according to increase and/or decrease in δ^{13}C and δ^{15}N values (0–90°: +δ^{13}C and +δ^{15}N; 90–180°: +δ^{13}C and −δ^{15}N; 180–270°: −δ^{13}C and −δ^{15}N; 270–360°: −δ^{13}C and +δ^{15}N). Length of arrows and colored background rasters illustrate modeled trajectory segment length at each station. Data from Espinasse et al. (2020)

the northern part of the modeled area. The ITMs suggested an overall recovering pattern between 2015 and 2017 with respect to the model defined in 2013, which was confirmed by an RDT < 0 for 76% of stations and a low overall mean of NCR values (0.21).

The TH (Figure 11) revealed that angle α ranging from 0 ° to 90° and 180° to 270° was the most frequent from 1998 to 2017. While SI trajectories characterized by increases in δ^{13}C and δ^{15}N values alternated with patterns of decrease in both isotope values and exhibited the major part of the overall changes, some fine scales patterns were also revealed at the beginning of the modeled period.

Discussion

The ITM provides a relevant visual synthesis of (1) spatio-temporal dynamics complementary to (2) modeled isoscapes. (1) ITM, including trajectories of two SI, highlight areas of high variability associated with eddies that enhanced local production in the open ocean (Espinasse et al., 2020). It also allowed the easy identification of areas with SI values that were stable over time, which is useful for animal tracking studies (Trueman & St John Glew, 2019). (2) Modeled isoscapes also illustrate this pattern beyond the decrease in δ^{13}C and δ^{15}N values from the coast to offshore (Espinasse et al., 2020). One solution to identify this second pattern in the ITM may exist in the addition of trajectory clusters (color of vectors) from a trajectory similarity analysis. In such cases, users should be careful with the figure readability. The main advantage of this concept of TM lies in its ability to synthesize spatio-temporal dynamics from four isoscapes, which is a major challenge when dealing with massive amounts of spatialized data.

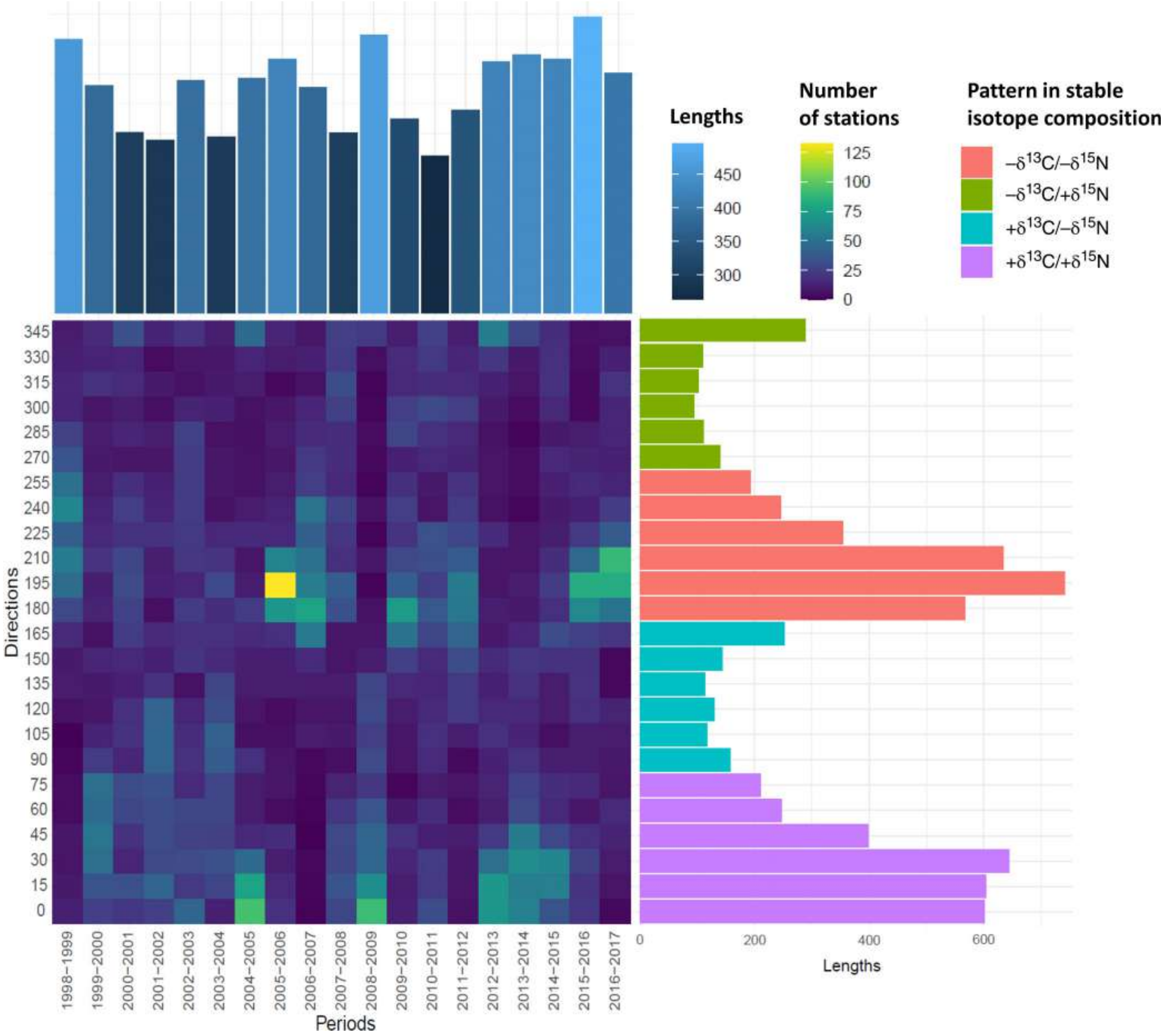

FIGURE 11 Trajectory heatmap. *Heatmap panel*: Angle α in the modeled 2D Ω_δ space exhibited by all stations within all pairs of dates (1998–1999, ... , 2016–2017) are represented by the range of direction (15°) according to period. Color gradient from dark blue to yellow indicates the number of stations exhibited by a given range of direction within a given period. *X* barplot: Sum of segment lengths across stations and times, exhibiting the chosen angle. The blue gradient indicates the net change magnitude. *Y* barplot: Overall net changes according to range of directions (angle α). Bars are colored according to increase and/or decrease in δ^{13}C and δ^{15}N values (Pink: 0–90°: $+\delta^{13}$C and $+\delta^{15}$N; Blue: 90–180°: $+\delta^{13}$C and $-\delta^{15}$N; Red: 180–270°: $-\delta^{13}$C and $-\delta^{15}$N; Green: 270–360°: $-\delta^{13}$C and $+\delta^{15}$N). Data from Espinasse et al. (2020)

The TH provides an effective synthesis of high temporal resolution SI dynamics for a 20 years period, highlighting cyclic patterns of enrichment and depletion in ^{13}C and ^{15}N isotopes. Coupled with quantitative SITA metrics, ITM and TH appear as promising tools for isoscapes space–time analyses. These innovative figure concepts allow the illustration of differences in the magnitude and nature of spatio-temporal SI dynamics, and they can be easily coupled with statistics to track accurately significant patterns in high resolutions data sets.

DISCUSSION

Building on previous works dealing with ecological dynamics in SI ecology, we adapted CTA to provide a formal and explicit framework for the analyses and representations of spatial and temporal trajectories in SI ecology. The different examples used here, sourced from marine, terrestrial, and freshwater ecosystems, illustrate the insights provided by this new analytic framework. SITA originates from the CTA framework, and we believe that the representation solutions proposed here (e.g., trajectory diagrams, TH) are also easily transferable to many different fields of ecology, including community ecology.

Tracking stable isotope dynamics with SITA metrics

Distance- and direction-based metrics provide quantitative synthetic information and allow effective comparisons at the individual, population, community, and ecosystem scales, all being relevant scales that are widely explored in ecology (Layman et al., 2012). Our approach was complementary to original analyses in the different application data sets. Coupled with the calculation of distance- and direction-based metrics, the analysis of trajectory similarity helped to highlight contrasted individual strategies that were not revealed from analysis at the population level, because they did not systematically follow species, age, or gender *a priori* classifications (EA1 and 3). When applied at the individual to the population levels, SITA allows the study of the shape and the magnitude of stable isotope trajectories to track for resource partitioning (EA1), adaptation to a changing environment (EA2, EA3 and EA4), or animal migrations (EA1). The SITA framework allows the measurement of changes in terms of both stable isotope composition (Ω_δ), and structure and functioning (Ω_γ), which is useful and relevant for understanding contrasted food web dynamics in response to environmental or anthropic pressures (EA4). The definition of recovering and departing patterns with respect to initial states highlights different dynamics through the distinction of sites characterized by long-term changes from those characterized by ecological periodicity (EA5), or unexplained, seemingly chaotic, variability. SITA can also identify shifts and cycles in the composition of sources (EA4, EA6). While not illustrated here, using mixing models to define Ω (see p-spaces defined in Newsome et al., 2007) supporting SITA seems a very promising avenue to track temporal changes in the proportion of resources fueling consumers and potential energy pathway dynamics.

SITA contributes to achieving the synthetic challenge inherent to high spatio-temporal resolution datasets, independently of the size of the study area and/or the length of the time series. This ability to deal with large datasets seems especially relevant in the context of isoscape dynamics in widespread and/or intensively studies area, as shown for SI dynamics in the northeast Pacific water body (EA6).

Differences in SITA metrics can be tested statistically as illustrated with circular statistics for direction-based metrics (EA1). Users are encouraged to use complementary statistical approaches, such as regression or correlation tests, to explore the relationship and the strength of the relationship between distance-based metrics and other explanatory variables under natural, anthropogenic, or experimental conditions.

Representing spatio-temporal dynamics in stable isotope ecology

The recent CTA extension (Sturbois et al., 2021) showed the importance of plotting trajectory metrics in specifically designed figure concepts, adapted for the representation of dynamics. Building on this, and on previous attempts in SI ecology (Agostinho et al., 2021; Cucherousset et al., 2013; Schmidt et al., 2007), we proposed here two new figure concepts specifically devoted to the representation of dynamics at large spatio-temporal scales: the ITM and the TH (Figures 10 and 11). Here, we have chosen the figure concepts that we deemed the most suitable for each ecological application. We believe that these entire figure concepts are strongly complementary and that users should explore all figure concepts and metrics, finally selecting the ones most adapted to the relevant hypotheses.

To improve the representation of dynamics through trajectory diagrams, users could innovate in the representation of trajectory metrics. For example, the customization of diagram traditionally used in SI ecology with arrows, density curve, net changes, and trajectory clusters together brings new perspectives in the visualization of ecological dynamics (EA1, EA2, EA4, and EA5). Trajectory roses offer innovative ways to represent directions. We went beyond the arrow diagrams proposed by Schmidt et al. (2007) by using the trajectory rose that allows representation of both angle distribution and length (EA3), or favoring the contrasted distribution of angles among different groups (trajectory cluster, population, anthropogenic factors, etc.) using a circular bar plot structure (EA1). We also developed the initial TM concept (Sturbois et al., 2021) devoted to the representation of trajectory metrics in synthetic maps (EA5), by the proposition of the ITM especially designed to illustrate SI dynamics at very large scales (EA6). Largely inspired by wind and current map, the ITM appears particularly relevant to detect patterns characterized by differences in the nature and magnitude of SI dynamics. To complement the representation of dynamics at high spatio-temporal resolution, we propose the TH concept, which provides synthetic perspectives to represent both the magnitude and the nature of changes and detect potential long-term SI cycles in large areas (EA6).

We believe that these entire figure concepts are far from being exhaustive and we suggest that users innovate in the representation of trajectory metrics and in the customization of R codes provided here (DataS1: SITA_R_Codes; Sturbois, Cucherousset, et al., 2021b).

Assumption, applications, and limitations of the proposed framework

Ecologists are increasingly using sophisticated methods for dealing with measured data (Fry, 2013) and SI ecology is no exception. While it is always tempting to favor approaches providing quantitative analyses, it is important to keep in mind the biological meaning of associated assumptions, and their inherent simplifications (Layman et al., 2012). If the SITA framework and the associated graphical representations constitute potential management and decision-making tools, we urge users interested in sharing this synthetic tools with stakeholders or managers that interpretation must be done carefully in the hands of experienced multivariate/SI ecologists (Sturbois et al., 2021).

"*A carpenter would never use a screwdriver to pound a nail*" (Layman & Post, 2008): SITA concepts and metrics were not intended as a universal tool to be applied in all situations or as a substitute for other available methods (Buckley, Day, Case, et al., 2021; Buckley, Day, Lear, et al., 2021), but as a new tool for the SI ecologists that could be useful in situations suitable for trajectory analysis. Similar to all analytical tools, there is a high likelihood that the SITA framework may be applied to datasets to which it is not well suited or that inexperienced users may misinterpret the results. Indeed, there is a considerable history of this in the SI literature concerning, for example, mixing models (Fry, 2013; Jackson et al., 2009; Phillips, 2001; Phillips et al., 2014). Users must consequently be aware of the assumptions, fields of application, and limitations associated with the SITA framework as described in this section.

Despite the speed of changes that allows dealing with variations in frequency of surveys, we encourage users to establish sampling strategies, implying synchronous sampling and similar frequency of surveys (De Cáceres et al., 2019; Sturbois, De Cáceres, et al., 2021). It is an essential condition to use at best the SITA framework.

Multivariate ecological methods are descriptive by nature. Despite SITA providing accurate measurements and representations of dynamics in stable isotope ecology, it shares limitations with CTA (De Cáceres et al., 2019; Sturbois et al., 2021). Consequently, SITA outputs must be completed by a strong examination of input datasets (stable isotope raw data or structural and functional indices) to improve the ecological interpretation of observed dynamics. Similarly, SITA may be complemented with additional analyses (Buckley, Day, Case, et al., 2021) to statistically test for other aspects of changes or to provide statistical backgrounds.

Note that ordination spaces are specifically constructed for each given data set. Therefore, any data transformation on the raw data or sampling decision is likely to affect trajectories and, subsequently, all metrics to be calculated. This effect should be tested before any overall transformations of raw data, such as scaling and/or baseline correction of SI values, or any biomass or abundance weighing prior to indices calculation.

Despite the SITA framework being not limited in terms of the number of components considered in metric calculations, some of the applications only considered part of the variability, if Ω_δ or Ω_γ contained more than two dimensions (reporting angles Θ, ω in a 0–360° system, angle α calculation). In this context, performing SITA requires a careful interpretation of the multivariate space to assess the consequences of such reduction.

SITA also shares numerous limitations inherent to stable isotope properties and analysis (Fry, 2008; Garvey & Whiles, 2017). Dynamics of basal source SI values influence the corresponding SI compositions of consumers (Matthews & Mazumder, 2004) and potentially the metrics used to describe the variability, and the food web structure and functioning. However, SITA offers the possibility to explore both source and consumer dynamics. Additionally, many other factors are known to influence food assimilation and finally the isotopic composition of consumers such as fractionation variability or the type of tissue analyzed (Fry, 2008).

In complex ecosystems characterized by similar SI composition of basal sources and in underdetermined cases in which multiple outcomes are feasible from isotope tracer measurements, different feeding pathways may lead to similar positions in δ space (Fry, 2013; Layman et al., 2007), a situation that cannot be disentangled by SITA and necessitates complementary approaches. For the opposite, SITA will be more relevant when differences in stable isotope values of basal sources induce contrasted positions of consumers. When performed at the population level, mean stable isotope values are used as input in SITA, which has the drawback of hiding the stable isotope composition variability at intraspecific levels (Bearhop et al., 2006; Matthews & Mazumder, 2004). In this case, intrapopulation variability could be shown as confidence intervals in trajectory diagrams or maps.

The metrics allow a real-time measurement of dynamics, and a qualitative and quantitative assessment of the potential degree of success in achieving conservations objectives or the impact of natural or anthropogenic changes in environmental conditions. All factors inherent to multivariate and stable isotope analyses, individually or combined, may influence SITA metric calculations, and we urge users for a careful check of such potential bias before defining their sampling design, performing SITA, and interpreting results. Alternatively, conclusions may lead to an incomplete picture and can mislead the description of dynamics with potential misdirecting conservation actions or overstating conservation progress.

Exporting trajectory analysis to other kinds of ecological data

Taking into account the strengths and limitations of the proposed framework, we consider that SITA brings insightful perspectives into the analysis of high-resolution temporal datasets using stable isotopes and/or other tracers in integrating organism tissues. Even though the SITA framework has been here defined based on stable isotope data, and builds on the CTA framework for community data, any other multidimensional input data are likely to be suitable for this approach. For instance, using trajectory analysis on multitrace element data, including SI or not, would provide appealing insights into subpopulation migratory patterns in fish populations based on otolith chemistry (Elsdon et al., 2008; Trueman et al., 2012). Similar applications can easily been foreseen at the individual scale from tree rings, in a dendrochronology context (Sleen et al., 2017), or from environmental signals recorded in bivalves shells (Butler et al., 2019), or bone growth layers (Merrett et al., 2021; Turner Tomaszewicz et al., 2016). As shown at the scale of the northeast Pacific water body (EA 6), sea water SI composition can be tracked to large spatio-temporal scales and may be tested for long-term or seasonal SI trajectories in rain and snowfall (Aizen et al., 2005; Tian et al., 2018), or ice (Schotterer et al., 1997; van Trigt et al., 2002; Werner et al., 2018). Other tracers are also increasingly used in association with SI, such as contaminants (Dietz et al., 2004, 2021) or fatty acids (Madgett et al., 2019), and the absence of limitation in the number of dimensions supporting SITA constitutes an important strength to improve the analysis of such complex multivariate datasets. As experimental studies involve very controlled protocols, SITA metrics can also be particularly relevant to depict experimental trajectories (EA3).

We hope that trajectory analysis using the new *ecotraj* package will contribute to the assessment of natural or man-induced environmental changes using the responses of chemical composition in biological archives, both in contemporary or archeological studies at local, to regional and global, scales. On a broader front, there are claims for an extension of the trajectory analysis concept to other fields in ecology. In this perspective, the adaptability to different type of ecological questions (compositional, functional, structural, trophic, etc.) given by the choice of the space of analysis Ω (i.e., raw variables and dissimilarity metric choice) constitutes the major strength of the approach. We strongly believe that coupling ecological trajectory analysis frameworks with traditional methods of analysis in studies dealing with long-term integrative data sets could bring interesting perspectives for a better understanding of ecosystem functioning, trends in ecosystems quality, and past and present global changes.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available as follows: Bestion et al. (2019b), Zenodo, https://doi.org/10.5281/ZENODO.3475401; Espinasse et al. (2020), Dryad, https://doi.org/10.5061/DRYAD.D2547D7Z6; Sturbois et al. (2021a), Zenodo, https://doi.org/10.5281/ZENODO.5519696. Code (Sturbois et al., 2021b) is available on Zenodo at https://doi.org/10.5281/ZENODO.5519693.

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Article III

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Characterizing spatio-temporal changes in benthic communities: Taxonomic and functional trajectories of intertidal assemblages in the bay of Saint-Brieuc (English Channel)

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ABSTRACT

Tracking and quantifying ecological changes at large and long-term scales is a central point for monitoring and conservation issues. The Community Trajectory Analysis Framework was used in complement with classical methods to analyse and represent long-term changes in marine habitats at 42 stations in the bay of Saint-Brieuc (western English Channel), sampled in 1987, 2001 and 2019. The taxonomic and functional trajectories of intertidal benthic assemblages were studied at local and assemblage scales. Whatever the perennial contribution of dominant prevalent species at the site scale, some species were highly variable over time and space, influencing the structuration of assemblages. Taxonomic changes were not systematically associated with significant changes in the functional properties at local and community scale. The consideration of local changes and variations at the species level explained the differences in composition observed at the scale of assemblages. Observed changes mainly reflected random population dynamics of structuring prevalent species in habitat under strong natural pressures, rather than specific changes of the community. Few species reveal the long-term effect of green tides in some assemblages. Overall, this study confirms the complexity to disentangle factors of changes in the absence of a monitoring strategy specifically devoted the measurement of environmental factors and anthropogenic pressures. The study also highlights the need for the development of benthic monitoring strategies at multiple spatial and temporal scales.

1. Introduction

Costal ecosystems face severe natural and anthropogenic pressures that affect, sometimes strongly, both the structure and functioning of benthic communities (Harris, 2012; Cimon and Cusson, 2018). Although assessment of stability/variability of benthic communities, often in relation with management considerations, has received a large attention by scientists, it remains a central point of ecological research and conservation (Ellis et al., 2000). Studying stability/variability in ecological systems requires the consideration of disturbances defined as "any discrete event in time that disrupt ecosystems, community or populations structure" (Picket and White, 1985). Ecological theory suggests that small scale disturbance events at intermediate frequencies may have positive effects on the system at larger scales whereas disturbance on larger scales are much more likely to reduce heterogeneity in communities and induce slower recovery rates (Bazzaz, 1983; Caswell and Cohen, 1991; Connell, 1978; Ellis et al., 2000). Understanding the effects of environmental changes on natural communities requires to distinguish natural and anthropogenic variability (Osenberg and Schmitt, 1996; Stewart-Oaten, 1996). However, the lack of reference, non-impacted sites in modern ecosystems, makes this task a real challenge (Boldina et al., 2014). Temporal surveys assessing the evolution of benthic communities are therefore essential to establish baselines and detect ecological changes (Desroy et al., 2002; Hardman-Mountford

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et al., 2005; Schückel et al., 2015; Veiga et al., 2017).

Benthic communities are commonly sampled *via* a network of stations and a sampling periodicity varying from seasonal to decadal. Such an approach allows detecting major changes in benthic macrofauna without being able to infer on the causes of changes (Bacouillard et al., 2020). The simultaneous sampling of several stations distributed in the area of interest makes possible to investigate temporal changes occurring at different inter-connected scales: (1) at the scale of a station, where local processes may drive the composition of communities (sedimentary changes, local anthropogenic pressures), and (2) at the scale of cluster of stations with similar composition (hereafter called assemblages), where processes operating at larger scale may drive the temporal variability (climate, diffuse and chronic anthropogenic disturbances).

Although there is a large consensus that diversity losses threaten ecosystem functioning, man-induced changes do not systematically impact diversity. Studying the temporal variability of benthic assemblages through analysis of composition and structure gains or losses seems consequently limited regarding functional considerations. For example, substantial changes in species composition and structure in space and time may not systematically results in proportional α diversity (Whittaker, 1972; Dornelas et al., 2014) and trait-based functional changes (McLean et al., 2019; de Sousa Gomes-Gonçalves et al., 2020). In this context, trait-based approaches offer a complementary integrative framework to link functional consequences to biodiversity changes (Suding et al., 2008; Boyé et al., 2019). Studies combining composition, structure and functioning assessments of assemblages in a multidimensional scale allow the detection of multi-faceted responses to environmental variability in faunal communities (McLean et al., 2019).

The detection of future potential changes in species distribution and assemblage compositions, which can be helpful for monitoring and conservation issues (Desroy et al., 2002; Schückel et al., 2013; Veiga et al., 2017), requires the establishment of baseline knowledge. In the English Channel, scientific studies have largely focused on benthic communities in the main coastal bays and estuaries (Desroy et al., 2002). In the bay of Saint-Brieuc (western English Channel), where intertidal habitats are partially protected since 1998 by a National Nature Reserve, the analysis of diachronic changes of benthic assemblages has not been updated for 20 years (Gros and Hamon, 2021). Previous studies underlined the close link between benthic resources and waders which prey on macro-invertebrates (Sturbois et al., 2015; Ponsero et al., 2016), highlighting the need to study and conserve benthic habitats. After two decades, an analysis of benthic assemblages using the same protocols as those used for the definition of historical baselines was needed to assess temporal changes of intertidal habitats in this bay representative of coastal areas characterized by range of impacts due to the complex co-occurrence of management's mosaic and anthropogenic uses (Ellis et al., 2000). Natural and anthropogenic contexts (Supplementary material, Appendix A) make the study site suitable to contribute to the debate about the definition of impact assessment at spatial and temporal scales and the feasibility of such research. It is also essential to provide up-to-date knowledge to policy makers and managers about the evolution of the composition, structure and functioning of benthic assemblages.

This study, based on a long-term survey in the intertidal soft-bottom sediments of the bay of Saint-Brieuc, aims to analyse the taxonomic and functional variability of benthic communities over the last 30 years at different spatial scales using 42 stations sampled in 1987 (Gros and Hamon, 2021), 2001 (Le Mao et al., 2002). and 2019. The approach specifically focused on the detection of trajectory patterns by applying the recent Community Trajectory Analysis Framework (De Cáceres et al., 2019; Sturbois et al., 2021b). Results were discussed regarding potential environmental and anthropogenic driving factors and some propositions were made for such long-term study approaches.

2. Material and methods

2.1. Study area

Fieldwork was conducted in the bay of Saint-Brieuc, France (Fig. 1). The study area includes about 2900 ha of tidal flats divided in two coves (Yffiniac and Morieux) mainly dominated by fine to medium sands. The most sheltered parts are dominated by salt marshes. The bay is under the influence of a semi-diurnal megatidal regime. Tidal range varies between 4 m at neap tides and nearly 13 m during spring tide (Fig. 2). Divagation of channels is particularly dynamic, with increasing magnitude in low levels (Supplementary material, Appendix B). A large part of the bay (1140 ha) is included in the National Nature Reserve of the bay of Saint-Brieuc, created in 1998 to protect wader populations (Fig. 1). The study area undergoes a variety of anthropogenic pressures (Supplementary material, Appendix A): sediment extraction conducted until 2004 (1000 m^3 y^{-1}, around stations 3 and 5) and muddy sediment deposits (near station 11) dredged from the Saint-Brieuc harbour since 2004 (120 000 m^3 y^{-1}). The bay also suffers from eutrophication, resulting in strong ephemeral macroalgae proliferation and cyclic green tides episodes. Professional (*Cerastoderma edule)* and recreational (*Cerastoderma edule, Pecten maximus, Arenicola marina*) fishing activities has been an important activity for many decades, especially in Yffiniac cove. In the lower level of Morieux cove, mussel farming on wooden poles, called “bouchots” (Fig. 1) has increased over the study period, from 277 ha in 1987 to 386 ha in 2001 and 312 ha in 2019.

2.2. Field sampling

Macrofauna was sampled during winter (March) in 1987, 2001 and 2019 at 42 stations, following the sampling grid (Fig. 1) and the protocol defined in 1987 by (Gros and Hamon, 2021). At each site, four replicates were collected for macrobenthos analysis using a 1/32 m^2 hand corer (diameter: 20 cm), at a depth of 25 cm. The content of the cores was gently sieved on site through 1-mm square mesh sieve. Retained material was preserved for analysis in 5% buffered formaldehyde. Density per m^2 of *Arenicola marina,* which is difficult to sample with a handcorer, was estimated visually by counting worm casts at each station within 10 quadrats of 1 m^2. A visual description of the sediment type was recorded and two samples of sediment were collected from additional cores (diameter 5 cm, depth 5 cm) and subsequently analysed for grain size distribution, and water and organic matter contents. All replicates were collected at the four corners of a 1 m^2 square, using GPS position-fixing (GPS Etrex Garmin).

2.3. Laboratory analysis

Macrofauna was identified to the lowest possible level (usually species level), counted, and abundances were expressed as densities per 1 m^2. Taxon were named following the World Register of Marine Species. For granulometric analysis, sediment was desalted with freshwater during 48 h before being dried at 60 °C for 48 h, sieved through AFNOR standard sieves (from 40 to 25000 μm), and weighed. Water and organic matter contents were respectively determined after drying (60 °C for 48 h) and combustion of sediment at 550 °C for 4 h (Hedges and Stern, 1984; Salonen, 1979).

2.4. Traits collection

The functional dataset was composed of six traits divided in 23 categories (Supplementary material, Appendix C). These traits characterized the morphology (body size, flexibility, fragility) and behavioural traits [feeding behaviour, living habit, tolerance (Degen and Faulwetter, 2019)]. This set of traits is related to the vulnerability of species to mechanical disturbances (associated to recreational and professional fishing activity and the circulation of vehicles) and organic enrichment

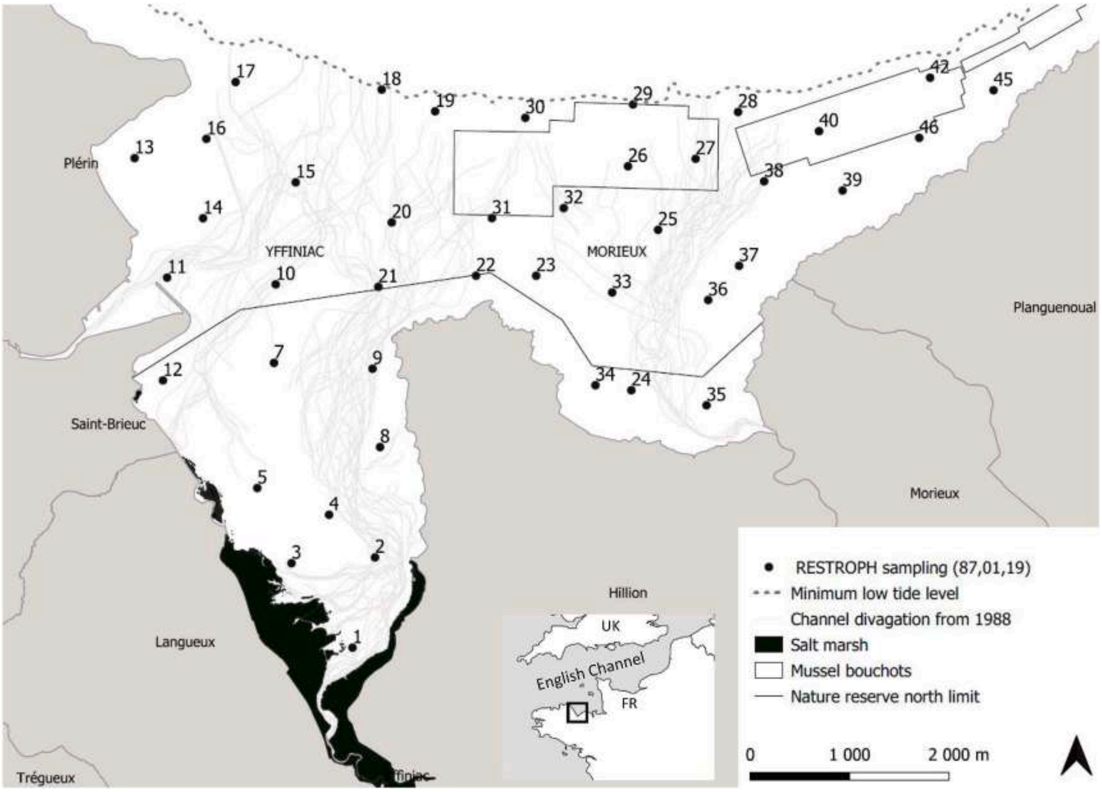


Fig. 1. Location of the study area and sampling strategy. Black dots corresponds to the 42 stations sampled in 1987, 2001 and 2019. The North limit of the Nature reserve is indicated by a black line and mussel bouchots by polygons.

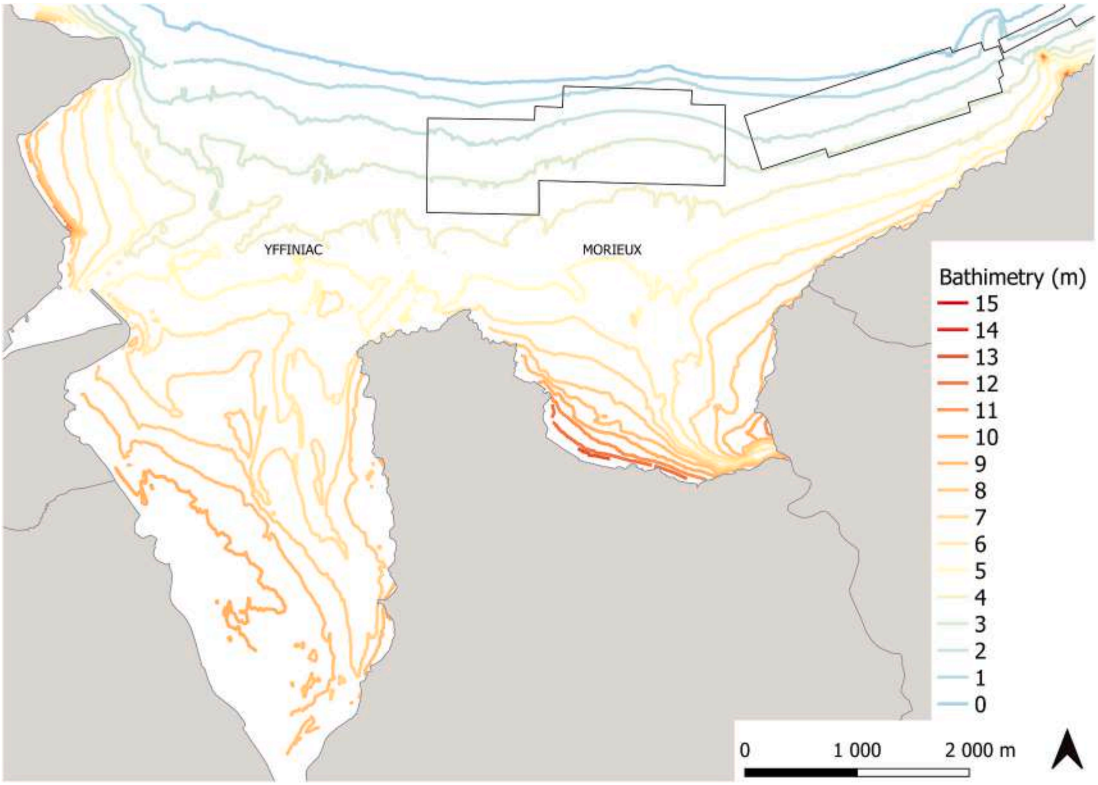


Fig. 2. Bathymetry of the study area. Isolines are coloured according to altitude from the top (red) to the low tide level (blue). Mussel bouchots are represented by polygones. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

(tolerance). They were chosen to analyse functional changes in the community, in relation to the main pressures identified in the study area. Information was retrieved from primary literature on specific taxa, expert knowledge and three publicly available databases: polytraits (http://polytraits.lifewatchgreece.eu), the World Register of Marine Species (WoRMS Editorial Board, 2020), and Biological Trait Information Catalogue (BIOTIC, http://www.marlin.ac.uk/biotic/). Scores were attributed to species according to their affinity to each category of traits, using a fuzzy coding from 0 (no affinity) to 3 [high affinity (Chevene et al., 1994)]. Community-weighted trait values (CWMs) were calculated to characterize the functional structure (Ricotta and Moretti, 2011).

2.5. *Data analysis*

Data collected in 1987, 2001 and 2019 were analysed to track taxonomic and functional changes. Analysis of sediments (sub-section 2.5.1) and α-diversity (2.5.2) were followed by spatial taxonomic clustering (2.5.3) and taxonomic and functional trajectory analysis (2.5.4). All the statistical analysis was performed with R 4.0.

2.5.1. *Sedimentary dataset*

Statistical description of sediments, based on grain-size distributions, was computed with the R package 'G2Sd' (Fournier et al., 2014). Ten sedimentary parameters were selected to describe sediment characteristics: water content (H_20), organic matter content (OMC), arithmetic mean, median (d50), gravel (>2 mm), coarse sand (1 mm–250 μm), fine sand (250–125 μm), very fine sand (125–63 μm), and mud (<63 μm) contents.

2.5.2. *Taxonomic α-diversity*

In order to assess the different components of α-diversity, the mean number of individuals per m^2 (N), taxa richness (S), Shannon-Weaver index (H′), Simpson index (D) and Pielou's species evenness (J) were calculated for each station prior to any transformations of the dataset.

2.5.3. *Spatial taxonomic clustering*

Hierarchical Cluster Analysis (HCA) was performed to distinguish benthic assemblages (*i.e.* site groups) at each campaign by using the Hellinger distance between each pair of samples (Legendre and Gallagher, 2001) and by applying the Ward's clustering method. The indicator value method (Indval) was performed to characterize assemblages (Dufrene and Legendre, 1997).

2.5.4. *Detecting trajectory patterns*

PCAs were performed on Hellinger transformed data and followed by Community Trajectory Analysis (CTA) using the package 'ecotraj' [De Cáceres et al. (2019), Sturbois et al. (2021b)]. CTA is based on geometrical properties of ecological trajectories (De Cáceres et al., 2019). The original framework and its new extension (Sturbois et al., 2021b) were used to study and represent temporal changes at the station scale taking into account all the dimensions of the multivariate analysis through trajectories of surveys in the multivariate space. A set of distance-based metrics were calculated. Segment-length represents, for a station, the distance between two consecutive surveys. S1 informs about changes between 1987 and 2001, and S2 between 2001 and 2019. The trajectory path represents the sum of segment length (S1+S2). Net changes were calculated to analyse trajectories between 1987 and 2019, considering the 1987 data set as an initial state (*i.e.* the first ecological state of the time series). Net changes informs about the overall change occurring during the study. The net change ratio represents the ratio between the net changes and the trajectory path. It informs about the straightness of recovering and or departing processes with respect to the initial state. Recovering and departing consecutive trajectory segments (RDT) were identified by subtracting Net change n-1 to Net change n (Sturbois et al., 2021b).

De Cáceres et al. (2019) developed a geometrically-based approach to trajectory resemblance which includes the shape, size, direction and position of trajectories with respect to the resemblance between all observations (state) belonging to a same trajectory. Dissimilarities between ecological trajectories (1987-2001-2019) were calculated to test their resemblance [Directed Segment Path Dissimilarity (De Cáceres et al., 2019)] and was used with the resulting symmetric matrix as input in a HCA (Ward.D2 clustering Method), to underline potential spatial patterns. Indicator value method (Dufrene and Legendre, 1997) was performed on taxonomic trajectory clusters to test differences between 1987, 2001 and 2019. The relative contribution of all categories of functional traits between 1987, 2001 and 2019 were compared for each functional trajectory clusters and at the scale of the whole study area.

3. Results

3.1. *General description of sediment*

The sampling area was dominated by fine sediment at the three sampling dates: (arithmetic means = 144.4 μm ± 52.5, 135.9 μm ± 44.9 and 159.5 μm ± 70.6 in 1987, 2001 and 2019, respectively). Sand was the most represented grain size class over the last three decades: 97.0% ± 1.9, 98.5% ± 4.1 and 95.6% ± 5.6. Mud and gravel were less represented and respectively ranged between 1.2% ± 4.0 to 3% ± 5.5, and 0.3% ± 0.8–1.4% ± 5.0. Overall, surficial sediment of the study area can be summarized as fine sands organised along a *continuum* of fine to very fine sands characterized by local variations in mud or gravel contributions.

3.2. *General description of the benthos*

The number of taxa reported in the intertidal flat was variable across the sampling period (Table 1): 50 in 1987, 53 in 2001 and 85 in 2019. In comparison to 1987, 11 taxa disappeared and 14 taxa appeared in 2001 and 14 taxa disappeared and 46 taxa appeared in 2019. 36 taxa were common to the three datasets and represented 95.5% ± 2.9 of the total abundance. Polychaetes, crustaceans, and molluscs were dominant. The number of taxa of these three dominant groups increased over the study

Table 1

General description of macrofauna (N: number of taxa).

	1987	2001	2019	All years
Total Richness	50	53	85	133
Mean Richness	10.4 (sd = 3.21)	10.8 (sd = 5.23)	16.8 (sd = 6.69)	
N Annelids	26	23	32	54
N Crustaceans	13	19	35	45
N Echinoderms	1	2	1	2
N Molluscs	9	9	15	24
N Nemertia	0	0	1	1
N Plathelminthe	0	0	1	1
N Sipuncles	1	0	0	1
N Constant taxa	7	4	12	
N Common taxa	5	13	12	
N Occasionnal taxa	13	11	11	
N Rare taxa	25	25	50	
Total abundance	34 222	95 991	50 639	
Mean abundance	815 (sd = 1617)	2286 (sd = 4496)	1206 (sd = 1530)	
Shannon (H)	1.62(sd = 0.46)	1.46 (sd = 0.76)	1.98 (sd = 0.70)	
Simpson (D)	0.696(sd = 0.153)	0.61 (sd = 0.29)	0.74 (sd = 0.21)	
Pielou (J)	0.704(sd = 0.153)	0.65 (sd = 0.29)	0.71 (sd = 0.21)	

period. Other categories contributed to less than 5% of the taxa richness, except for echinoderms, which represented 8.26% of the total abundance in 2019. The high total abundance observed in 2001 was due to a strong increase of the mollusc *Donax vittatus* in the low shore (Fig. 3), responsible for 51,8% of the total abundance.

In 1987, macrofauna was dominated by molluscs excepted in the low shore, where annelids were the most numerous group (Fig. 3). In 2019, distribution between taxonomic groups was less contrasted, especially in the low shore, mostly due to an increase in mollusc abundances. Abundance of crustaceans also increased in most of the study area and a clear extension of the echinoderms distribution was observed in the western part of the study area, mostly due to the ophiuroid *Acrocnida spatulispina*.

Taxa richness increases from high to low shore whereas abundances follow an inverse pattern (Table 1). Density, taxa richness and diversity (H, D) recorded from all samples were spatially and temporally variable. Compared to 1987, abundance (815 ind.m^{-2} ± 1617 vs 1206 ind.m^{-2} ± 1530), taxa richness (10.42 ± 3.21 vs 16.80 ± 6.69) and species diversity slightly increased in 2019.

3.3. Benthic assemblages

The hierarchical classification separated four clusters in 1987 and 2001 and five clusters in 2019. Mainly influenced by bathymetry (Fig. 2), the distribution and structuration of assemblages was stable from upper to lower flat, despite the south-westward extension of assemblage IV, and the apparition of a new assemblage in 2019 (Fig. 4).

Assemblage I, located in muddy sands on the upper part of the flat, was characterized *Pygospio elegans* in 1987, and *Peringia ulvae* in 2001 and 2019 (first rank indval, Table 2). *P. ulvae* was dominant in 1987 and 2019, whereas *Corophium arenarium* was the most abundant species in 2001. Assemblage II, associated to very fine to fine sand of the upper mid-flat, was characterized by *Macomangulus tenuis* in 1987 and 2019 *and Urothoe poseidonis* in 2019. *M. tenuis* remained the most abundant species over time. Assemblage III, associated to very fine to fine sand of the lower mid-flat, was characterized by *U. poseidonis* in *1987* and *Acrocnida spatulispina* in 2001, and 2019. This assemblage was dominated by *M. tenuis* in 1987, *U. poseidonis* in 2001, and *A. spatulispina* in 2019. Assemblage IV, associated to sands mainly located in low tide levels, was characterized by *Scoloplos armiger* in 1987, *Donax vittatus* in 2001, and *Magelona mirabilis* in 2019. It was dominated by *P. medusa* in

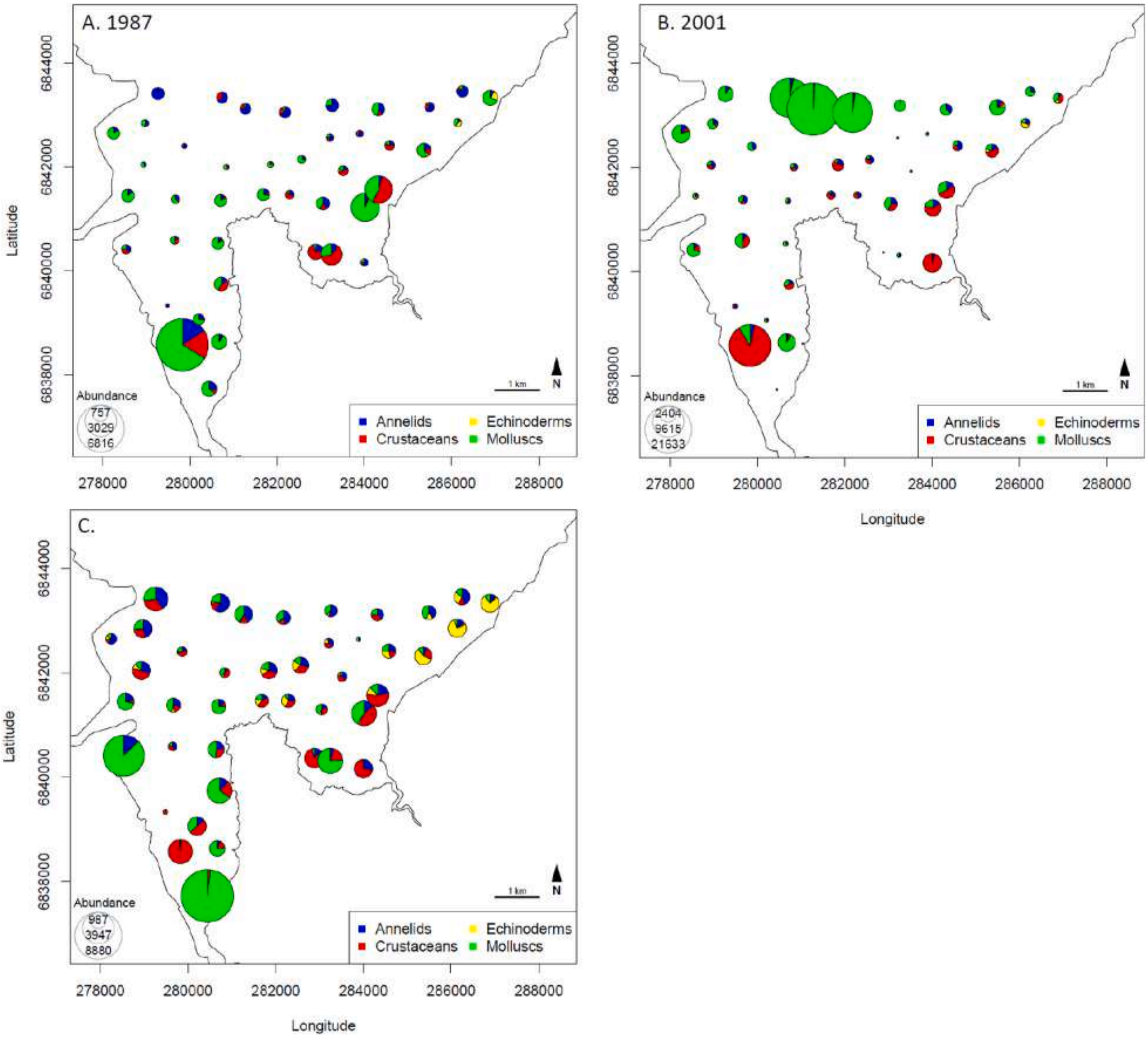


Fig. 3. Variations in relative abundance of the main numerous taxonomic group between 1987 (A), 2001 (B) and 2019 (C). Size of pies corresponds to total abundance and sections to taxonomic group contributions.

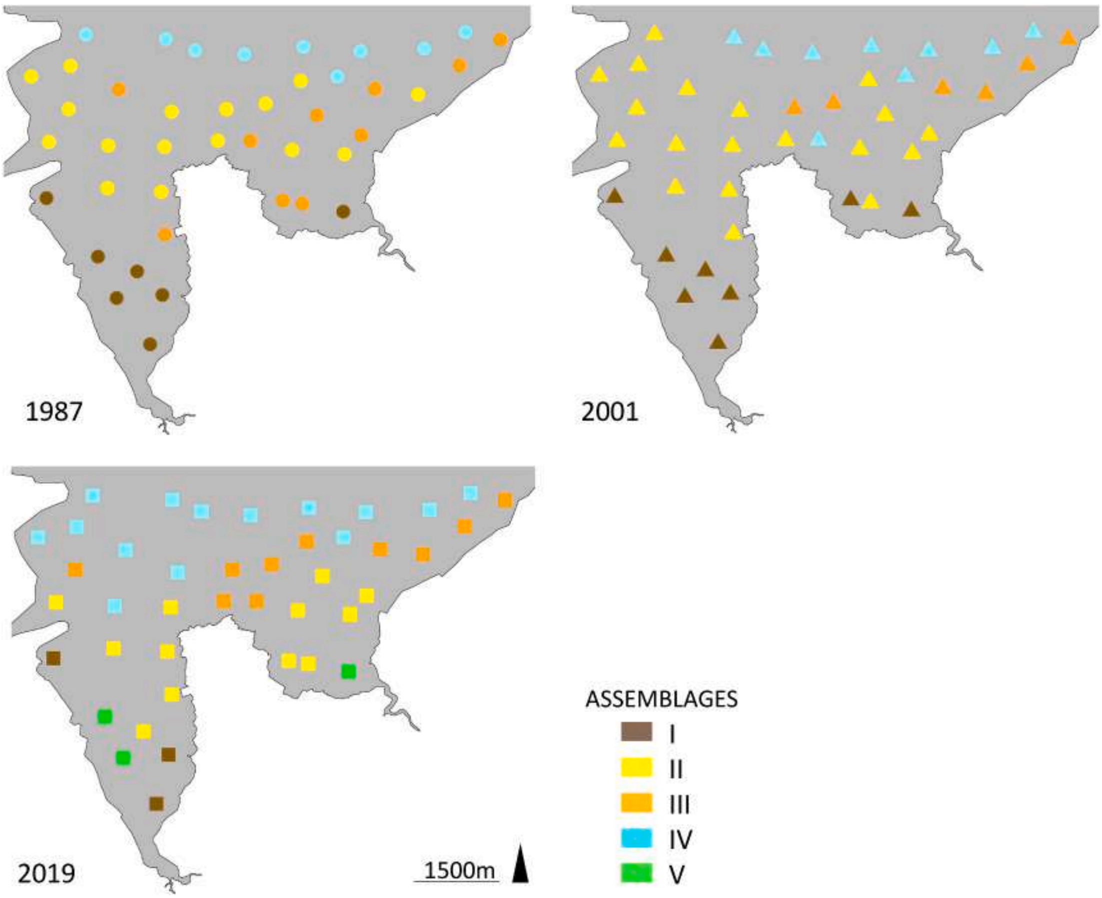


Fig. 4. Spatial distribution of benthic assemblages identified with Hierarchical Cluster Analysis performed on 42 stations in 1987, 2001 and 2019.

1987 and *D. vittatus* in 2001 and 2019. A new assemblage was identified in 2019, in the upper part of the shore, on bare sands associated to major sand intakes. *Eurydice affinis* characterized this assemblage and *Bathyporeia pilosa* was the most abundant species. Distribution maps of species used to describe assemblages (Table 2) are detailed in Supplementary material, Appendix D.

3.4. Detecting trajectory patterns

3.4.1. Taxonomic trajectories

The first period was characterized by less change (total S1 lengths = 453.05, mean = 10.79 ± 3.46) than the second [total S2 lengths = 582.34, mean = 13.87 ± 5.56 (Fig. 5, A)]. Highest net changes occurred in the low shore where eight stations concentrated 31% of changes (179.24). A positive correlation (0.529, p = 0.0002) was found between net change and latitude. RDT was positive for 31 stations (71.43%) and negative for 11 stations, showing an overall departure dynamics from the initial taxonomic state. Total net change (582.34) represented only 56% of the total trajectory path (1035.39). This low net change ratio (53.14% ± 0.12) indicated significant direction changes (*i.e.* driving species groups) in the multivariate space between 1987-2001 and 2001–2019 for departing trajectories, and included recovering ones.

The HCA performed on CTA of trajectory similarities separated four main clusters of taxonomic trajectories (Fig. 5B and C). Cluster A was composed of 8 stations from the sheltered part of the bay, and describing the evolution from an assemblage characterized *P. elegans* in 1987 and *B. pilosa* in 2019 and dominated by *P. ulvae* in 1987 and 2019 and *C. arenarium* in 2001. Cluster B, the most common group (28 stations), was characterized by *M. tenuis* in 1987, *U. poseidonis* in 2001 and *E. dolfusi* in 2019. *M. tenuis* remained the most numerous species over time. Cluster C (NC = 25.06 ± 0.38; TP = 35.33 ± 0.83) and D (NC = 20.78 ± 1.91; TP = 40.65 ± 5.28) were characterized by longer net changes and trajectory path compared to cluster A (NC = 10.49 ± 0.83; TP = 21.20 ± 1.43) and B (NC = 12.74 ± 0.81; TP = 23.94 ± 1.11), but represented a limited number of trajectories (14% of stations). Cluster C grouped 4 stations located in the north-west, characterized by *C. gibber* at the three campaigns and dominated by *P. medusa* in 1987 and *D. vittatus* in 2001 and 2019. Cluster D which regrouped only two stations located in the eastern low shore, was characterized by *Bathyporeia guilliamsoniana* in 1987, *P. medusa* in 2001 and *Nucula nitodosa* in 2019. *Magelona mirabilis* was the most numerous species in 1987 and 2019 and *D. vittatus* remained dominant in 2001. Distribution maps of species used to describe taxonomic trajectory clusters (Table 3) are detailed in Supplementary material, Appendix D.

3.4.2. Functional trajectories

Functional trajectory paths were, for all sites, similar for both periods, revealing similar level of functional variability between 1987 and 2001 (254.55, 6.06 ± 2.88) and 2001 and 2019 (223.41, 5.32 ± 2.61). Seven stations concentrated 30% (143.67) of the overall trajectory path, illustrating a high functional variability in these areas over the last 30 years. RDT revealed recovering trajectories for 25 stations (60%), evenly distributed in the study area (Fig. 6, A). The low net change ratio (46.78% ± 0.11) was influenced by recovering trajectories.

The HCA performed on CTA of trajectory similarities separated four main clusters according to the shape of functional trajectories (Fig. 6B and C).

Cluster E grouped six stations located in sheltered and upper parts of the shore and characterized by the highest net changes (7.50 ± 1.27) and moderate trajectory path (10.80 ± 1.09). Cluster E trajectories were mainly defined by an increase in the contribution of very sensitive, free living and small species (Fig. 7). Cluster F, which concerned only one

Table 2
Characteristics of assemblages identified with the Hierarchical Cluster Analysis in 1987, 2001 and 2019: Assemblages (Ass), number of station (N st), Taxa richness (S), Mean density per m^2 (M Dens), Shannon-Weaver Index (H), Simpson Index (D) and Pielou's evenness (J) (±= standard error). Distribution of species used to describe assemblages are detailed in Supplementary material, Appendix D.

Ass.	Indicator species	indval	p	Most numerous species	Mean.m^2 ± se		N st	S	Abund	H	D	J
I-87	***Pygospio elegans***	**0.857**	**0.0001**	***Peringia ulvae***	**1076.57**	**± 958.91**	7	8.29	1864.14	1.44	0.67	0.71
	Hediste diversicolor	**0.714**	**0.0001**	***Pygospio elegans***	**260.57**	**± 223.57**		±0.96	±1410.00	±0.15	±0.05	±0.07
	Peringia ulvae	0.714	0.0001	*Corophium arenarium*	194.29	±182.40						
	Limecola balthica	0.696	0.0001	*Limecola balthica*	148.57	±58.63						
	Arenicola marina	0.612	0.0003	*Bathyporeia pilosa*	98.29	±77.83						
II-87	***Macomangulus tenuis***	**0.595**	**0.0001**	***Macomangulus tenuis***	**344.75**	**± 152.13**	16	9.63	537.56	1.45	0.63	0.65
	Cerastoderma edule	**0.498**	**0.0026**	***Cerastoderma edule***	**59.94**	**± 20.50**		±0.60	±172.02	±0.12	±0.05	±0.04
				Nephtys hombergii	25.50	±6.42						
				Urothoe poseidonis	19.50	±6.89						
				Bathyporeia sarsi	12.00	±3.72						
III-87	***Urothoe poseidonis***	**0.502**	**0.0007**	***Macomangulus tenuis***	**238.4**	**± 118.43**	10	10.00	837.90	1.61	0.73	0.71
	Acrocnida spatulispina	**0.486**	**0.0021**	***Bathyporeia sarsi***	**225.6**	**± 101.72**		±0.70	±265.84	±0.09	±0.02	±0.03
				Urothoe poseidonis	163.2	±61.37						
				Acrocnida spatulispina	36.8	±19.93						
				Nephtys hombergii	35.2	±12.97						
IV-87	***Scoloplos armiger***	**0.947**	**0.0001**	***Polycirrus medusa***	**92.556**	**± 32.18**	9	14.00	465.89	2.07	0.81	0.79
	Chaetozone gibber	**0.889**	**0.0001**	***Magelona mirabilis***	**71.333**	**± 21.28**		±1.13	±45.52	±0.13	±0.03	±0.03
	Polycirrus medusa	0.763	0.0001	*Chaetozone gibber*	53.333	±17.44						
	Magelona filiformis	0.667	0.0001	*Fabulina fabula*	41.778	±25.11						
	Magelona mirabilis	0.613	0.0002	*Bathyporeia sarsi*	34.667	±16.71						
I-01	***Peringia ulvae***	**0.713**	**0.0002**	***Corophium arenarium***	**1371.33**	**± 1371.33**	9	6.89	2630.33	1.10	0.53	0.58
	Cerastoderma edule	**0.390**	**0.0179**	***Peringia ulvae***	**405.56**	**± 179.62**		±1.33	±1487.69	±0.23	±0.10	±0.12
	Eurydice affinis	0.351	0.0184	*Bathyporeia sarsi*	297.78	±297.78						
	Pygospio elegans	0.344	0.0287	*Cerastoderma edule*	180.44	±100.01						
				Macomangulus tenuis	128.89	±88.14						
II-01	***Macomangulus tenuis***	**0.544**	**0.0001**	***Macomangulus tenuis***	**382.07**	**± 116.231**	15	9.73	874.20	1.54	0.69	0.74
	Lekanesphera levii	**0.333**	**0.0142**	***Urothoe poseidonis***	**112.67**	**± 51.27**		±1.19	±206.65	±0.11	±0.04	±0.05
	Bathyporieia tenuipes	0.283	0.0335	*Cumospsis fagei*	72.87	±42.31						
				Spiophanes bombyx	57.73	±17.96						
				Nephtys hombergii	45.00	±11.32						
III-01	***Acrocnida spatulispina***	**0.870**	**0.0001**	***Urothoe poseidonis***	**122.70**	**± 30.46**	10	15.40	740.10	2.33	0.87	0.86
	Eocuma dollfusi	**0.692**	**0.0001**	***Macomangulus tenuis***	**94.60**	**± 26.62**		±0.75	±96.79	±0.06	±0.01	±0.02
	Sigalion mathildae	0.622	0.0001	*Acrocnida spatulispina*	74.40	±27.36						
	Urothoe poseidonis	0.581	0.0001	*Eocuma dollfusi*	56.20	±22.26						
	Malmgrenia arenicolae	0.524	0.0008	*Cumospsis fagei*	37.20	±10.64						
IV-01	***Donax vittatus***	**0.863**	**0.0001**	***Donax vittatus***	**6175.63**	**± 2846.18**	8	11.38	6475.50	0.61	0.25	0.30
				Magelona mirabilis	**52.25**	**± 24.80**		±2.24	±2880.00	±0.19	±0.09	±0.08
				Macomangulus tenuis	31.00	±12.14						
				Sigalion mathildae	22.50	±6.75						
				Polycirrus medusa	19.75	±13.64						
I-19	***Peringia ulvae***	**0.955**	**0.0001**	***Peringia ulvae***	**4437.33**	**± 2503.19**	3	11.67	5126.80	0.98	0.41	0.39
	Limecola balthica	**0.877**	**0.0010**	***Macomangulus tenuis***	**181.33**	**± 90.78**		±3.53	±2396.89	±0.50	±0.22	±0.19
				Pygospio elegans	157.33	±157.33						
				Cerastoderma edule	88.00	±84.03						
				Corophium arenarium	72.00	±46.88						
II-19	***Urothoe poseidonis***	**0.510**	**0.0004**	***Macomangulus tenuis***	**410.667**	**± 137.42**	12	14.67	1135.00	1.80	0.72	0.67
	Macomangulus tenuis	**0.451**	**0.0019**	***Urothoe poseidonis***	**194.000**	**± 73.74**		±0.82	±198.53	±0.13	±0.04	±0.04
	Cerastoderma edule	0.451	0.0287	*Bathyporeia sarsi*	144.667	±79.88						
				Cerastoderma edule	94.000	±27.35						
				Spio martinensis	44.667	±17.04						
III-19	***Acrocnida spatulispina***	**0.629**	**0.0001**	***Acrocnida spatulispina***	**324.80**	**± 307.86**	10	18.30	825.04	2.07	0.76	0.71
	Kurtiella bidentata	**0.62**	**0.0001**	***Kurtiella bidentata***	**66.40**	**± 33.742**		±1.69	±86.42	±0.20	±0.06	±0.06
	Malmgrenia marphysae	0.617	0.0079	*Bathyporeia elegans*	49.60	±52.092						
	Polycirrus medusa	0.497	0.0007	*Polycirrus medusa*	48.00	±38.088						
	Bathyporeia elegans	0.496	0.0125	*Cumopsis longipes*	45.60	±68.201						
IV-19	***Magelona mirabilis***	**0.595**	**0.0001**	***Donax vittatus***	**81.71**	**± 31.58**	14	20.50	730.37	2.49	0.88	0.85
	Donax vittatus	**0.505**	**0.0109**	***Magelona mirabilis***	**68.00**	**± 15.68**		±2.00	±128.38	±0.12	±0.01	±0.02
	Aponuphis bilineata	0.500	0.005	*Acrocnida spatulispina*	46.28	±15.69						
	Scoloplos armiger	0.486	0.0271	*Pseudocuma longicorne*	45.71	±34.59						
				Polycirrus medusa	43.42	±16.49						
V-19	***Eurydice affinis***	**1.000**	**0.0004**	***Bathyporeia pilosa***	**818.67**	**± 500.23**	3	7.33	1053.10	0.98	0.47	0.54
	Eurydice pulchra	**0.905**	**0.0004**	***Scolelepis squamata***	**85.33**	**± 85.33**		±2.03	±540.33	±0.28	±0.15	±0.17
	Bathyporeia pilosa	0.714	0.0003	*Eurydice pulchra*	64.00	±25.72						
				Nemertia	18.67	±14.85						
				Eurydice affinis	10.67	±2.67						

station, was characterized by the highest trajectory path (27.29) but one of the smallest net change (2.63) in relation with an effective recovering trajectory between 1987-2001 and 2001–2019. Cluster G was the most common pattern of functional trajectories (30 stations) characterized by moderate net changes (4.66 ± 0.28) and trajectory path (9.53 ± 0.48). This cluster was characterized by moderate functional changes, except for an increase in the contribution of flexible and small size species. Cluster H grouped five stations of the low shore characterized by high

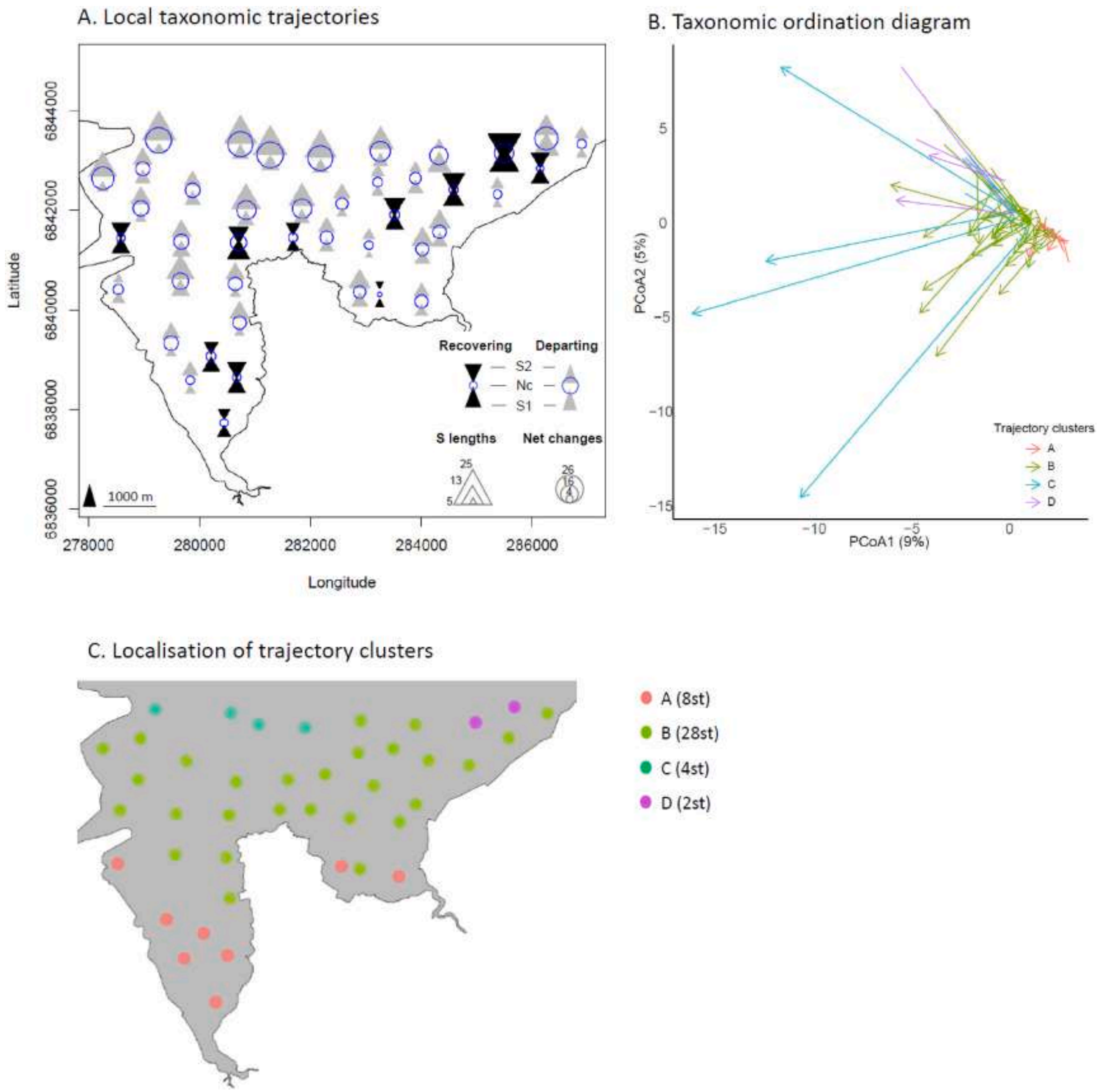


Fig. 5. Taxonomic trajectories. A.: Maps of local trajectories. Distance based metrics are represented with circular and triangle symbols. Net changes are represented with blue circles between 1987 and 2019. Bottom triangles represent the trajectory segment S1 (1987–2001) and top ones S2 (2001–2019). Size of symbols corresponds to lengths. For triangles, colors are used to distinguish recovering (black) from departing trajectories (grey). B: Trajectory ordination diagram. The three ecological state of each station were connected with arrows in order to represent the whole trajectory path. Each trajectory path was coloured according to taxonomic trajectory clusters defined with Hierarchical Cluster Analysis based on CTA trajectory similarity analysis. Despite trajectory distance-based metrics and dissimilarity were calculated considering all of the dimensions of the PCA, the first two dimensions show only 14% of the total variation, which may potentially hide some patterns. C.: Localisation of trajectory clusters within the study area. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

trajectory path (19.97 ± 1.72) and moderate net changes (5.71 ± 0.94), in relation with recovering trajectories occurring at this sites. The main functional shift in cluster H concerned a positive shift of suspension-feeders, free living, medium fragile, and rigid species, notably attributable to strong variation of *D. vittatus* observed at these stations.

Despite some local functional shift depending on functional trajectory clusters, and some slight significant shifts for some categories of traits, the overall functional properties remained stable over time at the site scale (Fig. 8).

4. Discussion

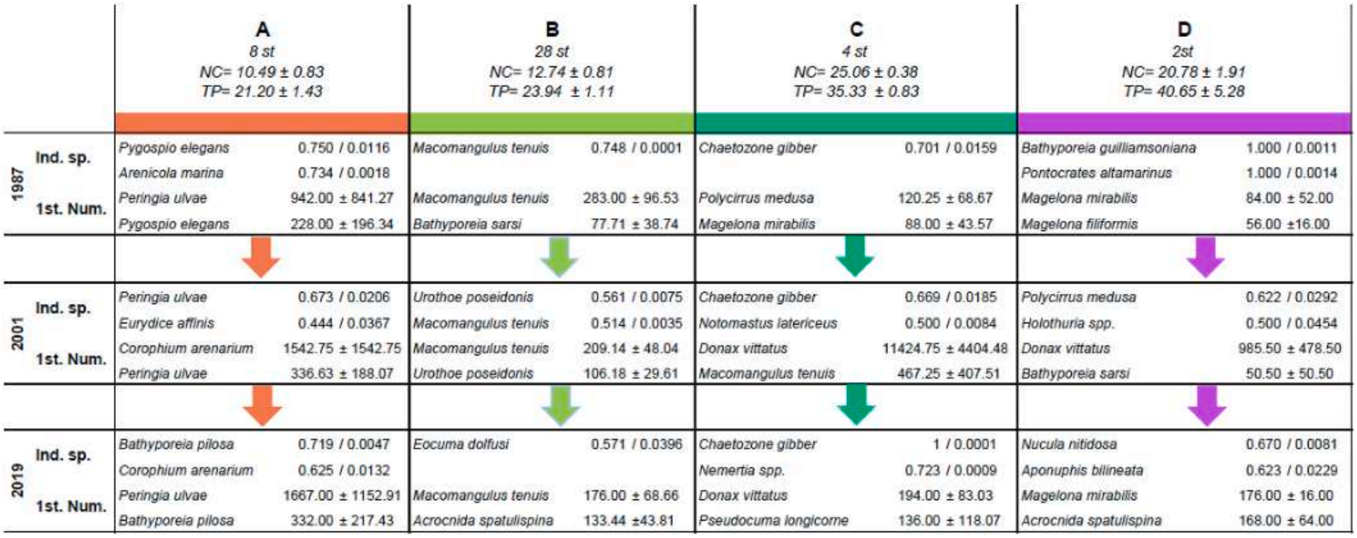
4.1. Local ecological dynamics influence benthic assemblages

As expected in such coastal environment (McLachlan and Brown, 2006), macrofauna was dominated by molluscs, polychaetes, and crustaceans, and 95.5% of the total abundance was due to 36 species common to the three sampling periods. This revealed a strong stability in the pool of species influencing community abundance and composition. Some gains and losses of occasional and rare species influenced variations of the relative contribution of taxonomic group to overall richness. Changes in assemblages mainly involved some of the prevalent species, suggesting a strong impact of fluctuating population dynamics rather than species replacement in the community. Different indicators and numerous species were involved in the definition of assemblages and taxonomic trajectory clusters but the contribution of some species to these descriptions was constant over time, notably *P.ulvae, L. balthica, U. poseidonis, C. edule, M. tenuis, C. gibber* and *M. mirabilis*. At the scale of stations, despite an overall departing taxonomic trend, we observed mainly recovering functional trajectories.

Two main mechanisms are involved in the long-term variability of benthic assemblages: the dynamics of structuring species and the existence of strong local variability.

Table 3

Characteristics of ecological states of trajectory clusters in 1987, 2001 and 2019. Taxonomic trajectory are coloured according to trajectory clusters and described with distance-based metrics mean ± se (NC: net change, TP: Trajectory path). Distribution of species used to describe taxonomic trajectory clusters (Ind.sp.: Indicative species, 1st. Num.: two first numerous species) are detailed in Supplementary material, Appendix D.



		A 8 st NC= 10.49 ± 0.83 TP= 21.20 ± 1.43		**B** 28 st NC= 12.74 ± 0.81 TP= 23.94 ± 1.11		**C** 4 st NC= 25.06 ± 0.38 TP= 35.33 ± 0.83		**D** 2st NC= 20.78 ± 1.91 TP= 40.65 ± 5.28	
1987	**Ind. sp.**	*Pygospio elegans*	0.750 / 0.0116	*Macomangulus tenuis*	0.748 / 0.0001	*Chaetozone gibber*	0.701 / 0.0159	*Bathyporeia guilliamsoniana*	1.000 / 0.0011
		Arenicola marina	0.734 / 0.0018					*Pontocrates altamarinus*	1.000 / 0.0014
	1st. Num.	*Peringia ulvae*	942.00 ± 841.27	*Macomangulus tenuis*	283.00 ± 96.53	*Polycirrus medusa*	120.25 ± 68.67	*Magelona mirabilis*	84.00 ± 52.00
		Pygospio elegans	228.00 ± 196.34	*Bathyporeia sarsi*	77.71 ± 38.74	*Magelona mirabilis*	88.00 ± 43.57	*Magelona filiformis*	56.00 ±16.00
		↓		↓		↓		↓	
2001	**Ind. sp.**	*Peringia ulvae*	0.673 / 0.0206	*Urothoe poseidonis*	0.561 / 0.0075	*Chaetozone gibber*	0.669 / 0.0185	*Polycirrus medusa*	0.622 / 0.0292
		Eurydice affinis	0.444 / 0.0367	*Macomangulus tenuis*	0.514 / 0.0035	*Notomastus latericeus*	0.500 / 0.0084	*Holothuria spp.*	0.500 / 0.0454
	1st. Num.	*Corophium arenarium*	1542.75 ± 1542.75	*Macomangulus tenuis*	209.14 ± 48.04	*Donax vittatus*	11424.75 ± 4404.48	*Donax vittatus*	985.50 ± 478.50
		Peringia ulvae	336.63 ± 188.07	*Urothoe poseidonis*	106.18 ± 29.61	*Macomangulus tenuis*	467.25 ± 407.51	*Bathyporeia sarsi*	50.50 ± 50.50
		↓		↓		↓		↓	
2019	**Ind. sp.**	*Bathyporeia pilosa*	0.719 / 0.0047	*Eocuma dolfusi*	0.571 / 0.0396	*Chaetozone gibber*	1 / 0.0001	*Nucula nitidosa*	0.670 / 0.0081
		Corophium arenarium	0.625 / 0.0132			*Nemertia spp.*	0.723 / 0.0009	*Aponuphis bilineata*	0.623 / 0.0229
	1st. Num.	*Peringia ulvae*	1667.00 ± 1152.91	*Macomangulus tenuis*	176.00 ± 68.66	*Donax vittatus*	194.00 ± 83.03	*Magelona mirabilis*	176.00 ± 16.00
		Bathyporeia pilosa	332.00 ± 217.43	*Acrocnida spatulispina*	133.44 ±43.81	*Pseudocuma longicorne*	136.00 ± 118.07	*Acrocnida spatulispina*	168.00 ± 64.00

1. Coupled with random gain or losses of species (Legendre, 2019), the dynamics of structuring species results in moderate specific taxonomic changes in the multivariate structure of assemblages. However, several species can induce strong trends, such as *D. vittatus*, whose abundance varied from 13.4 ± 15 ind.m^2 (20 stations) in 1987–3107 ± 6347 ind.m^2 (16 stations) in 2001 and 72.8 ± 101 ind.m^2 (19 stations) in 2019 or *A. spatulispina* and *Kurtiella bidentata*, whose occurrence and abundance increased. In assemblage I, the decline in *L. balthica* populations is potentially attributable to climate change (temperature increase) as suggested by different works in European regions (Beukema et al., 2009; Genelt-Yanovskiy et al., 2017; Jansen et al., 2007; Ong et al., 2017; Philippart et al., 2003; Van Colen et al., 2018). The bay of Saint-Brieuc being located in the southern part of *L. balthica*'s distribution, populations are likely to be affected by climate warming.
2. The stronger local variability is able to induce changes in assemblage definition, according to the initial state defined in 1987. The identification of a new assemblage in 2019, in relation to sedimentary variations, and the re-affectation of some stations to different assemblages illustrate such spatial changes. The distribution of *A. spatulispina* and *K. bidentata* in particular significantly extended in the sampling area over time.

At some stations, local taxonomic variability was of higher magnitude than the within-assemblages dispersion observed in 1987, which resulted in changes in the affectation of assemblage over time. Depending on stations, differences between assemblages were driven by differences in species compositions and/or dynamic of densities (see differences in Table 2). Some stations were also located at the border of some assemblages implying that they can be influenced by one assemblage or another depending on the year. Because changes in species composition and/or abundance (maybe favoured by hydrodynamics and/or sediments), some stations move from one assemblage to another. For instance, the station 15 located at the border of two assemblages in an area of high tidal channels dynamic was characterized by successive changes over time: some species were sampled at least at two dates (e.g. *Cerastoderma edule, Sigalion mathildae, Macomangulus tenuis* or *Bathyporeia sarsi*) whereas others rised high abundance at only one date (e.g. *Scolelepis squamata* in 1987; *Macomangulus tenuis* and *Polycirrus medusa* in 2001; *Bathyporeia elegans, Cumopsis longipes* in 2019).

At the opposite, others trajectories buffered local functional changes in some stations at the assemblage scale, especially in the low part of the shore. Taken separately, stations were characterized by different functional trajectories, and the concentration of local recovering trajectories in these assemblages contributed to explain the overall functional persistence. Macrobenthic communities are often associated to a mosaic of micro-habitats where natural disturbance events result in the creation of patches characterized by different recovering stages (Defeo et al., 2009; Ellis et al., 2000).

According to Grimm and Wissel (1997), persistence is defined as a stability property of ecological systems which nevertheless integrate moderate temporal variations. It differs of the concept of constancy, which describes unchanged systems. Despites changes observed at the scale of assemblages coupled with fluctuating population dynamics of structuring species, we assume an overall persistence of the whole benthic community in the bay of Saint-Brieuc. Such assumptions are in accordance with Bacouillard et al. (2020), which suggest that local turnover can be very high, especially in response of hydrologic and sedimentary dynamics (Desroy et al., 2007), without adversely affecting the long-term persistence of the community.

4.2. *Low shore concentrates taxonomic changes*

The CTA approach revealed that the taxonomic variability increased following an inshore-offshore gradient. In the upper flat, sheltered conditions, strong influence of salinity variations and emersion time limit the number of species and the variability due to species gain. Inversely, the taxa richness increasing towards the lower flat contributes to the magnitude of change in low levels. As observed in 2019 for *Aponuphis bilineata* and *Nucula nitidosa*, the local presence of subtidal species on the intertidal flat constitutes a source of variation.

The northwest part of the bay, characterized by professional and recreational fishing activities known to impact benthic community properties (Boldina et al., 2014; Mosbahi et al., 2016), concentrated the highest net changes. Tides associated to hydrodynamics, particularly strong in our study area, is recognized as a dominant factor shaping the

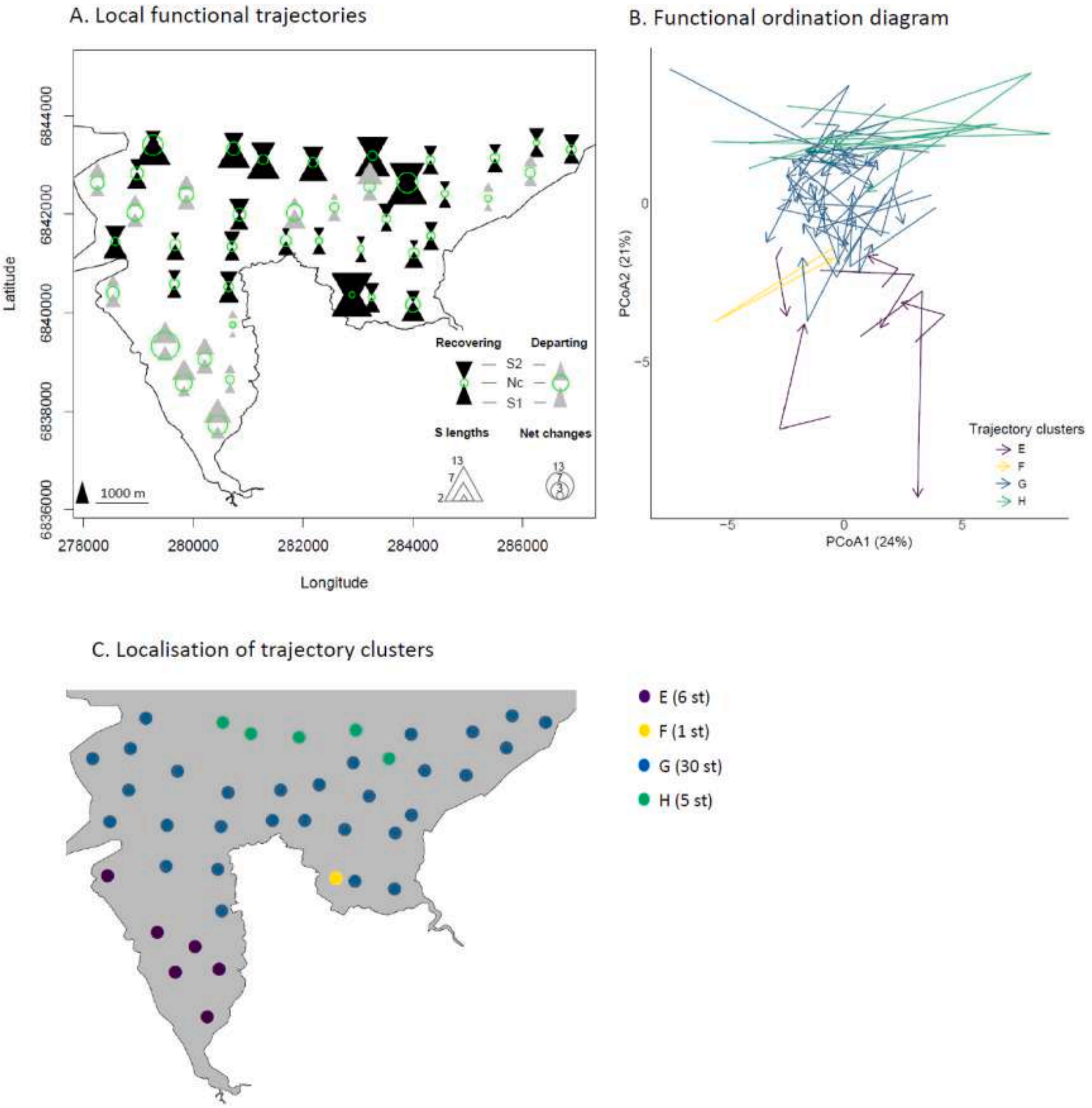


Fig. 6. Functional trajectories. A.: Maps of local trajectories. Distance based metrics are represented with circular and triangle symbols. Net changes are represented with green circles between 1987 and 2019. Bottom triangles represent the trajectory segment S1 (1987–2001) and top ones S2 (2001–2019). Size of symbols corresponds to lengths. For triangles, colors are used to distinguish recovering (black) from departing trajectories (grey). B: Trajectory ordination diagram. The three ecological state of each station were connected with arrows in order to represent the whole trajectory path. Each trajectory path was coloured according to functional trajectory clusters defined with Hierarchical Cluster Analysis based on CTA trajectory similarity analysis. C.: Localisation of trajectory clusters within the study area. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

variability of coastal systems (Monbet, 1992; Wildish, 1977; Wildish and Kristmanson, 1979). This factor is responsible for surficial sediment coverage and, consequently, for the dynamics of the distribution of macrofauna as demonstrated by Fujii (2007) in the Humber estuary (UK), Compton et al. (2013) in the Wadden sea, or Veiga et al. (2017) on North Portuguese coasts. The influence of intertidal channels divagation (within a 1420 ha area since 1988, Supplementary material, Appendix A) must also be considered as a driver of sediments resuspension and habitat resetting, particularly important in the low western shore. In the eastern part, low net changes associated with high trajectory path and recovering trajectories could be explained by sand banks displacement from north to south. Such impact of sediment transport has already been highlighted in different coastal areas in New Zealand (Thrush et al., 2003), France (Gouleau et al., 2000) or experimentally in the UK (Whomersley et al., 2010). In this way, we expect any anthropogenic activity potentially modifying sedimentary parameters (bio deposition, sediment deposition, beach nourishment, dredging …) to, in turn, modify intensely the composition, structure and functioning of soft bottom assemblages as suggested by Veiga et al. (2017).

Whomersley et al. (2010) suggested that benthic communities frequently disturbed by sediment movements or other natural environmental conditions would show greater resilience against further physical disturbance. Such resilient responses to disturbance, due to the selection of adapted species, depend on the history of prior disturbance and on the inherent ecological plasticity exhibited by species (Davic, 2003). In our study, 36 prevalent species contribute to the persistence of the community over time. Most of these species are adapted to living in mobile sediments (McLachlan and Brown, 2006) and facing erosion and sedimentation. They could then persist because of their tolerance to the harshness of the environment as suggested by Callaway (2016).

In many coastal ecosystems, multiple disturbance sources, both natural and anthropogenic, are often confounded (Whomersley et al., 2010), which makes difficult the definition of their respective contribution (Harris, 2012). Our study confirms the complexity to disentangle factors of changes in dynamic areas, where strong natural variability results in regular community resets (Defeo and McLachlan, 2013), which

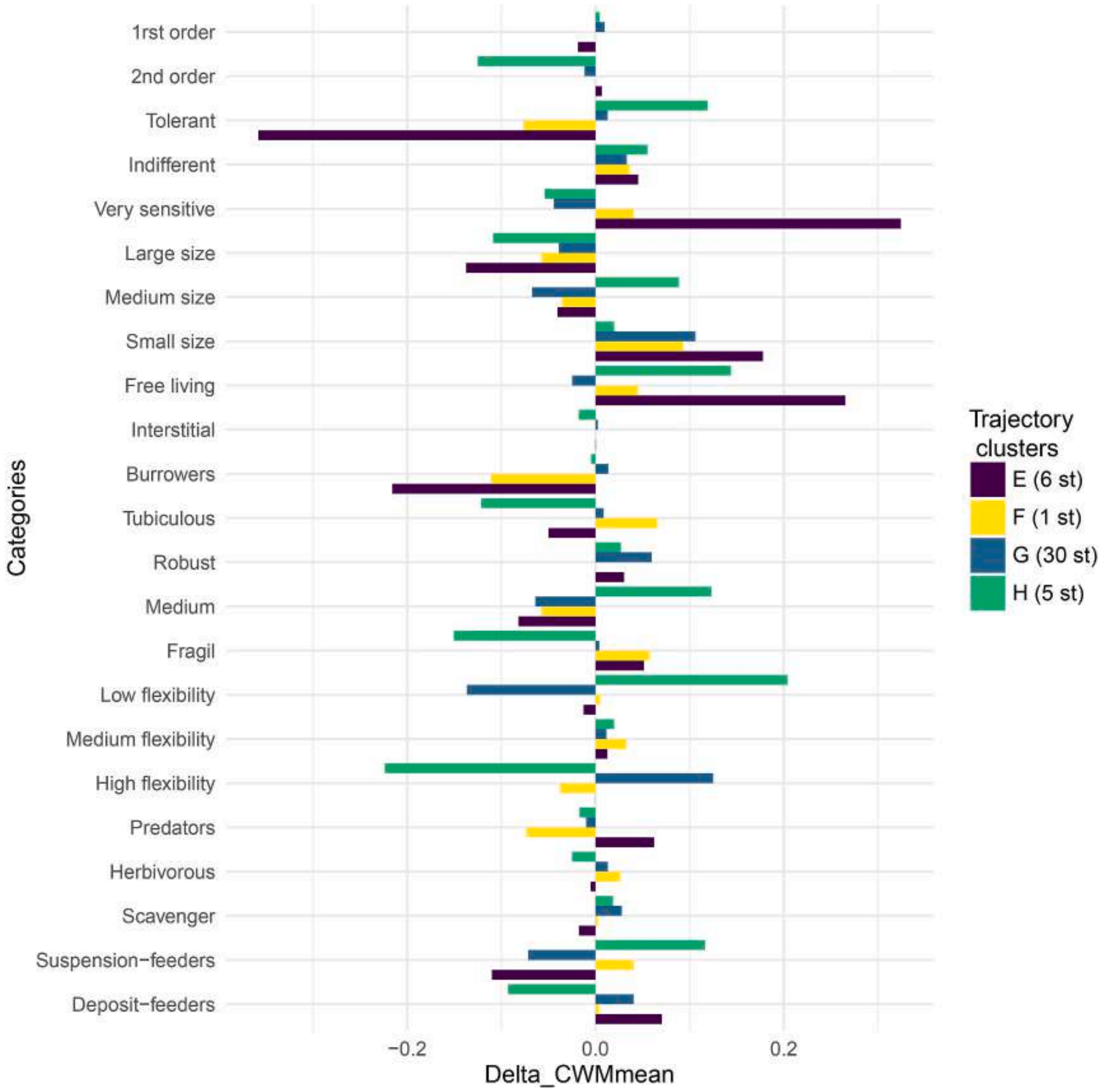


Fig. 7. Barplots of Community-weighted trait values (CWM) values shift for each categories of traits (mean 2019 – mean 1987). Bars are coloured according to functional trajectory clusters.

may overshadow anthropogenic impact. On the opposite, areas characterized by low hydrodynamics where benthic communities are not naturally adapted to disturbances would therefore be very sensitive to additional physical disturbance as showed by Jac et al. (2020). In the bay of Saint-Brieuc characterized by severe natural constrains, further studies coupling experimental and high frequency field samplings should deal with the respective role of hydrodynamics and anthropogenic activities in resetting benthic communities (shear stress measurement in area concerned and not by the circulation of vehicles from mussels farming, analysis of the benthic macrofauna variability coupled with different gradients of fishing activities and or local dynamics…).

4.3. Functional properties of the community persist over time

The CTA resulted in contrasted taxonomic and functional trajectory patterns (*i.e.* net changes, departing and recovering trajectory). Clare et al. (2015) showed that density compensation by redundant taxa buffers ecological functioning changes, but that functional stability is subjected to aperiodic disruption due to substitutions of dissimilar taxa or uncompensated population fluctuations. Accordingly, high trajectory paths observed in the low shore reflected an important functional variability, but recovering trajectories notably influenced by *D. vittatus* fluctuating population dynamics led to low net changes. Functional properties persisted over time at the scale of the whole community. Low sensitivity of traits such as body size, flexibility, fragility to genus and, in a lesser extent, species changes also contribute to limit the influence of taxonomic variability on the functional stability. Lower influence of traits relative to feeding behaviour finally suggested no major changes at the scale of intertidal sedimentary habitats, in accordance with (Sturbois et al., 2021b) who showed that high sedimentary variability was limited to few sites.

To choose the set of traits in relation to main pressures, we hypothesised that fishing activities in the lower flat may influence benthic assemblages over time according to changes in relative values of body size, flexibility, fragility. Low net changes in the lower part of the shore for the widespread functional trajectory cluster G and the influence of *D. vittatus* in the functional trajectory of cluster H does not support such a functional response to human pressures.

A similar interest was devoted to the tolerance of species to organic matter enrichment according to the eutrophication process, mainly due to green tides. No major change was observed at the scale of the whole study area in the contribution of the different categories of tolerance. In accordance, changes were moderate in the different functional clusters except in cluster E characterized by an important positive shift in the contribution of very sensitive species. Despite a slow long-term water quality improvement trend and a progressive decrease of green tides

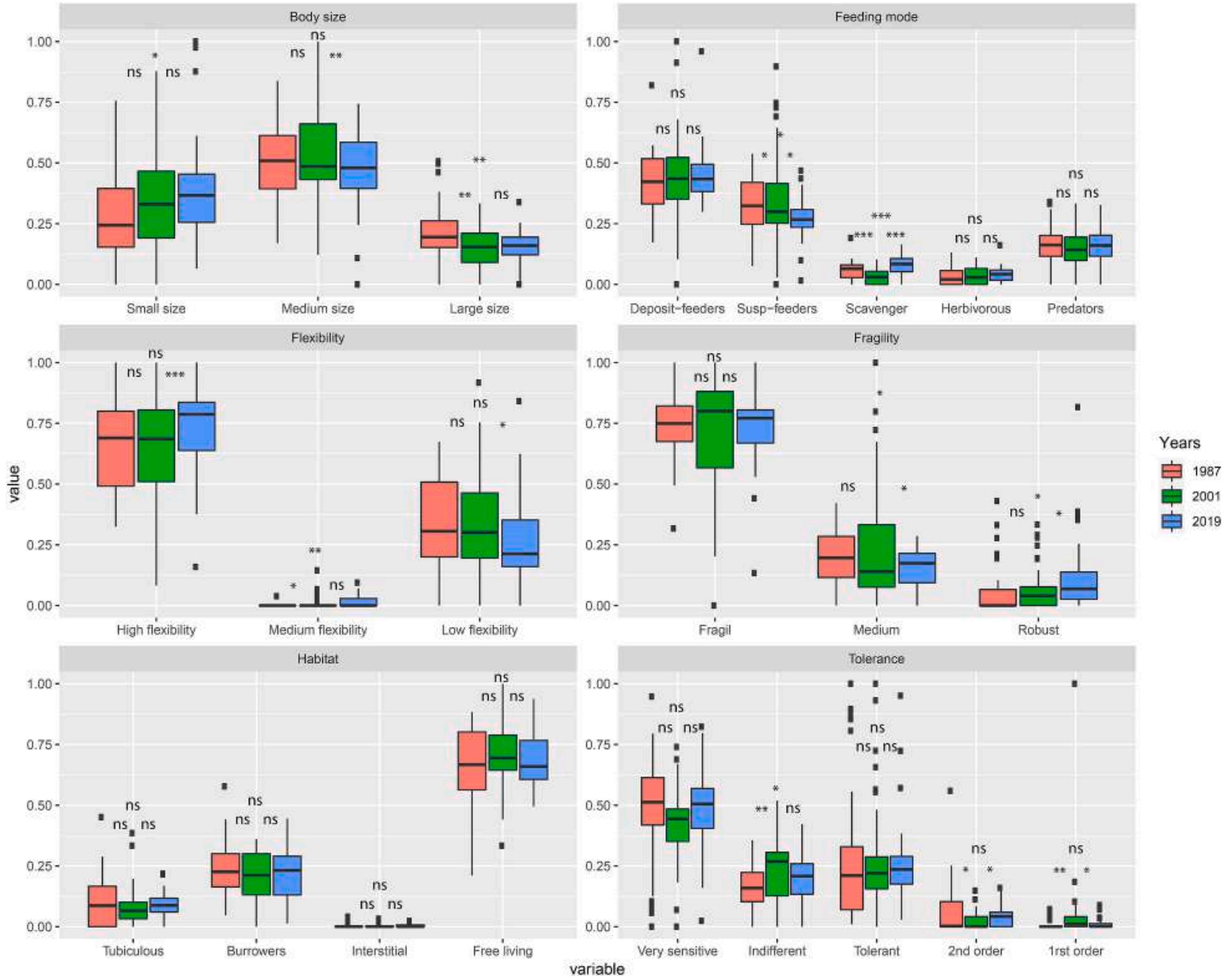


Fig. 8. Box plots of Community-weighted trait values (CWM) traits values in levels of respective categories according to year (1987: red; 2001: green; 2019: blue). Box plot indicates the median (line in the box), the first and third quartiles (hinges) and extreme data points (black points). Significance of student permutation paired tests are indicated for each category traits (ns: non significant; *: pval<0.05; **: pval<0.01; *** pval:<0.001). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

associated to local water development and management plan, these events still strongly affect the study area. Quillien et al. (2015a) discussed the potential influence of *Ulva* sp. mats on abundance peak of *D. vittatus* (improved recruitments and negative effect on predators of larvae), which could explain high densities reaching 21 487 ind.m^2 in 2001 and 14 685 ind.m^2 in 2011 in the bay of Saint-Brieuc (unpublished data). Quillien et al. (2015b) also highlighted large-scale effects of green tides on macrotidal sandy beaches in Brittany, showing notably that the echinoderm *A. spatulispina* and the mollusc *K. bidentata* were stimulated in soft bottom sediments impacted by green tides, contrary to the crustaceans *B. elegans* and *Cumopsis* spp., which were impacted. In our study, the abundance and occurrence of these four taxa increased over the study period, revealing a more complex gradient of sensitivity to green tides and/or nutrient enrichment and the implication of other driving factors. As suggested by Bolam et al. (2000), Everett (1994), and Raffaelli et al. (1999), generalisations on the effect of algae mat are not straightforward. In the study area, we believe that the important green-tides associated to nutrient uptake buffer the influence of nutrient enrichment on macrofauna.

4.4. *The crucial need of data at multiple spatial and temporal scales*

The CTA applied to marine communities offers new trajectory metrics and tools (De Cáceres et al., 2019; Sturbois et al., 2021b), useful to the accurate quantification and description of changes as suggested by Cimon and Cusson (2018), which claimed for the development of new metrics to document effects on community dynamics. The potential and the interest of such framework focused on the analysis of ecological dynamics increases significantly with the size of the time series.

There is virtually no appropriate benchmark data describing natural standards and alterations of most environmental systems concerned by impacts accumulation (Ellis et al., 2000). Like many estuarine and coastal areas, the bay of Saint-Brieuc has been exposed to strong human influence over the last decades. The ecological state identified in 1987 and considered as the initial state in this study, was defined under a pressure context already well established (notably nutrient enrichment, macroalgae proliferation, mussel farming, fishing activities). The absence of a pristine reference state constitutes a strong limitation in the analysis of long-term trends (Hardman-Mountford et al., 2005; Rubal et al., 2014; Veiga et al., 2017). Furthermore, our study suffers from the absence of long-term measurements of environmental factors and anthropogenic pressures, especially to disentangle natural vs anthropogenic changes.

Our results illustrate the value of historical data for marine and coastal management, as well as the importance of maintaining consistent protocols, as underlined by Callaway (2016). Overall, the complementary methods and scales used to analyse the data set contributed to the research frameworks focused on the definition of changes and impact assessments at spatial and temporal scales in marine ecosystems. However, it pointed the limitations of sampling strategies that only imply long-term networks. The patterns of changes described were based only on three sampling occasions, which limits the understanding of processes occurring between each surveys, and potentially overshadowing important intermediate changes (e.g. occasional dominance by very large numbers from very few species as observed for *D. vittatus*). As suggested by Bacouillard et al. (2020), the coupling of different spatial and temporal scales in sampling strategy [few stations with high frequency sampling (Hewitt et al., 2016) *vs* low frequency larger sampling networks (Kröncke et al., 2011)] could help to track changes between long-term networks. Bacouillard et al. (2020) propose in the bay of Seine 60 stations sampled every five years to assess long-term changes in the beta diversity (i.e. assemblages distributions) and five stations sampled at least once a year to analyse the heterogeneity in the responses of local community to multiple stressors. Sturbois et al. (2021a) have also demonstrated such interests of coupling different spatial and temporal scales by the use of two complementary data sets (38 stations in 1987 and 2019, and one station from 2005 to 2019). In this study, the 15 years time series suggested that changes observed in a subtidal benthic community over the last 30 years occurred probably from 2015. It claims for the local development of an ambitious monitoring strategy in the intertidal area based on the 42 stations network sampled every 10 years coupled with at least one station sampled once a year in each assemblage.

An overarching question in conservation biology is the assessment of marine protected area effect on marine habitats (Appolloni et al., 2017; Bevilacqua et al., 2006; Day et al., 2012; Klein et al., 2015; Thompson et al., 2012). In this study, it was not possible to assess accurately any conservation effect of the National Nature Reserve as 1) species and assemblages remained locally very contrasted between unprotected and protected areas and 2) such assessment ideally requires a global network of protected and unprotected areas.

However, this study provides an up-to-date assessment to policy makers and managers about the evolution of the composition, structure and functioning of benthic assemblages. This knowledge will integrate future governance rounds, in a multi-scale approach involving policy makers and stakeholders, and will make marine habitats, a central part of the conservation process (Greathead et al., 2020), which aim notably to extend the current natural reserve perimeter. Such approaches should not only focus on aggregating local present day practices, but also on exploring future visions and potential scenarios (Pereira L., 2021).

5. Conclusion

The CTA framework brings new quantitative and qualitative insights to characterize and illustrate changes in marine habitats. The consideration of both local changes and variations at population levels helps to explain the differences observed at the scale of assemblages. Observed changes mainly reflected random population dynamics of structuring prevalent species in habitat under strong natural constrains, rather than strong specific changes of the community. Few species may underline the long-term effect of green tides in some assemblages. This study also claims for ambitious monitoring strategy in order to integrate multiple spatial and temporal scales, and efficient measurements of environmental and anthropogenic driven factors.

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CRediT authorship contribution statement

A. Sturbois: Conceptualization, Methodology, Validation, Formal analysis, Data curation, Writing – original draft, Visualization, Project administration, Funding acquisition, Investigation. **G. Cormy:** Writing – review & editing, Investigation. **G. Schaal:** Methodology, Writing – review & editing, Investigation, Supervision, Validation. **O. Gauthier:** Methodology, Writing – review & editing, Validation. **A. Ponsero:** Writing – review & editing, Visualization, Investigation. **P. Le Mao:** Writing – review & editing, Investigation. **P. Riera:** Writing – review & editing. **N. Desroy:** Methodology, Writing – review & editing, Investigation, Supervision, Validation.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Anthony STURBOIS reports financial support was provided by Agence de l'Eau Loire Bretagne. Anthony STURBOIS reports financial support was provided by Region Bretagne. Anthony STURBOIS reports financial support was provided by Europe for the European maritime and fisheries fund. Anthony STURBOIS reports financial support was provided by Ministery de la Transition Ecologique et Solidaire.

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Appendix A. Supplementary data

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Article IV

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RESEARCH ARTICLE

WILEY

Using ecological trajectories to track long-term taxonomic and functional changes in benthic shallow soft-bottom communities (Bay of Saint-Brieuc, English Channel)

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Abstract

1. Taxonomic and functional trajectories of benthic assemblages were studied in shallow soft-bottom sediments in the bay of Saint-Brieuc (Western English Channel). Changes were assessed at different spatial and temporal scales using a macrobenthic dataset based on 38 stations sampled in 1987 and 2019, coupled with data from one station sampled annually between 2005 and 2019 as part of the European Water Framework Directive monitoring programme.
2. Taxonomic trajectories indicated 1) changes in the structure and distribution of benthic assemblages, 2) an homogenization of the assemblages, and 3) significant functional shifts.
3. Fishing activities and nutrient enrichment are probably strong drivers of the observed changes, as suggested by the higher mortality rate of fragile, flexible, tubiculous and burrowing species, and the increase in the abundance of opportunistic species in the assemblages. Certain populations of macroinvertebrates seem jointly controlled by climate change and by the aforementioned local factors of disturbance.
4. The Community Trajectory Analysis framework appears as a new and interesting method to track ecological changes in marine ecosystems by measuring change with respect to a baseline state, to help define ecological recovery (station returning to the initial ecological state) and departure (station presenting increased changes over time), and to analyse trajectory similarity.
5. According to the degradation of habitat over time, we identify the need for the implementation of knowledge-based conservation strategies, especially within Natura 2000 sites.

KEYWORDS

benthic assemblages, community trajectory analysis, conservation, ecological trajectories, eutrophication, long-term changes, macrofauna, Natura 2000, scallop dredging

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Oceanic cruse: Desroy N., 2019. RESTRO 19 cruise, RV Thalia, https://doi.org/10.17600/18000934

1 | INTRODUCTION

Worldwide, marine ecosystems are suffering severe taxonomic and functional changes in response to cumulative effects of anthropogenic disturbances including overfishing, pollution, global climate change, habitat degradation and introduction of non-indigenous species (Gray, 1997; Claudet & Fraschetti, 2010). Human influences induce both acute and chronic effects over various temporal and spatial scales, and can ultimately lead to broad-scale loss of productive habitats, and alteration of community structure and function (Ellis, Norkko & Thrush, 2000). As a result, 60% of major marine ecosystems worldwide are currently degraded or suffer from unsustainable levels of exploitation, leading to the adoption of conservation policies by many countries (Convention on Biological Diversity, 2010; UNEP, 2011). The European Water Framework Directive (WFD, Directive 2000/60/EC) and the Marine Strategy Framework Directive (European MSFD, Directive 2008/56/EC) require that European Member States implement measures to achieve a good environmental status of their water bodies.

The comparison to reference conditions based on pristine or slightly disturbed areas is recommended by the European WFD to track changes in environmental status, although it is generally recognized that non-disturbed marine and estuarine habitats are rare (Borja, Dauer & Grémare, 2012), and that historical data rarely constitute a pristine state (Callaway, 2016; Bacouillard et al., 2020). In this context, acceptable levels of disturbance can be used to define reference conditions (Borja, Dauer & Grémare, 2012). Such an approach requires repeated and standardized surveys over time to: 1) track changes with respect to baselines conditions, and 2) provide up-to-date ecological state to stakeholders involved in the development of management plans for coastal and marine areas. Benthic macrofauna has been considered as a relevant descriptor to characterize the biological status of water bodies by the European WFD (Borja, Muxika & Rodríguez, 2009; Borja, Dauer & Grémare, 2012), as this compartment influences nutrient cycling, represents an important food resource for higher trophic levels (Snelgrove, 1997; McLusky & Elliott, 2004), and reacts rapidly to disturbances (Gray, 1997; Claudet & Fraschetti, 2010).

Among sublittoral macrobenthic assemblages, very shallow subtidal habitats (0-15 m), accessible for sampling only during high tide, are often excluded from sampling programmes and remain, to a large extent, poorly monitored (Desroy et al., 2002). Very shallow communities are notably characterized by high diversity and productivity levels (Gray, 1997; Snelgrove, 1999; Levinton, 2001). This knowledge gap and the scarcity of data constitute a serious impediment for the implementation of conservation strategies (Ellis, Norkko & Thrush, 2000).

On the French coast of the English Channel, scientific studies have largely focused on benthic communities of the main coastal bays and estuaries [e.g. Rance estuary, (Desroy & Retière, 2004), bay of Seine (Dauvin & Desroy, 2005; Desroy et al., 2007; Bacouillard et al., 2020) or bay of Mont-Saint-Michel (Trigui, 2009)]. In the bay of Saint-Brieuc (Western English Channel), the ecological state of subtidal communities defined in 1987 by Gros & Hamon (1988) has never been updated, contrasting with the monitoring strategy deployed in the adjacent intertidal area, partially protected since 1998 by a National Nature Reserve primarily devoted to the conservation of birds and, *de facto*, to benthic habitats (Sturbois et al., accepted). This shallow subtidal area, belonging to the "Baie de Saint-Brieuc – Est" Natura 2000 site, supports intense fishing activities (dominated by scallop dredging) and mussel rope culture.

Historical data are rare in this very shallow area, and limited to the ecological assessment carried out in 1987 by Gros & Hamon (1988) and to the WFD monitoring conducted at one station from 2005 to 2019.

This study, based on a resampling of the stations sampled in 1987 in the bay of Saint-Brieuc and on the WFD long-term monitoring of the benthic assemblage at one shallow station, aims to analyse taxonomic and functional trajectories of benthic assemblages in order to: (1) detect patterns of changes over the last 30 years at different spatial scales using the 38 stations sampled in 1987 and 2019, and (2) analyse recent dynamics at one station sampled yearly from 2005 to 2019 as part of the WFD monitoring programme. As single or multiple disturbances differently affect species composition and structure, temporal changes of the benthic community were tracked, with both α and β-diversity metrics (Ellis, Norkko & Thrush, 2000; Cimon & Cusson, 2018). In accordance with Dornelas et al. (2013), Magurran et al. (2019), and Yang (2020) recommendations to develop new multivariate metrics devoted to the study of temporal ecological changes and response to disturbance (Cimon & Cusson, 2018), we specifically focused on taxonomic and functional spatio-temporal trajectories coupling classic multivariate analysis with the recent Community Trajectory Analysis framework (De Cáceres et al., 2019; Sturbois et al., 2021), finally discussing conservation prospects for such coastal areas.

2 | MATERIAL AND METHODS

2.1 | Study area

Fieldwork was conducted in the bay of Saint-Brieuc (France, Figure 1). The study area encloses 11,700 ha of very shallow soft-bottom sediments. The bay is under the influence of a semi-diurnal megatidal regime. Tidal range varies between 4 m at neap tides and nearly 13 m during spring tides. Despite bordering the National Nature Reserve of the bay of Saint-Brieuc and partially belonging to the Natura 2000 "Baie de Saint-Brieuc-Est" site (FR5300066), the study area is exposed to a number of anthropogenic pressures including mussel culture, scallop dredging and eutrophication. Mussels are farmed on bouchots (wooden poles, Figure 1) in the north-eastern part of the intertidal area, occupying 277 ha and 312 ha in 1987 and 2019, respectively (Sturbois et al., accepted) and are also farmed on ropes in the western part of the study area, around stations 81, 99 and 100. The sea bed is also exposed to long-term scallop dredging activities as the bay of Saint-Brieuc is characterized by the

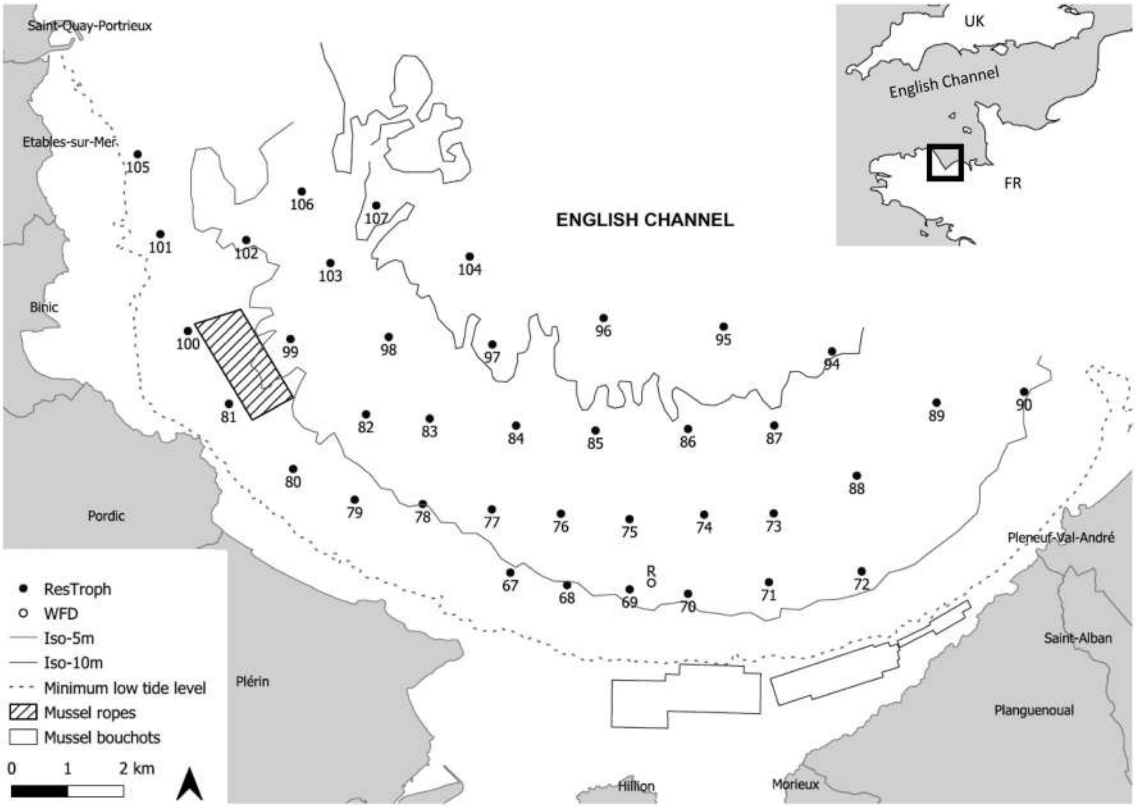


FIGURE 1 Location of the study area and sampling strategy. Black dots correspond to the 38 stations of the ResTroph research programme sampled in 1987 and 2019 and the white one (station R) to the Water Framework Directive (WFD) monitoring programme conducted from 2005 to 2019. Water depth is represented by dotted (0 m) and continuous lines (5 and 10 m) and mussel culture on bouchots and ropes by polygons

highest fishing pressure in Brittany (Appendix A-1). Regulation changes have led, since 2010, to the concentration of dredging, at the beginning of the fishing season, in areas colonized by the non-indigenous slipper limpet *Crepidula fornicata* (Appendix A-2). The bay also suffers from eutrophication resulting in macroalgae proliferation and cyclic green tides episodes (Charlier et al., 2007; Gravier, 2012), which notably impact fish nursery grounds (Le Luherne et al., 2016; Le Luherne et al., 2017) and influence the dynamics of some benthic populations of invertebrates of the intertidal area (Sturbois et al., accepted).

2.2 | Field sampling

Benthic macrofauna were sampled at 38 stations during winter (March) in 1987 and 2019 (ResTroph research programme) following the grid (Figure 1) and the protocol defined in 1987 by Gros & Hamon (1988). During both surveys, five replicates were collected at each station with a small Hamon grab (1/8m^2) for macrobenthos analyses. The grab contents were gently sieved on board either through: 1) a 2 mm circular mesh sieve (1 replicate) to describe benthic assemblages, or 2) a 5 mm circular mesh sieve (4 replicates) to specifically analyse bivalve populations. The retained material was preserved for analysis in 5% buffered formaldehyde. Only the replicate sieved on a 2 mm mesh was used for the long-term comparison of the benthic community. Two samples of sediment were collected in one additional grab using a handcorer, and subsequently analysed for grain size distribution and organic matter content respectively. All replicates were collected at a maximal distance of 50 m from each station, using DGPS position-fixing. As part of the ecological status monitoring, one station (R) was additionally sampled yearly (nine replicates, following national recommendation of the REBENT benthic network as part of the WFD) in March from 2005 to 2019, with a Smith McIntyre grab (0.1 m^2), and sieved on a 1 mm circular mesh sieve. Data at station R were used to assess the year-to-year variability of taxonomic and functional diversity at this site.

2.3 | Laboratory analyses

Macrofauna were identified to the lowest possible taxonomic level (usually species level), counted, and abundances were standardized to 1 m^2. Taxon names follow the World Register of Marine Species (WoRMS Editorial Board, 2020).

For granulometric analysis, sediment was desalted with fresh water and left to settle for 48 h. Sediment was then dried at 60 °C for 48 h and sieved through AFNOR standard sieves, before weighing. Organic matter content was determined after drying (60 °C for 48 h) and combustion of sediment at 550 °C for 4 h (Salonen, 1979; Hedges & Stern, 1984).

2.4 | Traits collection

The functional dataset was composed of six traits representing a total of 25 categories (Appendix B). These traits characterized the morphology (body size, flexibility, fragility) and behaviour (feeding behaviour, living habit, tolerance to organic enrichment) (Degen & Faulwetter, 2019). This set of traits is related to vulnerability to mechanical disturbance (fishing activities), and to tolerance to organic enrichment (eutrophication) and was chosen to analyse functional changes in benthic fauna, in relation to the main pressures identified in the study area. Information was collected from primary literature on specific taxa, expert knowledge and the databases polytraits (http://polytraits.lifewatchgreece.eu), the World Register of Marine Species (WoRMS Editorial Board, 2020), and Biological Trait Information Catalogue (BIOTIC, http://www.marlin.ac.uk/biotic/). Scores were attributed to species according to their affinity to each category of traits using a fuzzy coding from 0 (no affinity) to 3 (high affinity) (Chevene, Doleadec & Chessel, 1994). Community-weighted trait values (CWMs) were calculated to characterize the functional community structure for both datasets (Ricotta & Moretti, 2011).

2.5 | Data analysis

Long-term (38 stations, 1987 vs 2019) and inter-annual (station R; 2005 to 2019) datasets were analysed to track for taxonomic and functional changes. The study focused specifically on the analysis of ecological trajectories depicted at different temporal scales taking the advantage of both data sets: 32 year long-term comparison vs 15 year long-term series. All statistical analyses were performed with R 4.0 (R Development Core Team, 2020).

2.5.1 | Sedimentary dataset

Statistical description of sediments, based on grain-size distributions, was computed with the R package 'G2Sd' (Fournier, Gallon & Paris, 2014). Sediment characteristics and changes were described from ten sedimentary parameters and tested with a Wilcoxon paired-test: organic matter content (OMC), mean and median (d50) particle size, gravel (>2 mm), coarse sand (2 mm to 500 μm), fine sand (250 to 125 μm), very fine sand (125 to 63 μm), and mud (<63 μm) contents (%).

2.5.2 | Taxonomic α-diversity

In order to assess the different components of taxonomic α-diversity, the mean number of individuals per m^2 (N), species richness (S), Shannon-Weaver index (H′), Simpson index (D) and Pielou's species evenness (J) were calculated for each station (2 mm circular mesh sieve) prior to any transformations of the dataset.

2.5.3 | Spatial and temporal taxonomic clustering

Hierarchical Cluster Analyses (HCA) were performed on both taxonomic datasets to distinguish benthic assemblages (i.e. stations/surveys groups) by using the Hellinger distance between each pair of samples/dates (Legendre & Gallagher, 2001) and by applying the Ward's clustering method. The indicator value method (Indval) was performed for characterizing assemblages (Dufrene & Legendre, 1997).

2.5.4 | Detecting trajectory patterns

On ResTroph and WFD datasets, PCAs were performed on Hellinger-transformed data and followed by Community Trajectory Analysis (CTA). CTA is based on geometrical properties of ecological trajectories (De Cáceres et al., 2019). The original framework and its new extension (Sturbois et al., 2021) were used to study and represent temporal changes at the station scale taking into account all the dimensions of the multivariate analysis through trajectories of surveys in the multivariate space.

Long-term comparison

Net changes between 1987 and 2019 were calculated to analyse trajectories considering the 1987 data set as the initial state. Dissimilarities between ecological trajectories were calculated to test their resemblance (De Cáceres et al., 2019) and underline potential spatial patterns in temporal variations with HCAs. 1) For taxonomic trajectories, the Indicator value method (Dufrene & Legendre, 1997) was performed on taxonomic trajectories clusters to test differences between 1987 and 2019. 2) For functional trajectories, the relative contribution of all categories of functional traits between 1987 and 2019 were compared for each functional trajectory cluster and tested at the scale of the whole community (paired samples Student's permutation tests; $p < 0.05$).

Inter-annual dynamics

For the long-term WFD dataset (yearly sampling from 2005 to 2019), Trajectory segments lengths (i.e. S1 = 2005 to 2006, S2 = 2006 to 2007, … S14 = 2018 to 2019), Net change, Directionality and Net change ratio were calculated. Recovering (station returning to an initial ecological state) and departing (station where change increased over time) consecutive trajectory segments were identified by subtracting Net change n-1 by Net change n (Sturbois et al., 2021).

2.5.5 | Relation between taxonomic structure and environmental and spatial variables

Multi-collinearity in sedimentary variables was detected with the Variable Inflation Factors methods (VIF). Variables characterized by highest VIF were excluded for further analysis. (1) Redundancy analyses (RDA) were performed to determine the part of variance respectively explained by sedimentary variables in the taxonomic Restroph dataset (Blanchet, Legendre & Borcard, 2008). When significant, (2) a forward selection was used to test the significance of each variable. (3) Linear and non-linear multi-scale structures of the spatial model were analysed and a linear spatial model was performed to determine the variance explained by spatial variables (Legendre & Legendre, 2012). (4) A variation partitioning analysis was undertaken to assess the variation explained and shared by sedimentary and spatial variables (Legendre & Legendre, 2012).

2.5.6 | Species changes in bivalve populations

The evolution of the abundance (raw data) of the main bivalve species (four replicates sieved on 5 mm circular mesh) was analysed and differences were tested with paired samples Student's permutation tests ($p < 0.05$).

3 | RESULTS

3.1 | General description of sediment

Sediments were dominated by sands in 1987 (74.33% ± 12.85, mean $+/-$ sd) and 2019 (78.74% ± 12.35) (Appendix C). Fine sands (125–250 μm) were the most represented sedimentary class in both years (42.34% ± 17.92 in 1987; 46.60% ± 17.99 in 2019). Mud content significantly decreased in 79% of stations (−11.12% ± 6.89; min = −0.79%; max = −31.15%, $P < 0.001$). In contrast, 21% of stations were characterized by an increase in mud content (+11.53% ± 17.56) especially at stations 101 (+52.46%), 81 (+16.16%), and 100 (+13.61%). Gravel accounted for 8.43% ± 10.59 in 1987 and 10.23% ± 6.96 in 2019. Mean particle size (356.55 μm ± 258.94 vs 421.54 μm ± 192.55) slightly but significantly increased ($P < 0.001$) over the study period.

Sediment properties at station R varied inter-annually (Appendix D): after an initial period of high inter-annual variability between 2005 and 2014, sediment granulometry was less variable from 2015 onwards.

3.2 | General description of the macrofauna

Overall, 208 taxa were collected on the 2 mm mesh size sieves (with 72 taxa common to both datasets). Between 1987 and 2019, 57 taxa were lost and 79 taxa gained. Macrofauna was dominated by annelids, molluscs and crustaceans (Appendix E). In 1987, annelids were the most numerous taxonomic group (9,344 ind., 55.73%) ahead of molluscs (3,168 ind., 18.89%) and crustaceans (3,080 ind., 18.37%). Molluscs were the most numerous group in 2019 (6,600 ind., 42.26%) ahead of annelids (6,080 ind., 38.93%) and crustaceans (2,448 ind., 15.68%). Sipunculids, echinoderms, platyhelminths and nemerteans contributed less than 5% of the total species richness and abundance. H′, D, J and mean Richness all slightly decreased over time while total richness increased.

A total of 202 taxa were reported over 15 years at the station R. Richness (63.47 ± 11.27) and abundance (928.52 ind.m^{-2} ± 593.83) increased over the study period. Annelids, molluscs and crustaceans dominated the community (Appendix E). *Chaetozone gibber* (133.07 ind.m^{-2} ± 94.14), *Varicorbula gibba* (95.87 ind.m^{-2} ± 187.35), *Aponuphis bilineata* (60.07 ind.m^{-2} ± 34.39), *Abra alba* (44.67 ind. m^{-2} ± 92.79), *Ampelisca sarsi* (44.00 ind.m^{-2} ± 128.14), *Notomastus latericeus* (25.67 ind.m^{-2} ± 26.07), and *Ampelisca brevicornis* (24.93 ind.m^{-2} ± 30.93) were dominant over the period studied. Some of them exhibited strong temporal variations, especially in the second part of the time series between 2012 and 2019 (Figure 2).

Changes were observed in the contribution of the main taxonomic groups to total local abundance between 1987 and 2019 (Figure 3a and b): the contribution of molluscs increased at most stations, especially in the southern part of the study area. This change, also visible in the fauna of the station R occurred around 2015 (Figure 3c). Before 2015, the abundance of each taxonomic group at station R was similar to the abundances measured in 1987 at the southern stations of the bay of Saint-Brieuc (stations 62 to 72).

3.3 | Taxonomic clustering

3.3.1 | Spatial clustering in 1987 and 2019

In both campaigns, HCAs separated the stations into four main clusters (i.e. benthic assemblages) (Figure 4). In 1987, according to indicator values ($P < 0.05$), the southern assemblage I-87 was characterized by *C. gibber* and *Sigalion mathildae*, species that occur in shallower fine sands (Table 1). *Chaetozone gibber* and *A. bilineata* were the most abundant species. Assemblage II-87, mainly located in western muddy-sands, was characterized by *A. brevicornis* and *V. gibba* and dominated by *A. brevicornis* and *Euclymene oerstedii*. Assemblage III-87, mainly located in the central part of the study area, occurred in muddy heterogeneous sediment. It was characterized by *Ampharete* spp. and dominated by *Ampharete* spp. and *Crepidula fornicata*. Assemblage IV-87 was located in the north of the study area, characterized by *Nototropis vedlomensis* and *N. latericeus*, and dominated by *N. latericeus* and *Nucula hanleyi*.

In 2019, the southern cluster was the most widespread assemblage (I-19, 19 stations), occurring in fine to muddy sands located between the southern and the central part of the study area. It was characterized by *V. gibba* and *Phyllodoce groenlandica* and

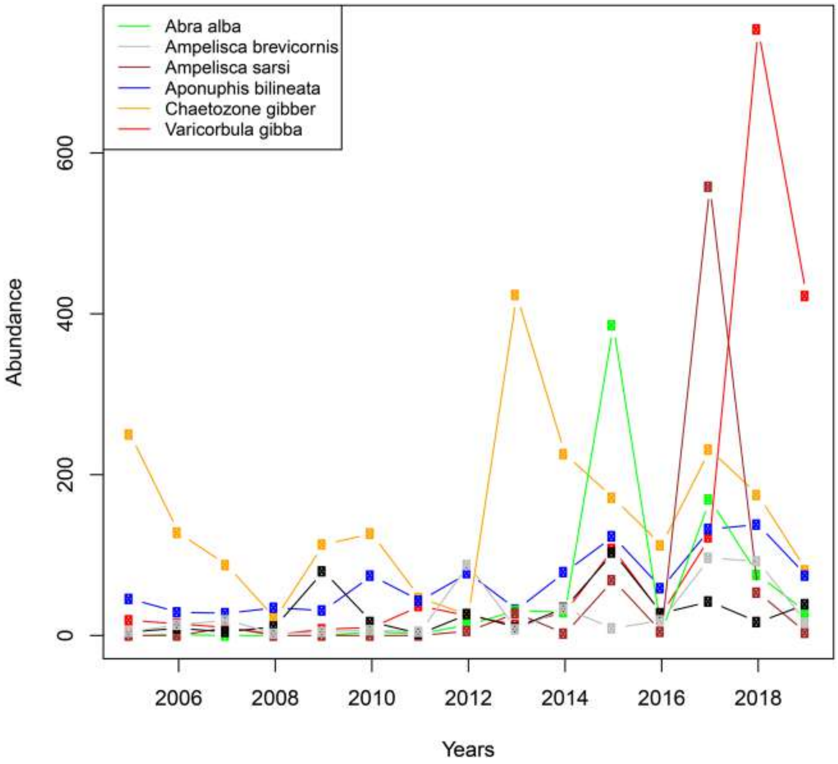


FIGURE 2 Abundance (ind.m^{-2}) of dominant species sampled at station R

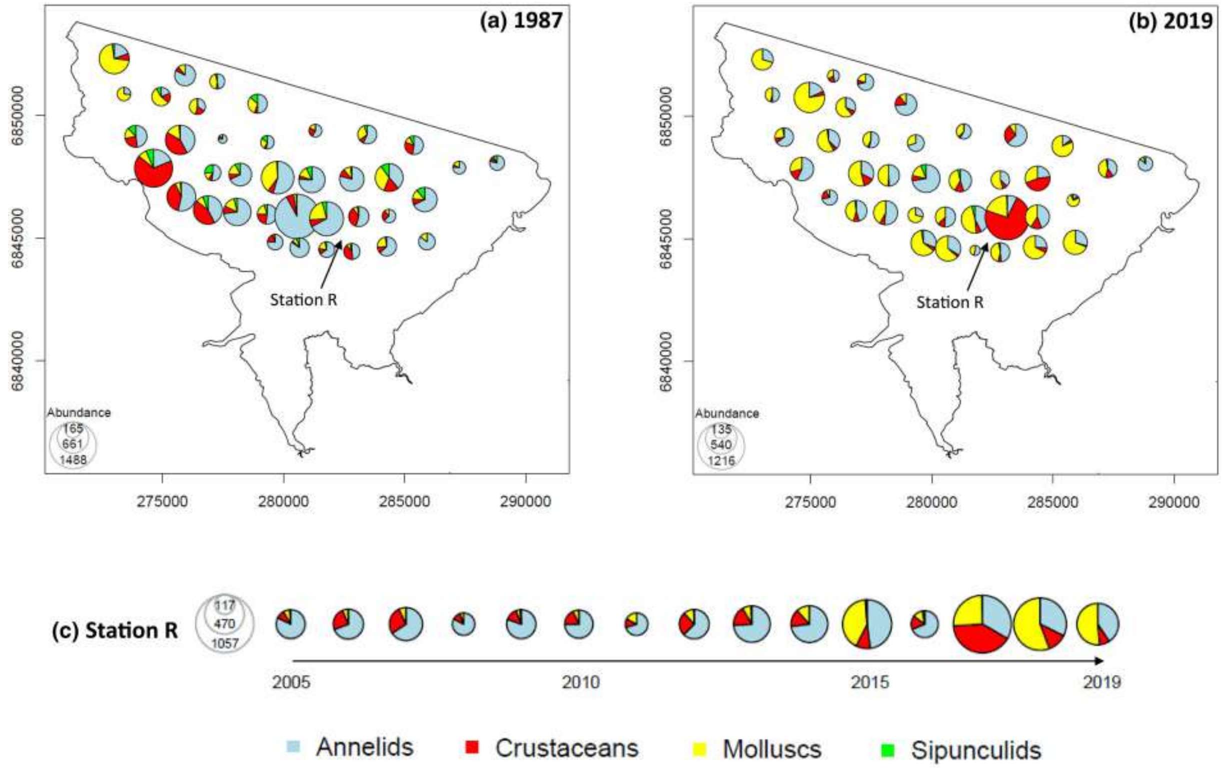


FIGURE 3 Distribution maps of main taxonomic groups. Colours represent the following groups: Annelids (blue), Crustaceans (red), Molluscs (yellow) and Sipunculids (green). Pie sections correspond to the relative abundance of each taxonomic group and size to total abundance. (a) and (b) represent 1987 and 2019 ResTroph surveys and (c) represents surveys conducted from 2005 to 2019 at station R

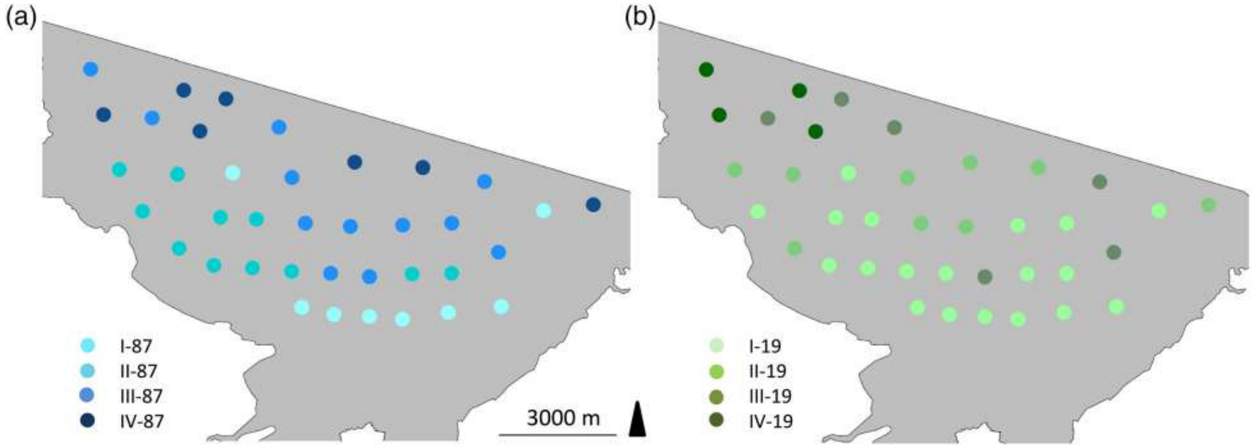


FIGURE 4 Spatial distribution of benthic assemblages identified with Hierarchical Cluster Analysis of the ResTroph data set (38 stations) in (a) 1987 and (b) 2019

dominated by *V. gibba* and *A. tenuicornis*. Assemblage II-19, occurring at nine stations mainly located in the northern-central part, was characterized by *Nephtys hombergii* and dominated by *N. latericeus* and *V. gibba*. Assemblage III-19 (6 stations) was identified in muddy heterogeneous sediments in the north and central parts, and typified by *C. fornicata* and *P. maximus* and dominated by *C. fornicata* and *N. latericeus*. Assemblage IV-19 was characterized and dominated by *Timoclea ovata* and *N. hanleyi* and limited to four north-western stations.

Species diversity was variable among assemblages (Table 1). In 2019, the lowest H′ values were observed in assemblages I-19 and IV-19. Temporal changes in the distribution of assemblages were concentrated in the southern part of the bay (Figure 4). The overall diversity (H′, D, J) decreased in the shallower parts, as a consequence of the increase of *V. gibba*, and shallower bottoms gradually homogenized as shown by the assemblage I-19 distribution (50% of stations).

3.3.2 | Temporal clustering from 2005 to 2019

The HCA performed on the station R dataset identified three clusters (Table 2). Cluster I, composed of seven years, was characterized by *Caulleriella alata* and *Edwardsia claparedii*. Cluster II (4 years) was characterized by *Cirratulidae* spp. and *Tritia varicosa*. Cluster III, composed of four of the most recent surveys (2015, 2017, 2018, 2019), was typified by *Calyptraea chinensis* and *Spisula elliptica*. *Chaetozone gibber*, *A. bilineata* and *Ampelisca* spp. remained in the first five highest-ranking species in terms of abundance over the entire study period, and *V. gibba* and *A. alba* became dominant during the more recent surveys. Taxonomic diversity indices were quite stable between clusters except richness and abundance, which increased during recent observations (cluster III, Table 2).

3.4 | Species changes in bivalve populations

The abundance (Table 3) and distribution (Appendix F) of the main bivalve species changed over time. Significant increases in abundance were detected for *Varicorbula gibba*, *Anomia ephippium*, *Bosemprella incarnata*, *Moerella donacina*, *N. hanleyi*, *Nucula nitidosa*, *Timoclea ovata* and *Pecten maximus*. Conversely *Polititapes rhomboides* and to a lesser extent *Fabulina fabula* decreased significantly over time.

3.5 | Detecting trajectory patterns

3.5.1 | Taxonomic trajectories

Long-term comparison

All sampling stations were characterized by taxonomic changes over time (Figure 5a and b). Mean net change (± sd) calculated on the 38 stations was variable spatially (15.5 ± 2.23), ranging from 11.4 (station 74) to 21.5 (station 104). The HCA performed on CTA analysis of trajectory similarities identified four trajectory clusters according to the shape of taxonomic trajectories (Figure 5a, b and c). Cluster A was composed of 20 stations describing the evolution from an assemblage dominated by *Ampharete* spp. and *A. brevicornis* in 1987 to an assemblage dominated by *V. gibba* and *C. fornicata* in 2019. Cluster B grouped 13 stations characterized by *A. bilineata* in 1987 and *V. gibba* in 2019. A shift between the dominant species *A. brevicornis* and *A. bilineata* (1987) to *V. gibba* and *A. tenuicornis* (2019) was observed. Mean net changes (± se) were slightly lower in cluster B (16.59 ± 1.09) than in cluster A (20.35 ± 0.66). The two other clusters characterized a limited number of specific trajectories exhibiting a longer trajectory path in the northern part of the study area (stations 105 and 106, and stations 107,104 and 94).

Most stations encountered similar changes in the multivariate space, as indicated by the similar trajectory directions. Direction

TABLE 1 Characteristics of the assemblages identified by the Hierarchical Cluster Analysis in 1987 and 2019: number of stations (N st), Specific richness (S), Mean density per m^2 (Abund), Shannon-Weaver Index (H), Simpson Index (D) and Pielou's evenness (J) (± standard error). Assemblages are characterized by indicator and dominant species

Assemblages		Indicator species	indval	*P*	Most numerous species	Mean.m^{-2} ± SE	N st	S	Abund	H	D	J
1987	**I-87**	***Chaetozone gibber***	**0.555**	**0.0006**	***Chaetozone gibber***	**42.00 ± 12.98**	8	12.25	219	2.18	0.85	0.88
		Sigalion mathildae	**0.547**	**0.0007**	***Aponuphis bilineata***	**35.00 ± 11.60**		± 1.05	± 28.20	± 0.07	± 0.01	± 0.02
		Magelona filiformis	0.500	0.0016	*Ampelisca brevicornis*	21.00 ± 6.22						
		Spiophanes bombyx	0.487	0.0032	*Spiophanes bombyx*	18.00 ± 6.18						
		Aponuphis bilineata	0.442	0.0067	*Sigalion mathildae*	11.00 ± 3.00						
	II-87	***Ampelisca brevicornis***	**0.536**	**0.0004**	***Ampelisca brevicornis***	**145.45 ± 59.49**	11	21.09	535.27	2.53	0.87	0.84
		Varicorbula gibba	**0.470**	**0.0013**	***Euclymene oerstedii***	**37.09 ± 14.56**		± 1.79	± 88.98	± 0.01	± 0.02	± 0.03
		Ampelisca tenuicornis	0.431	0.0073	*Ampelisca tenuicornis*	37.09 ± 11.63						
		Euclymene oerstedii	0.415	0.0143	*Notomastus latericeus*	36.36 ± 7.50						
		Nephtys hombergii	0.368	0.0362	*Aponuphis bilineata*	31.27 ± 6.95						
	III-87	***Ampharete spp.***	**0.554**	**0.0005**	***Ampharete spp.***	**150.67 ± 98.61**	12	24.92	629.33	2.60	0.85	0.82
		Golfingia (golfingia) elongata	**0.532**	**0.0004**	***Crepidula fornicata***	**71.33 ± 34.54**		± 1.96	± 115.25	± 0.16	± 0.04	± 0.04
		Crepidula fornicata	0.443	0.0055	*Notomastus latericeus*	37.33 ± 9.96						
		Polycirrus medusa	0.438	0.0051	*Polycirrus medusa*	32.00 ± 9.08						
		Sthenelais boa	0.419	0.0085	*Golfingia (Golfingia) elongata*	21.33 ± 4.33						
	IV-87	***Nototropis vedlomensis***	**0.384**	**0.0031**	***Notomastus latericeus***	**21.71 ± 7.75**	7	15.43	225.14	2.43	0.87	0.90
		Notomastus latericeus	**0.357**	**0.0273**	***Nucula hanleyi***	**14.86 ± 13.57**		± 2.08	± 29.90	± 0.17	± 0.03	± 0.03
		Hilbigneris gracilis	0.351	0.0387	*Hilbigneris gracilis*	12.57 ± 5.20						
		Glycera capitata	0.286	0.0296	*Polycirrus medusa*	9.14 ± 9.14						
		Protomystides bidentata	0.286	0.0293	*Fabulina fabula*	9.14 ± 4.43						
2019	**I-19**	***Varicorbula gibba***	**0.612**	**0.0001**	***Varicorbula gibba***	**160.84 ± 19.63**	19	16.53	466.11	2.08	0.77	0.76
		Phyllodoce groenlandica	**0.368**	**0.0310**	***Ampelisca tenuicornis***	**64.42 ± 63.54**		± 1.04	± 74.66	± 0.09	± 0.02	± 0.03
					Glycinde nordmanni	20.63 ± 4.07						
					Streblosoma bairdi	17.26 ± 4.63						
					Aponuphis bilineata	16.42 ± 6.69						
	II-19	***Nephtys hombergii***	**0.483**	**0.0004**	***Notomastus latericeus***	**29.33 ± 7.06**	9	18.78	352.00	2.60	0.90	0.90
					Varicorbula gibba	**27.56 ± 10.16**		± 2.14	± 56.04	± 0.10	± 0.01	± 0.01
					Nephtys hombergii	25.78 ± 5.62						
					Anomia ephippium	18.67 ± 10.67						
					Pista cristata	17.78 ± 6.77						
	III-19	***Crepidula fornicata***	**0.728**	**0.0004**	***Crepidula fornicata***	**160.00 ± 66.58**	6	18.83	430.67	2.29	0.80	0.80
		Pecten maximus	**0.446**	**0.0239**	***Notomastus latericeus***	**21.33 ± 7.35**		± 2.68	± 103.08	± 0.21	± 0.05	± 0.06
		Syllis garciai	0.333	0.0313	*Aponuphis bilineata*	16.00 ± 10.93						

TABLE 1 (Continued)

Assemblages	Indicator species	indval	P	Most numerous species	Mean.m^{-2} ± SE	N st	S	Abund	H	D	J
	Amphipholis squamata	0.333	0.0304	*Nephtys hombergii*	10.67 ± 5.72						
	Aequipecten opercularis	0.333	0.0290	*Anomia ephippium*	10.67 ± 9.16						
IV-19	***Nucula hanleyi***	**0.611**	**0.0024**	***Timoclea ovata***	**34.00 ± 28.73**	4	10.50	252.00	1.97	0.81	0.85
	Timoclea ovata	**0.596**	**0.0031**	***Nucula hanleyi***	**30.00 ± 11.94**		± 1.32	± 62.18	± 0.08	± 0.01	± 0.03
	Glycera alba	0.481	0.0069	*Crepidula fornicata*	30.00 ± 30.00						
				Notomastus latericeus	26.00 ± 17.09						
				Polititapes rhomboides	18.00 ± 18.00						

(i.e. specific initial and final composition) and trajectory length seemed mainly responsible for the separation of clusters. The convergence of most trajectories, especially from clusters A and B, which grouped 87% of trajectories, illustrate an homogenization over time with respect to the ecological state described in 1987.

Inter-annual dynamics

A first period from 2005 to 2014 was characterized by lower net changes than measured at the end of the time series, indicating a greater stability during this first period as underlined by consecutive departing and recovering patterns. This period was followed by a recent period of higher variability in composition and characterized by higher net change values (Figure 6a). Even if *C. gibber* and *A. bilineata* remained among the five most dominant species, the trajectory underlined: 1) the shift in dominance by different *Ampelisca* spp., and 2) the dominance of *V. gibba* and *A. alba* in recent surveys (Table 2). The alternation of recovering and departing dynamics resulted in low directionality (0.359) and low net change ratio (10.11%).

3.5.2 | Functional trajectories

Long-term comparison

Net change was variable spatially (7.94 ± 2.53), ranging from 3.97 (station 87) to 15.24 (station 88). The HCA performed on CTA analysis of trajectory similarities separated three clusters of functional trajectories (Figure 7a,b and c). Trajectory length and direction were mainly responsible for the separation of clusters. Cluster E contained 27 stations (7.34 ± 0.36) in which the highest net change values were mainly located in the southern part of the study area, and were characterized by a decrease in the relative contribution of the following categories: 1) medium size, flexible, fragile; and 2) tubiculous, burrowers and tolerant species. Simultaneously, the contribution of suspension-feeders, predators and scavengers increased, as well as rigid, robust, and large and small species. Free-living species became dominant and the contribution of second-order opportunistic species increased. Cluster F grouped six trajectories characterized by higher net changes (10.59 ± 1.64). The main functional changes were in a decrease of deposit-feeders, tubiculous, and flexible and fragile species. This group of trajectories was specifically characterized by an important increase of CWM values of very sensitive species, and attached species mainly represented by *A. ephippium*. Cluster G comprised five trajectories (7.96 ± 0.79). In addition to a similar pattern concerning deposivorous and tubiculous species, these trajectories were specifically characterized by an increase in the contribution of predator, flexible, fragile, and burrowing species and a decrease of rigid, suspension-feeders and tolerant species.

At the scale of the whole area including all stations, a similar global pattern was observed (Figure 8). Compared to 1987, the community was dominated by suspension-feeders and free-living species in 2019. Even if significant functional shifts in morphological

TABLE 2 Characteristics of survey clusters identified by the Hierarchical Cluster Analysis performed on the WFD data set (2005 to 2015): number of stations (N st), Specific richness (S), Mean density per m^2 (Abund), Shannon-Weaver Index (H), Simpson Index (D) and Pielou's evenness (J) (± standard error). Assemblages are characterized by indicator and dominant species

Assemblages	Indicator species	indval	P	Most numerous species	Mean.m^{-2} ± SE	N st	S	Abund	H	D	J
R-I	***Caulleriella alata***	**0.643**	**0.0003**	***Chaetozone gibber***	**170.95 ± 52.62**	7	62.57	647.30	3.10	0.89	0.75
	Edwardsia claparedii	**0.576**	**0.0259**	***Aponuphis bilineata***	**52.54 ± 7.52**		± 3.62	± 82.30	± 0.12	± 0.03	± 0.03
	Magelona filiformis	0.563	0.0009	*Notomastus latericeus*	26.51 ± 10.09						
	Scoloplos armiger	0.530	0.0023	*Ampelisca brevicornis*	23.02 ± 11.53						
	Apseudpsis latreillii	0.471	0.0263	*Varicorbula gibba*	22.38 ± 3.70						
R-II	***Cirratulidae spp.***	**0.758**	**0.0039**	***Chaetozone gibber***	**90.83 ± 25.03**	4	53.00	576.67	3.03	0.92	0.77
	Tritia varicosa	**0.750**	**0.0194**	***Cirratulidae spp.***	**74.72 ± 24.46**		± 3.34	± 88.18	± 0.07	± 0.01	± 0.01
	Ampelisca spinimana	0.725	0.0001	*Ampelisca tenuicornis*	50.00 ± 16.22						
	Nephtys hombergii	0.645	0.0269	*Aponuphis bilineata*	41.39 ± 11.12						
	Ampelisca tenuicornis	0.590	0.0002	*Chaetozone zetlandica*	29.72 ± 7.39						
R-III	***Calyptraea chinensis***	**1**	**0.0022**	***Varicorbula gibba***	**351.39 ± 152.33**	4	75.50	1772.50	2.92	0.87	0.67
	Spisula elliptica	**0.925**	**0.0010**	***Ampelisca sarsi***	**170.83 ± 129.74**		± 2.40	± 234.74	± 0.11	± 0.02	± 0.02
	Ampelisca spinipes	0.860	0.0035	*Abra alba*	164.72 ± 31.00						
	Thyasira fexuosa	0.790	0.0016	*Chaetozone gibber*	164.44 ± 14.47						
	Amphictene auricoma	0.750	0.0150	*Aponuphis bilineata*	116.94 ± 19.90						

TABLE 3 Main bivalve species identified in the four replicates sieved on the 5 mm circular mesh size at the 38 Restroph stations in 1987 and 2001 (N: total abundance, SD: standard deviation). The significance of trends was tested with a student permutation paired-test (ns: no trend; −: decrease; +: increase). Distribution maps are detailed in appendix F

	1987		2019				
Species	**N**	**Mean ± SD**	**N**	**Mean ± SD**	**Trend**	**p_val t perm. Paired test**	
Acanthocardia echinata	14	0.37 ± 1.02	2	0.05 ± 0.32		0.162	ns
Anomia ephippium	24	0.63 ± 1.68	194	5.11 ± 7.71	+	0.002	***
Arcopagia crassa	8	0.21 ± 1.30	10	0.26 ± 1.62		0.954	ns
Bosemprella incarnata	16	0.42 ± 1.24	142	3.74 ± 6.10	+	0.002	***
Varicorbula gibba	380	10.00 ± 13.91	3,564	93.79 ± 101.08	+	0.002	***
Fabulina fabula	38	1.00 ± 3.15	2	0.05 ± 0.32	−	0.046	*
Glycymeris glycymeris	4	0.11 ± 0.45	54	1.42 ± 5.95		0.362	ns
Laevicardium crassum	6	0.16 ± 0.55	46	1.21 ± 1.71	+	0.004	**
Moerella donacina	4	0.11 ± 0.45	112	2.95 ± 4.18	+	0.002	***
Nucula hanleyi	4	0.11 ± 0.45	166	4.37 ± 9.36	+	0.002	***
Nucula nitidosa	2	0.05 ± 0.32	166	4.37 ± 6.47	+	0.002	***
Pandora albida	10	0.26 ± 0.83	18	0.47 ± 1.18		0.456	ns
Parvicardium scabrum	0	0.00 ± 0.00	22	0.58 ± 1.39	+	0.010	*
Pecten maximus	0	0.00 ± 0.00	56	1.47 ± 2.17	+	0.002	***
Polititapes rhomboides	226	5.95 ± 9.01	48	1.26 ± 4.89	−	0.002	***
Spisula elliptica	6	0.16 ± 0.55	6	0.16 ± 0.72		1.000	ns
Timoclea ovata	10	0.26 ± 0.83	176	4.63 ± 17.47	+	0.006	**

traits were observed over time, the fauna remained dominated by medium size, flexible and fragile species. According to the tolerance to nutrient enrichment trait, fauna remained dominated by very sensitive and indifferent species.

Inter-annual dynamics

Functional net change increased over time (Figure 6b). Different categories of traits influenced the functional stability: axis I (41.4%) contrasted filter feeding, living free, rigid and robust organisms to deposit feeding, tube dwelling and highly flexible organisms (Appendix H). The alternation of recovering and departing dynamics resulted in low directionality (0.387) and net change ratio (10.04%).

3.6 | Relation between taxonomic structure and environmental and spatial variables

According to the VIF analysis, coarse sand and mean particle size were excluded from the following analysis. The part of the variance explained by sedimentary variables was higher in 1987 (R^2adj = 0.177; F = 2.547; Pr(>F) = 0.001) than in 2019 (R^2adj = 0.055; F = 1.420; Pr(>F) = 0.003). Sedimentary variables characterized by finest grain size were significantly correlated to the taxonomic structure in 1987: fine sand (R^2adj = 0.157), mud (R^2adj = 0.123), and very fine sand (R^2adj = 0.059). In 2019, two sedimentary variables were correlated: mud (R^2adj = 0.050) and D50 (R^2adj = 0.032).

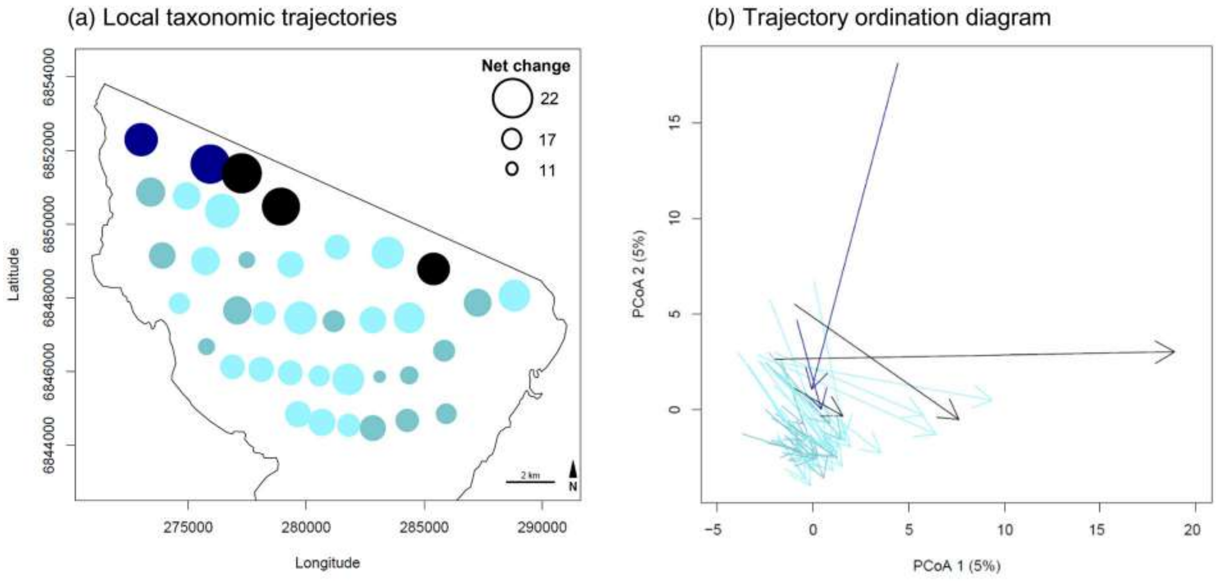
A linear spatial structure was revealed for both years (R^2adj = 0.089; F = 2.752; Pr(>F) = 0.001 in 1987 vs R^2adj = 0.100; F = 2.994; Pr(>F) = 0.001 in 2019). In 1987, sedimentary and spatial variables explained 12% and 5% of the variance, respectively, while 4% was shared. In 2019, the part of the explained variance decreased and the contribution of spatial variables was higher (sedimentary: 2%, spatial: 7%, shared: 3%).

4 | DISCUSSION

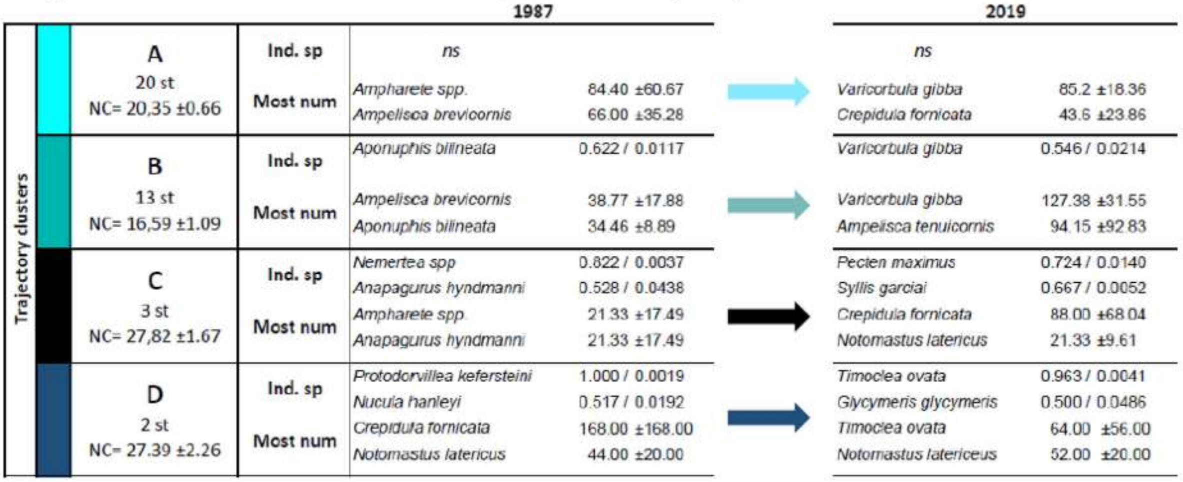
4.1 | Changes probably occurred recently

The results highlight the relevance of the Community Trajectory Analysis method to assess long-term changes in the spatial structure of benthic assemblages over the study area, based on the comparison of historical and up-to-date data in multivariate spaces.

Among the four taxonomic clusters identified in 2019, two of them, representing 74% of stations, pointed towards a potential degradation of habitats indicated by: 1) the numerical increase of the opportunistic species *V. gibba*, and 2) the lower species diversity in one of the two assemblages. This was further confirmed by the analysis of trajectory similarity, which revealed that 87% of the stations (clusters A and B) were characterized by increases in the



(c) Characterization of initial and final ecological states of trajectory clusters



Trajectory clusters		1987		2019	
A 20 st NC= 20,35 ±0.66	**Ind. sp**	*ns*		*ns*	
	Most num	*Ampharete spp.*	84.40 ±60.67	*Varicorbula gibba*	85.2 ±18.36
		Ampelisca brevicornis	66.00 ±35.28	*Crepidula fornicata*	43.6 ±23.86
B 13 st NC= 16,59 ±1.09	**Ind. sp**	*Aponuphis bilineata*	0.622 / 0.0117	*Varicorbula gibba*	0.546 / 0.0214
	Most num	*Ampelisca brevicornis*	38.77 ±17.88	*Varicorbula gibba*	127.38 ±31.55
		Aponuphis bilineata	34.46 ±8.89	*Ampelisca tenuicornis*	94.15 ±92.83
C 3 st NC= 27,82 ±1.67	**Ind. sp**	*Nemertea spp*	0.822 / 0.0037	*Pecten maximus*	0.724 / 0.0140
		Anapagurus hyndmanni	0.528 / 0.0438	*Syllis garciai*	0.667 / 0.0052
	Most num	*Ampharete spp*	21.33 ±17.49	*Crepidula fornicata*	88.00 ±68.04
		Anapagurus hyndmanni	21.33 ±17.49	*Notomastus latericus*	21.33 ±9.61
D 2 st NC= 27.39 ±2.26	**Ind. sp**	*Protodorvillea kefersteini*	1.000 / 0.0019	*Timoclea ovata*	0.963 / 0.0041
		Nucula hanleyi	0.517 / 0.0192	*Glycymeris glycymeris*	0.500 / 0.0486
	Most num	*Crepidula fornicata*	168.00 ±168.00	*Timoclea ovata*	64.00 ±56.00
		Notomastus latericus	44.00 ±20.00	*Notomastus lateriiceus*	52.00 ±20.00

FIGURE 5 Taxonomic trajectories. (a) Map of local trajectories. Circle size corresponds to net change between 1987 and 2019 and colours to clusters of trajectories determined by Hierarchical Cluster Analysis on trajectory similarity analysis. All the dimensions of the multivariate space were considered in net change calculation and analysis of trajectory similarities. (b) Trajectory ordination diagram. Only two dimensions are shown. (c) Characteristics of initial and final taxonomic ecological states of trajectory clusters. Taxonomic trajectory is coloured according to trajectory clusters (blue gradient), and described with distance-based metrics mean ± se (NC: net change, TP: Trajectory path), the two first indicative (Ind.sp.) and numerous species (1st. Num)

density of *V. gibba* from 1987 to 2019. At the scale of the study area, however, decreases of β species diversity remained moderate (Appendix E).

Inter-annual dynamics at station R suggests that these changes are very recent (Figure 3). The lower variability observed at station R from 2005 to 2014 may depict natural dynamics, while recent changes since 2015 seem driven by a strong and cumulative disturbance regime. The recent shift in the taxonomic multivariate structure was driven by variations in the abundance of a few dominant species, such as *V. gibba*, *A. alba*, *C. chinensis* and *S. elliptica*. Interestingly, although benthic communities were highly variable over the last five years, sediment properties and organic matter content did not exhibit such variability, suggesting that the recent pattern in benthic community structure may not be strictly related to habitat characteristics.

4.2 | Functional shifts

Ecological processes shaping energy flows in ecosystems are induced by a complex feedback system reflecting species adaptation to their environment, while the environment is, in turn, constantly modified by biological activities (Levins & Lewontin, 1985; Díaz & Cabido, 2001; Pacheco et al., 2011).

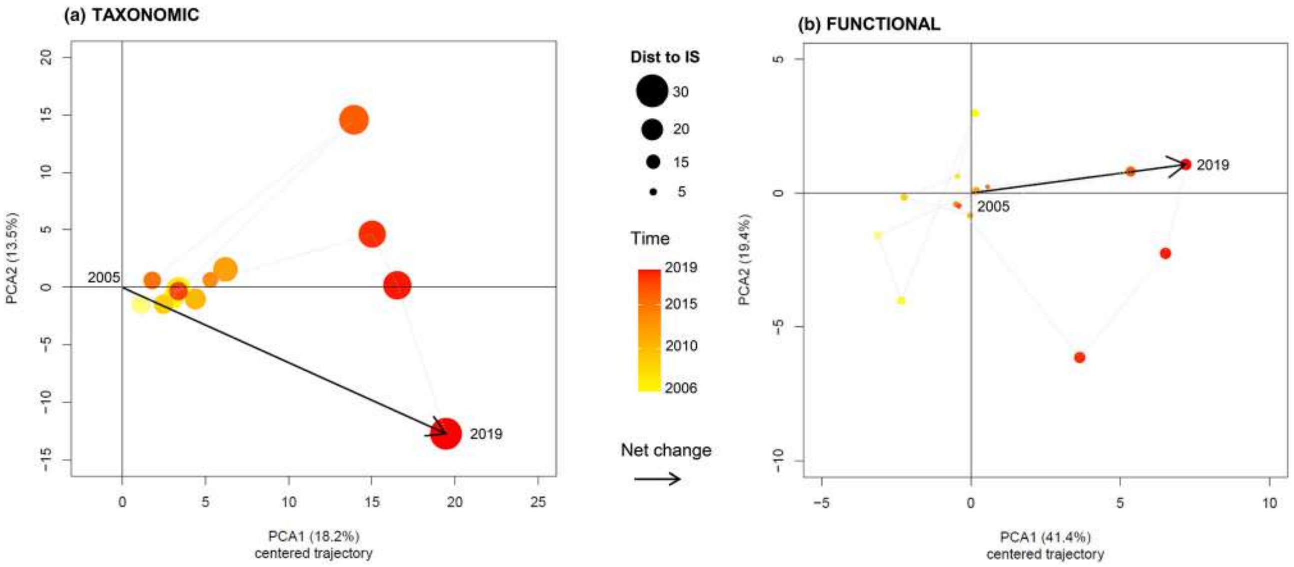


FIGURE 6 Trajectory of the station R between 2005 and 2019. The origin of the ordination diagram represents the initial state characterized in 2005 after trajectory centring. Only two dimensions are shown. Points correspond to intermediate ecological states (size = length of each state to initial state (IS) considering all PCA components) and are coloured according to time (yellow (2005) to red (2019)). Lines represent segments between transitional states. The black arrows represent the net change between 2005 and 2019

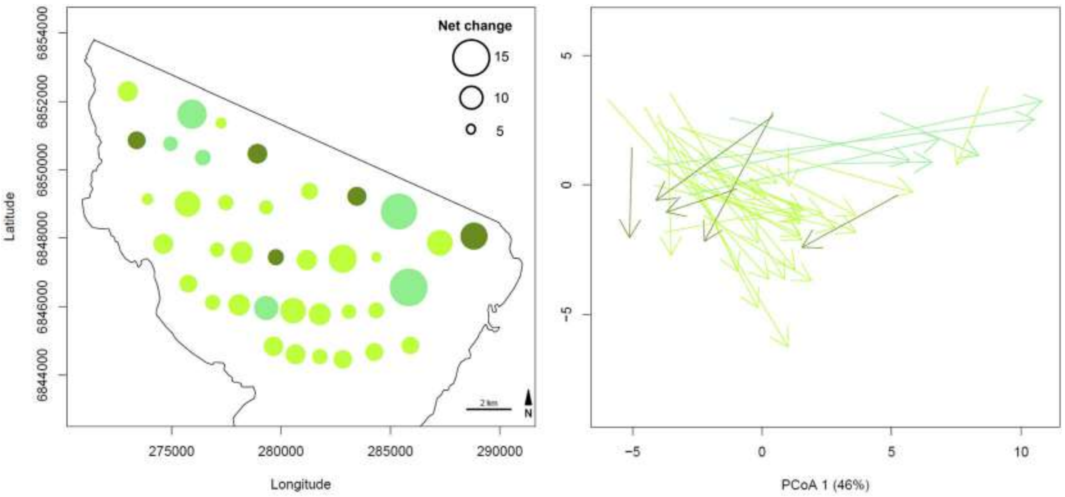
Trait-based approaches have been widely used to characterize functional shifts, in response to different natural or human disturbances (Thrush & Dayton, 2002; van Denderen et al., 2015; Bolam et al., 2017). The use of biological traits is expected to provide a good view of functional shifts over space and time (Pacheco et al., 2011). In our study, traits were chosen to assess the potential impacts of: 1) fishing activities (size, flexibility, fragility, habitats, feeding habits), and 2) organic matter enrichment (tolerance, feeding habits).

4.2.1 | Fishing activities

Trawling and dredging fishing activities are responsible of many impacts on the sea bed, such as the modification of benthic communities and sedimentary habitats (Newell, Seiderer & Hitchcock, 1998; Ellis, Norkko & Thrush, 2000; Thrush & Dayton, 2002; Eigaard et al., 2017). Watling & Norse (1998) compared the consequences of disturbance induced on the sea bed by mobile fishing gear to forest clear cutting. Scallop dredging in the Irish Sea has been shown to significantly modify benthic communities and *P. maximus* populations under experimental and commercial fishing pressure conditions (Bradshaw et al., 2001). Dredging activities tend to modify the structure of mounds, tubes, and burrows created by organisms living on the sediment surface, and limit small scale habitat structure heterogeneity (Thrush & Dayton, 2002). As underlined by Gray et al. (2006), the homogenization of heterogeneous habitats and the reduction of three-dimensional structures above and below the sediment–water interface constitute one of the most damaging effects of fishing activities.

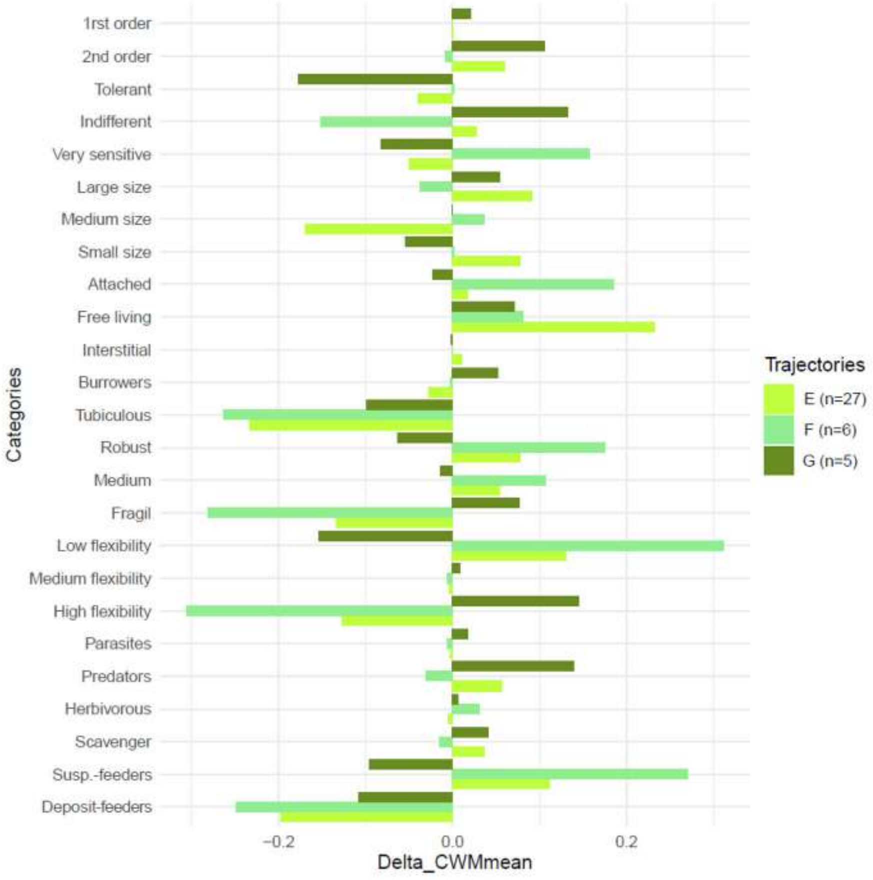
In our study, current functional shifts within assemblages led to a relative dominance of robust, rigid and free living species which suggests selective mortality processes of fragile, flexible, and sedentary species due to fishing pressure and human disturbances (Jennings et al., 2001; Duplisea et al., 2002; Kaiser et al., 2006; Constantino et al., 2009; Pedersen et al., 2009). Despite concentrating the highest scallop dredging pressure in Brittany (Appendix A-1), no accurate spatio-temporal assessment of fishing pressure is available for the bay of Saint-Brieuc. The existence of a potential impact of fishing activities on macrobenthos may seem at odds with the increase of suspension-feeder abundances over time in the study area. Van Denderen et al. (2015) studied benthic functional response to fishing activities according to natural disturbance regimes. They showed that fishing impacts are smaller or absent in areas exposed to high natural disturbance, leading to the hypothesis that, depending on local hydrodynamics, natural and fishing disturbances may affect benthic communities in similar ways. The local wave regime has been broadly stable over the last 30 years (SHOM, Appendix H) ruling out a strong influence of hydrodynamics on the observed patterns.

Overall sedimentary changes may also have contributed to the decrease of deposit-feeders in the study area, as dredging activities are known to homogenize the sediment. Mengual et al. (2016, 2019) showed for example an overall erosion of muddy areas in the bay of Biscay in relation with fishing activities, and a coarsening trend of surface sediments (5 cm). Morys, Brüchert & Bradshaw (2021) showed a significant decrease of surface organic matter content in a recent experiment into the impact of bottom trawling on benthic biogeochemistry. Such organic matter content decrease was observed at station R from 2014 (Appendix D). In our study, sedimentary



(a) Local functional trajectories

(b) Trajectory ordination diagram



(c) Differences in mean CWM values of categories of traits within functional trajectory cluster

FIGURE 7 Functional trajectories. (a) Map of local trajectories. Circle size corresponds to net change between 1987 and 2019 and colours to clusters of trajectories determined by HCA on CTA trajectory similarity analysis. All the dimensions of the multivariate space were considered in net change calculation and analysis of trajectory similarities. (b) Trajectory ordination diagram. Only two dimensions are shown. Functional trajectories are coloured according to trajectory clusters (green gradient). (c) Barplots of Community-weighted trait values (CWM) values shift for each categories of traits (mean 2019 – mean 1987). Bars are coloured according to functional trajectory clusters

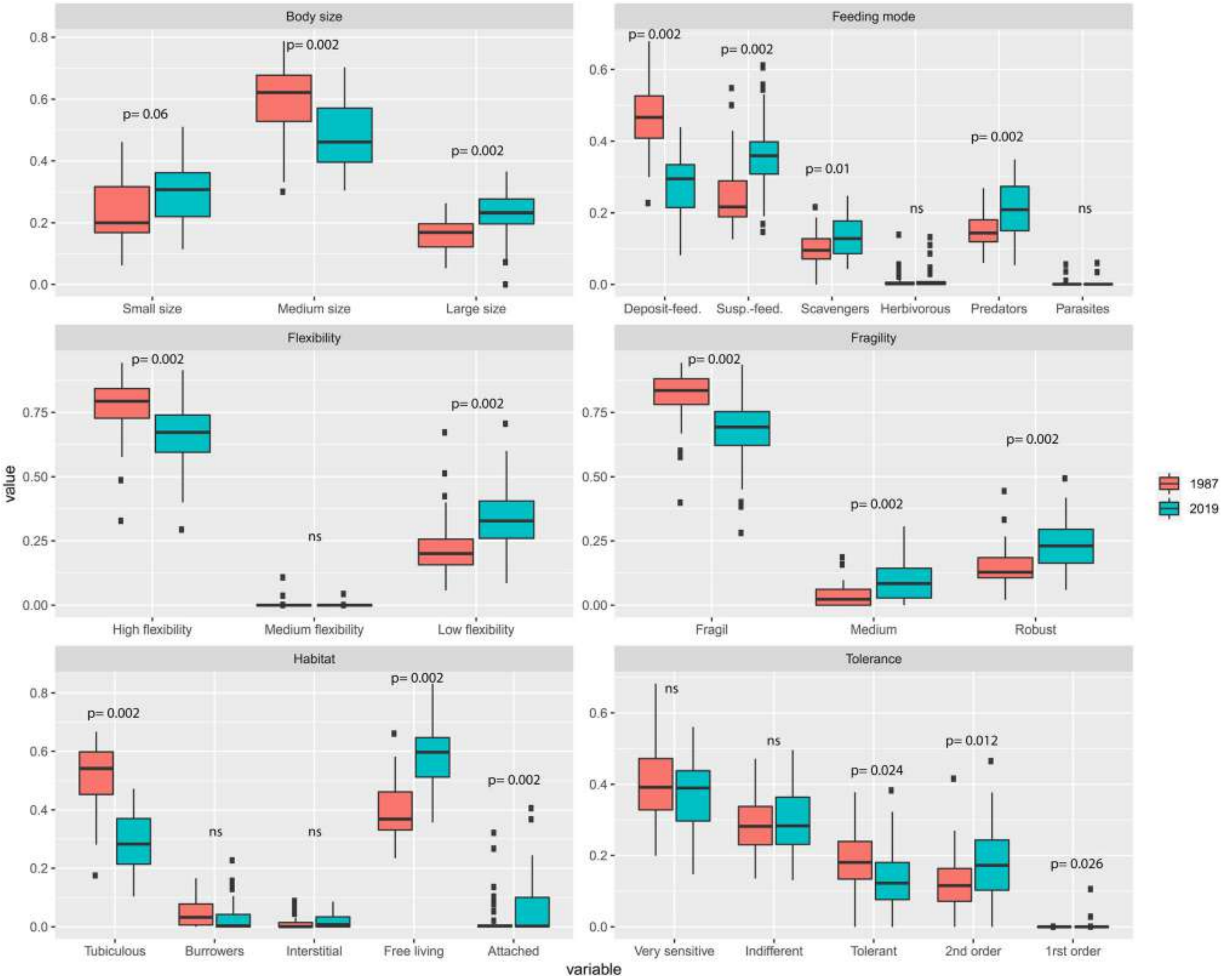


FIGURE 8 Boxplots of Community-weighted trait values (CWM) values for each category of traits and by year (1987: red; 2019: green). Boxplot indicates the median (line in the box), the first and third quartiles (hinges) and extreme data points (black points). Significance of student permutation paired-tests are indicated for each trait level

parameters partly shaped the taxonomic multivariate structure of the benthic community, but the amount of explained variance decreased between 1987 and 2019 indicating that sedimentary variables explain only a limited part of the observed changes.

4.2.2 | Organic enrichment

The positive functional shift observed for second-order opportunistic species, and particularly *V. gibba*, seems to indicate an impact of organic matter enrichment in accordance with Hrs-Brenko (2006) who suggested that eutrophication increases the fecundity of *V. gibba*. During our study, small individuals of *V. gibba* were observed attached by their byssus to drifting *Ulva* sp., suggesting: (1) a potential influence of algal mats offering new attachment substrates for early recruitment stages, and (2) individuals could drift when attached to algal mats, hence facilitating the colonization of new areas. In the western English Channel, eutrophication can also extend the spawning season of *Abra alba* (Dauvin & Gentil, 1989) which could be partly responsible for its high abundance observed at station R in 2015 and 2017. Local disturbance, predation/competition, and climatic factors are also known to control *A. alba* populations (Dauvin et al., 1993). The persistence of the observed changes needs to be confirmed as *A. alba* and *V. gibba* are known to present high population variations in such soft-bottom communities (Cabioch, 1968), however, such high inter-annual variability was not observed until the mid 2010s.

Despite the fact the positive shift of second-order species was mainly driven by *V. gibba*, the community was still dominated by species very sensitive to nutrient enrichment in 2019, some molluscs - *B. incarnata*, *Laevicardium crassum*, *T. ovata*, *M. donacina*, *N. hanleyi*, *P. maximus* having increased in abundance and occurrence. The diversity of temporal dynamics suggests a complex gradient of sensitivity to organic matter enrichment and the implication of additional driving factors. Indeed, (1) discards from scallop dredging could promote opportunistic species and scavengers leading to increases in their abundances (Depestele et al., 2019), and (2) by capturing nutrients, green tides are particularly suspected to buffer the influence of nutrient enrichment on macrofauna as discussed by Ponsero & Le Mao (2011) and Sturbois et al. (accepted) concerning the neighbouring intertidal area.

As in other ecosystems impacted by anthropogenic activities, changes observed in the bay of Saint-Brieuc result from different pressures acting simultaneously at different spatio-temporal scales. The selective mortality of fragile, flexible, tubiculous and burrower organisms suggests the influence of a physical disturbance. As the wave regime was stable over the survey period (SHOM: Supplementary material, Appendix H), dredging activities appear as the most likely factor of disturbance. The magnitude of fishing influence is difficult to assess because of the lack of accurate data concerning dredging pressure. However, changes in fisheries regulations (i.e. fishing ground zonation) in 2010 and 2017, coupled to an increase in the *P. maximus* population, has led to an increase in scallop dredging activities and inherent mechanical disturbances of the sea bed and associated benthic macrofauna. Nutrient enrichment probably drove the ecological response of the primary disturbed benthic assemblages by the stimulation of opportunistic-species, and concomitantly other suspension-feeder species. Climate change occurring at a larger scale, combined with the aforementioned local factors of disturbance, may also jointly control some other bivalve's populations.

4.3 | Regional scale insights

Recent fishing ground assessments have shown a large increase in the populations of *P. maximus* from the English Channel, and particularly in the Normano-Breton gulf where landings have increased from 1,200 tons in 1989 to an average of 7,000 tons since the early 2000s (Foucher et al., 2015; Foucher, 2017; Le Mao et al., 2019). Over the last 10 years, *P. maximus* densities across all age classes have increased in the lowest levels of the intertidal area (pers. obs.) suggesting a similar scenario in shallow sea bed between the low water mark and a depth of 5 m. The management of *P. maximus* populations by fishermen in collaboration with scientists, as well as climate change, have favoured this stock increase (Shephard et al., 2010). Fishing activities in the bay, associated to recruitment fluctuations, may be involved in the drastic decline of other bivalve populations, such as *Polititapes rhomboides*, which was commercially harvested in the bay until recently (Huet & Pitel, 2006).

Among other bivalve species, *Moerella donacina* and to a lesser extent *Timoclea ovata* increased in abundance and occurrence. These trends are congruent with those reported by Gaudin et al. (2018) who tracked changes in response to climate change in the English Channel. They notably showed, between the 1960s and 2014, large and moderate increases in occurrence and eastward movements of populations (i.e. tracking colder conditions) for *M. donacina* and *T. ovata*, respectively. Climate change (temperature increase) is also suspected to be responsible for changes in the abundance of *A. alba* at station R [Dauvin et al., 1993; Thiébaut & Houbin (comm. Pers.)], and of *Limecola balthica* in the nearby intertidal mudflats of the bay of Saint-Brieuc (Sturbois et al., accepted).

In the past decades, the slipper limpet *Crepidula fornicata* has progressively become an important component of soft-bottom benthic ecosystems in the English Channel (Blanchard et al., 2001; Blanchard, 2005). Total stock reached an estimated 450,000 tons in the bays of Saint-Brieuc and Mont Saint-Michel in the early 2000s (Blanchard & Hamon, 2006). Current trends are not documented, except in the bay of Brest, where Blanchet-Aurigny et al. (2012) reported that historical *C. fornicata* beds are currently mainly made up of dead shells. In our study, a decrease in the mean density of *C. fornicata* was observed (40.21 ind.m^{-2} ± 182.42 in 1987 vs 21.11 ind.m^{-2} ± 48.46 in 2019), but this overall trend is driven by change observed at a single station (105), while densities remained stable for the rest of the bay.

4.4 | What conservation perspectives for such coastal areas?

Among the different species sampled in this study, *V. gibba* experienced the greatest increase in abundance, especially in the southern part of the study area. *Varicorbula gibba* is considered as an indicator of environmental instability whose strong increase across Europe has been largely associated to various disturbances (Hrs-Brenko, 2006), particularly pollution and sedimentary instability (Pearson & Rosenberg, 1978; Salen-Picard, 1981; FAO & UNEP, 1985; Pranovi, Da Ponte & Torricelli, 2007). Unstable conditions have been reported to promote *V. gibba* populations (Rosenberg, 1977; Pranovi, Giovanardi & Franceschini, 1998). Cabioch (1968) already noted an alternation between *V. gibba* and *A. alba* abundance peaks in the western English Channel, similar to what we observed at station R.

High larval settlement of *V. gibba* is known to frequently appear after catastrophic events (Hrs-Brenko, 2006). This species, which grows rapidly (Jensen, 1990), shows strong survival capacity to different abiotic (resistant to pollution, turbidity, hypoxia, and sedimentation) and biotic stressors. In Australia, where this species is invasive, dramatic rises in abundance can have negative effects on the growth rate of *Pecten fumatus* juveniles, a commercial species, as demonstrated experimentally by Talman & Keough (2001). The bay of Saint-Brieuc, which suffers from eutrophication (but without hypoxic episodes) and supports intensive scallop dredging activities, appears to be a favourable area for the proliferation of this species.

The massive recruitment of *V. gibba* also characterizes the pioneer stages of benthic community dynamics following a perturbation (Pranovi, Giovanardi & Franceschini, 1998). Bonvicini-Pagliai & Serpagli (1988) called this species “a time recorder of environmental stress”. As a dominant suspension-feeder, with rapid juvenile and adult growth, *V. gibba* plays an important role in the food web by transfering pelagic production to the benthic compartment (Hrs-Brenko, 2006). Once the disturbance regime decreases, biotic interactions will progressively regulate *V. gibba* populations (Olafsson, Peterson & Ambrose, 1994). Knowledge on the level of disturbance required for the persistence of an abundant *V. gibba* population and its ability to increase in abundance in the absence of a primary disturbance factor is crucial to disentangle effects of natural and anthropogenic factors (Australian Government, 2008).

When developing management plans for marine areas and benthic resources, stakeholders must consider that benthic communities have the capacity to adapt to a predictable and moderate level of anthropogenic disturbance. However, there is a threshold beyond which populations, even composed of 'resistant' species, will collapse and cause the impoverishment of communities, with loss of major ecological functions and inevitable negative feedbacks, even on target species (Pranovi, Giovanardi & Franceschini, 1998).

The ecological state defined in 1987 does not constitute a reference state, and even less a conservation target, as nutrient enrichment and fishing pressures were probably already well established. CTA could bring new perspectives to the assessment of the ecological distance between current and reference status (Borja, Dauer & Grémare, 2012), by measuring net changes with respect to a predefined reference state. Ideally, such ecological baseline should be defined within an ecological entity, in unaffected areas. In the absence of a local pristine state, or of an ecological state that could be considered as a conservation target, it should be possible to include data from similar ecosystems located in the same region in the analysis to define a reference state in the multivariate space (e.g. a centroid of samples considered as a potential conservation target, including natural variability). Net change calculations over time, with respect to the reference status, may allow the accurate measurement of the restoration process through recovering trajectories. The definition of conservation targets in multivariate spaces could underline the degradation level, with respect to historical data, and help local governance adapt management perspectives.

Activities with potentially conflicting goals are concentrated in the "Baie de Saint-Brieuc-Est" Natura 2000 site with fishing on the one hand and benthic habitat conservation on the other. The assessment of fishing impacts on Natura 2000 sites requires high-resolution spatial environmental data, including distribution of natural habitats and species, as well as fine-scale data on the distribution of ongoing fishing activities that overlap with high-value conservation zones (Pedersen et al., 2009; AFB et al., 2019; Lusenius et al., 2019). In this context, this study: (1) underlines the value of historical data, even if they do not constitute a pristine state, and the limitations in their use as conservation targets, (2) provides up-to-date information about the distribution of benthic assemblages and associated species, and (3) confirms the necessity of measuring the fishing pressure to correctly interpret changes in marine ecosystems attributable to human activities. In our study, the use of the station R dataset was essential to the better understanding of long-term changes observed between only two sampling dates (1987 vs 2019). It confirms that the coupling of different spatial and temporal scales in any sampling strategy [few stations with high frequency sampling (Hewitt, Ellis & Thrush, 2016) *vs* low frequency larger sampling networks (Kröncke et al., 2011)] helps to track changes between long-term sampling networks as suggested by Bacouillard et al. (2020) and Callaway (2016) and that the development of such a monitoring strategy is important for the future.

This study clearly suffers from the lack of knowledge concerning fishing pressure and potential control areas free of fishing impacts. Unfortunately, there is no area free of dredging activity in the study site or in peripheral areas. Alternatives to characterize the impact of fishing activities in the study area could consist of a study of the response of benthic communities to a gradient of fishing pressures as proposed by van Denderen et al. (2015), or within an experimental area closed to commercial fishing as tested by Bradshaw et al. (2001). Further work is needed to 1) quantify fishing efforts in the shallow area (via abrasion maps) as such accurate information is lacking, and 2) design a strategy based on the comparison between dredged and un-dredged areas.

Overall, access to highly resolved information about fishing activities is paramount to help understand changes in benthic communities and distinguish the impact of fishing activities and other factors (nutrient enrichment, sediment instability, climate change) on benthic communities. Up-to-date documented reports on ecological changes and conservation status must be shared with stakeholders to effectively inform public debates (Eastwood et al., 2007; Pedersen et al., 2009). Consultation processes should involve policy makers, members of fishing institutions, fishermen, environmental organizations, and managers of Marine Protected Areas (MPAs) when present. This step should ideally lead to the implementation of fishery management measures to reduce threats, and achieve conservation objectives (Pedersen et al., 2009; AFB et al., 2019; Lusenius et al., 2019).

Although progress in expanding the coverage of MPAs has been made, the application of management tools has not yet been implemented in most of these areas (Torriente et al., 2019). Conservation of the marine environment is effectively a relatively new phenomenon and is currently playing 'catch-up' with its terrestrial counterpart where protected areas have been established for many decades (Morris et al., 2014). Despite the need for a worldwide improvement in the designation and management processes of marine areas, it has already been demonstrated that local human impacts on the marine environment could be effectively reduced within networks of Natura 2000 and Marine Protected Areas (Fraschetti et al., 2018; Zupan et al., 2018). Management plans are recommended for Natura 2000 sites but are not mandatory under the Habitats Directive. Nevertheless, they appear to be an appropriate solution to reflect transparent conservation objectives (European Commission, 2011). Despite their complexity, fishing regulations implemented through a consultation process and management scheme have been shown to represent win-win scenarios for economic and conservation goals in different marine protected areas around the world (N2K group, 2018). In the bay of Saint-Brieuc, the implementation of such win-win scenarios enabled the long-term management of *P. maximus* population with benefits for the fishermen, and more modestly, the cockle fishing grounds (Ponsero, Dabouineau & Allain, 2009). Similar trends were reported in the Irish Sea by Bradshaw et al. (2001), who showed positive effects of commercial fishing area closures on *P. maximus* (and indirectly on fishermen) and on benthic communities which became more diverse.

These results clearly show there has been a degradation of soft-bottom macrobenthos and it is important that this new knowledge is taken into account in implementing new governance processes and developing an integrated conservation strategy.

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CONFLICT OF INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

AUTHOR CONTRIBUTION

Anthony Sturbois: Conceptualization, Methodology, Validation, Formal analysis, Data curation, Writing - original draft, Visualization, Project administration, Funding acquisition, Investigation (Restro 19). **Gaëtan Cormy:** Writing - review & editing, Investigation (Restro 19). **Alexandre Le Moal:** Writing - review & editing, Investigation (Restro 19). **Gauthier Schaal:** Writing - review & editing, Investigation (Restro 19), Supervision. **Caroline Broudin:** Writing - review & editing, Investigation (WFD). **Eric Thiébault:** Writing - review & editing, Investigation (WFD). **Alain Ponsero:** Writing - review & editing, Visualization, Investigation (Restro 19). **Patrick Le Mao:** Writing - review & editing, Investigation (Restro 19). **Auriane Jones:** Writing - review & editing. **Pascal Riera:** Writing - review & editing. **Olivier Gauthier:** Methodology, Writing - review & editing, Validation. **Nicolas Desroy:** Methodology, Writing - review & editing, Investigation (Restro 19), Supervision, Validation.

DATA AVAILABILITY STATEMENT

Author elects to not share data.

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Spatio-temporal patterns in stable isotope composition of a benthic intertidal food web reveal limited influence from salt marsh vegetation and green tide

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ABSTRACT

Assessing fluxes of matter and energy in food webs within and across benthic habitats is important to understand the ecological functioning in bays and estuaries, where the productivity is favoured by a wide diversity of primary producers. The temporal variability (March vs September 2019) in the carbon and nitrogen stable isotope composition of primary food sources and benthic invertebrates consumers was investigated in a large intertidal area (Western English-Channel, France). The study area is influenced by megatidal conditions and characterised by salt marshes in the sheltered part, and seasonal *Ulva* spp. blooms. The spatio-temporal variability in the structure of the benthic food web was analysed at the scales of both the whole bay and the different assemblages, which constitute the mosaic of habitats. Inferences on potential sources fuelling the food web were supported by spatio-temporal patterns based on covariations and stable isotope trajectory analysis. Results highlighted that phytoplankton, microphytobenthos and SOM were, most likely, the main food sources. The trophic connectivity between salt marsh and benthic habitats within the bay was limited to some macrofauna species inhabiting muddy creeks within the salt marsh. Unexpectedly, the influence of *Ulva* spp. blooms appeared also limited. Spatial patterns illustrates the constancy of the spatial variability in the benthic pelagic coupling, with a higher influence of microphytobenthos in the upper shore compared to low shore assemblages. This first attempt to characterize intertidal benthic food web constitutes a relevant baseline for the conservation of the bay of Saint-Brieuc where a national Nature Reserve has been created in 1998 for the conservation of overwintering birds. The spatial and temporal patterns of the benthic food web observed in this study (1) confirm the importance to consider food web variability at spatial and temporal scales from sampling designs to data analysis, and (2) demonstrate the ability of the stable isotope trajectory analysis framework to highlight food web dynamics.

1. Introduction

Coastal areas are among the most productive marine systems in the world, sustaining many ecological processes and ecosystems services (Costanza et al., 1997). The production of bays and estuaries is provided by a wide diversity of primary producers, including phytoplankton, seaweeds, seagrass, mangroves, salt marsh plants, macroalgae, and benthic diatoms (Bouillon et al., 2011). All these primary producers contribute to an important pool of detrital organic matter, which plays a major role in the biogeochemistry and ecology of bays and estuaries ecosystems. Due to this diversity, understanding the fate of primary production within coastal ecosystems, and especially within food webs, is challenging (Mann, 1982). Furthermore, the contribution of these different producers to local food webs has been reported to vary within and among coastal systems (Chanton and Lewis, 2002; Deegan and Garritt, 1997; Domingos and Lana, 2017), leading to a lack of a

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commonly accepted paradigm for food web functioning across variable spatial and temporal scales.

Because coastal food webs depend on primary food sources which can be either sessile or mobile, assessing vertical (i.e. benthic-pelagic coupling) and horizontal (i.e. organic matter fluxes across habitats/ecosystems) trophic connectivity between adjacent habitat is crucial (Kang et al., 2015; Schaal et al., 2008). Trophic connectivity varies among systems from near total isolation to strong mixing. Water motion facilitates the movement of carbon as dissolved or particulate matter in aquatic ecosystems (Guimond and Tamborski, 2021; Polis et al., 1997).

Hydrodynamics influences coastal productivity through a variety of mechanisms (Largier, 1993). In tidal environments, the periodic movement of the tide is responsible for organic matter redistribution, enhancing trophic connectivity among different habitats and assemblages (Polis et al., 1997). Redistribution range depends on tidal amplitude across meso, macro and megatidal systems (Domingos and Lana, 2017; Ziegler et al., 2019). Resulting hydrodynamics can lead to the accumulation and/or dispersal of water column constituents, including sediment, phytoplankton, and particulate detritus (Young et al., 2021), and potentially influence production pathways and food web structure. Higher water motion increases material processing (e.g. microphytobenthos resuspension) between benthic and pelagic compartments (Ubertini et al., 2012) which can be amplified by biological factors, such as bioturbation (Rakotomalala et al., 2015).

Bay and estuaries are known to be influenced by seasonal and inter-annual variability in marine and freshwater inputs. This variability affects the abundance and distribution of resources and consumers and may drive food web dynamics (Bouillon et al., 2011). The consideration of trophic dynamics is consequently crucial to take into account the spatio-temporal variability of food sources in terms of composition and availability.

In shallow bays under the influence of mega-tidal conditions, bathymetry influences submersion/emersion time of intertidal habitats, affecting the time available for feeding. Tidal conditions coupled with sediment characteristics also have a pronounced effect on benthic macrofauna species distribution limiting for example the distribution of species requiring stable conditions to sheltered parts (Blanchet et al., 2014; França et al., 2009). Such a broad spatial-pattern in the distribution of intertidal benthic species can be strongly consistent over time, leading to the persistence of contrasting benthic assemblages along inshore/offshore and sheltered/exposed gradients in intertidal soft bottom-habitats (Sturbois et al., 2021a).

Organic matter inputs (e.g. detrital plants or algae) from vegetated systems may diversify food webs structure and energy pathways (Hyndes and Lavery, 2005; Nordström et al., 2015; Quillien et al., 2016; Schaal et al., 2008). Such additional food resources may originate from close productive habitats such as salt marshes (Nordström et al., 2014). It may also results from seasonal eutrophication with the proliferation of green algae, which may have important consequences on the structure of benthic food webs (Quillien et al., 2016) and fish assemblages (Jones et al., 2020).

For decades, stable isotope analysis has been widely used in trophic ecology studies to understand feeding behaviour, trophic relationship and organic matter flow within and across marine food webs (Fry, 2008; Peterson, B.J., 1999). Carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) are the most commonly used stable isotope in trophic studies. The carbon isotope ratio, expressed as $\delta^{13}C$, is particularly relevant to determine the origin of organic matter supporting consumers (e.g. benthic vs pelagic or freshwater vs marine), while the nitrogen isotope ratio ($\delta^{15}N$) allow the estimation of trophic positions (Fry, 2008). More recently, the development of numerous isotopic metrics has allowed to better assess stable isotope measurements at the community scale, providing relevant information about ecosystems structure and functioning (Cucherousset and Villéger, 2015; Layman et al., 2007, 2012; Rigolet et al., 2015).

In this study, we focused on the structure and the dominant sources that support the food web in an intertidal sandflat influenced by megatidal conditions and characterised by a variety of primary producers. We specifically explored $\delta^{13}C$ and $\delta^{15}N$ values from sources to benthic invertebrates consumers at the scale of the entire sandflat and for benthic assemblages which constitute the mosaic of habitat within the bay. Classical analyses ($\delta^{13}C$ versus $\delta^{15}N$ raw values, graphical inference, indices of structure) were coupled with distance- and direction-based metrics of the new Stable Isotope Trajectory Analysis (SITA) framework (Sturbois et al., 2021b). This new method provides an assessment of stable isotope data at different levels of biological organization, from individuals to ecosystems to derive structural and functional trajectories. We hypothesized that: (1) due to the aforementioned characteristics of the bay, spatial gradients and temporal variability would drive the sources supporting the food web, (2) the variability would induces spatial and temporal difference in the food web structure among habitats. Implications in sampling strategy and conservation processes were finally discussed.

2. Material and methods

2.1. Study area and sampling design

Fieldwork was conducted in the bay of Saint-Brieuc, France (Fig. 1), a 2900 ha tidal flat divided in two coves (Yffiniac and Morieux coves). The area is mainly dominated by fine to medium sands, while the most sheltered parts are characterised by muddy sands. The bay is under the influence of a semi-diurnal megatidal regime. Tidal range varies between 4 m at neap tides and nearly 13 m during spring tides, generating strong tide currents rising between 0.3 and 0.5 m/s in this part of the bay.

The upper shore is dominated by salt marshes (125 ha) characterised by a current dynamic of extension and a good conservation status (Sturbois and Bioret, 2019).

The bay suffers from eutrophication, resulting in strong ephemeral macroalgae proliferation and cyclic green tides episodes (Charlier et al., 2007; Gravier, 2012) (Supplementary material, Appendix A). The national Nature Reserve of Saint-Brieuc was created in 1998 for the protection of shore birds. Because overwintering and migratory waders forage on macrofauna (Ponsero et al., 2016; Ponsero and Le Mao, 2011; Sturbois et al., 2015), their protection required the conservation of marine habitats and benthic resources.

The bathymetry and hydrodynamics strongly influence the structure of benthic assemblages on the study area: from muddy sands assemblage, on the upper shore, to medium sands. Following the main benthic assemblages characterized by Sturbois et al. (2021a), sampling of macrofauna was carried out on four soft-bottom habitats in the bay of Saint-Brieuc from the top to the low flat: salt marsh muddy creeks (2 stations), and muddy (5 stations), fine (9 stations) and medium sands (6 stations, Fig. 1). The bathymetric gradient among habitats leads to differences in mean daily submersion time: salt marsh (2:07 h per 24 h), muddy sands (4:59 ± 3:09), fine sands (12:21 ± 6:05) and medium sands (20:35 ± 3:31).

2.2. Sample collection and laboratory processes

Sources – Samples were collected in early March and September 2019. Sedimentary organic matter (SOM) was collected at each station by scraping the upper 1 cm of the sediment during the low tide. For each station, one subsample was acidified (10% HCl) and re-dried overnight at 60 °C, whereas the other subsample remained untreated. Values of $\delta^{13}C$ from acidified subsamples were combined with those of $\delta^{15}N$ from untreated subsamples to compute the SOM isotope values undisturbed by calcium carbonate residues ($\delta^{13}C$) and by acidification ($\delta^{15}N$) (Androuin et al., 2019). Benthic diatoms (Microphytobenthos, MPB), abundant in the muddy/sandy sediments of the area at the end of spring/early summer, were collected in June 2019 and July 2020 by scrapping the surface of the sediment and extracted according to a

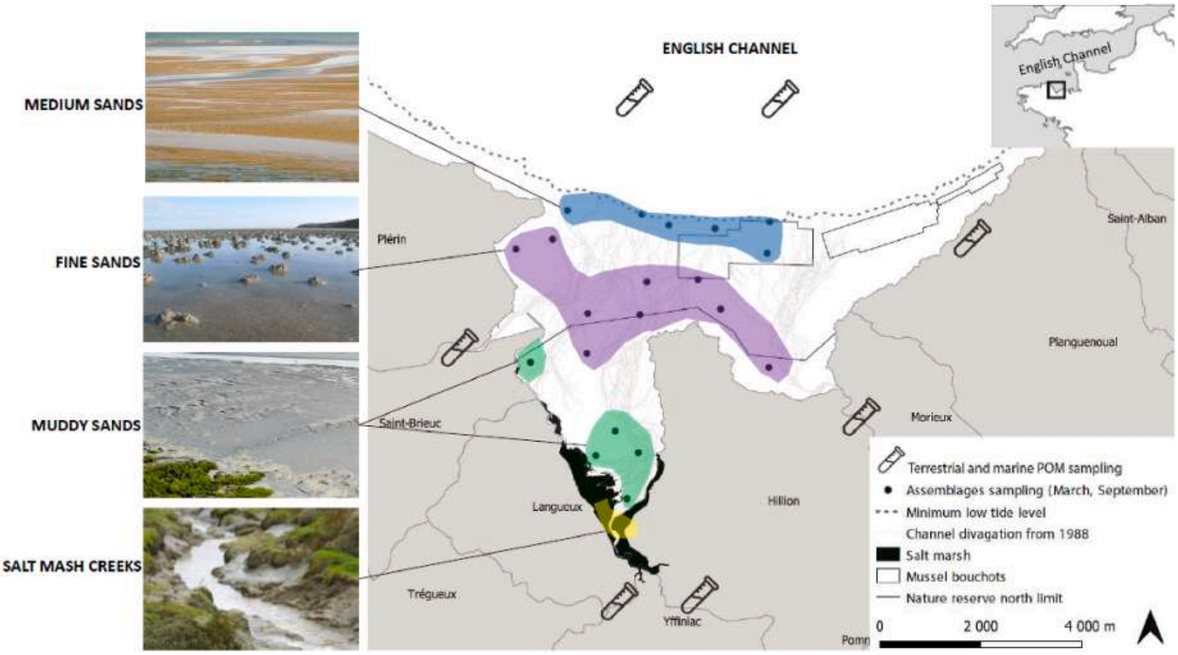

Fig. 1. Location of the study area and sampling stations. Dots correspond to the stations sampled in the different habitats. Colors of polygons correspond to the four assemblages (i.e habitats) sampled: salt marsh creeks (yellow), muddy sands (green), fine sands (purple) and medium sands (blue).

method of Couch (1989), modified by Riera et al. (1999). The diatoms were collected on previously combusted glass fiber filters, briefly washed with 10% HCl and rinsed with Milli-Q water and kept frozen (−20 °C) until analysis. Stable isotope compositions of 2019 and 2020 were averaged.

Marine and freshwater samples collected for suspended particulate organic matter (POM) were pre-filtered through a 90-μm-mesh to remove large detritus and then filtered on precombusted (500 °C, 5 h) Whathman GF/F filters. POM collected from river basins (POM_TER, 5 stations), and offshore (POM_SEA, 2 stations) were differentiated in further analysis.

Leaves and twigs of the most representative vascular plants colonizing salt marshes (Sturbois and Bioret, 2019) were sampled by hand at low tide, as well as fresh stranded algae (*Ulva* spp.) whenever present on the flat (fine and medium sand habitats). Samples were rinsed at the laboratory to be cleaned from epibionts, dried at 60 °C for 48 h, and ground into a fine powder using a marble mortar.

Consumers - Benthic macrofauna was sampled in March and September 2019 from the four assemblages using a 1/32 m^2 hand corer (diameter: 20 cm), at a depth of 25 cm (Supplementary material, Appendix B). Sampling was coupled with spade prospection for over-dispersed megafauna, or for species typically difficult to sample using hand corers (e.g. the lugworm *Arenicola marina*). The content of the cores was gently sieved through a 1-mm square mesh sieve. Macrofauna was then sorted on the field and preserved in plastic vials. The beach-hopper *Orchestia gammarellus* was captured by hand in the vegetation bordering salt marsh creeks. In the laboratory, animals were identified to the lowest possible taxonomic level, rinsed and stored at −20 °C until further treatment. Samples consisted of individual muscle tissues of large species (bivalves, annelids, echinoderms) or, whenever necessary for small species, pooled individuals (for the small gastropod *Peringia ulvae*) and whole individual (for amphipods species). Species containing calcium carbonates (e.g. the burrowing brittle-star *Acrocnida spatulispina* or the slippershell snail *Crepidula fornicata*) were split into two acidified and non-acidified subsamples. Values of $\delta^{13}C$ from acidified subsamples and $\delta^{15}N$ and from untreated subsamples were combined. All samples were rinsed, dried at 60 °C for 48 h, and ground into fine powder using a marble mortar.

At least three replicates were analysed per species when possible, but for several taxa less replicates were available (Supplementary material, Appendix B). As much as possible, the different replicates were chosen among available samples to cover the widest part of each assemblage.

2.3. Stable isotope analysis

Ground samples were packed into 5×8 mm ultra-clean tin capsules and analysed using an elemental analyser (EA Flash 2000 from ThermoFisher Scientific) coupled with an isotope ratio mass spectrometer (Delta V Plus from ThermoFisher Scientific) at the stable isotope platform of the Pole Spectrométrie Océan at the University of Bretagne Occidentale (Brest, France). Stable isotope ratios were reported in the standard δ notation as units of parts peer thousands (‰) relative to the international reference standard: $\delta X = [(R_{Sample}/R_{Standard})\text{-}1] * 10^3$ where X is ^{13}C and ^{15}N and R is the corresponding ratio of $^{13}C/^{12}C$ and $^{15}N/^{14}N$. Reference standard used were Vienna-Pee Dee Belemnite for ^{13}C and atmospheric N_2 for ^{15}N (precision: 0.1).

2.4. Data analysis

Data sets were investigated to analyse spatial patterns and temporal variability of the intertidal benthic food web between March and September. Analyses were conducted in terms of composition and structure at the bay scale (i.e. entire community), and at the finer scale of the different benthic assemblages. Each species has been assigned to a trophic group: carnivores, deposit-feeders, deposit-suspension-feeders, suspension-feeders, grazers, omnivores. This assignation was performed with respect to primary literature on specific taxa, expert knowledge and three publicly available databases: polytraits (http://polytraits.lifewatchgreece.eu), the World Register of Marine Species (WoRMS Editorial Board, 2020), and Biological Trait Information Catalogue (BIOTIC, http://www.marlin.ac.uk/biotic/). Trajectory analysis was performed to quantify and characterize the magnitude (distance) and the nature (direction) of temporal shift in the $\delta^{13}C/\delta^{15}N$-space for trophic groups. All analyses were performed within the R environment.

Spatial differences in $\delta^{13}C$ and $\delta^{15}N$ were tested with a one-way ANOVA against the factor ‘Assemblages’. The food web structure was analysed though community-wide metrics (Layman et al., 2007):

- *$\delta^{13}C$ range* (CR): Distance between the highest and the lowest $\delta^{13}C$ values of the community (i.e., maximum $\delta^{13}C$ - minimum $\delta^{13}C$). CR is one representation of basal source diversity within a food web;
- *$\delta^{15}N$ Range* (NR): Distance between highest and the lowest $\delta^{15}N$ values of the community (i.e., maximum $\delta^{15}N$ - minimum $\delta^{15}N$). NR is one representation of the total length (i.e. total number of trophic levels) within a food web;
- *Total Area* (TA): Convex hull area encompassed by all species in the $\delta^{13}C$-$\delta^{15}N$ 2D δ space. This represents a measure of the total amount of niche space occupied, and thus a proxy for the total extent of trophic diversity within a food web;
- *Mean distance to centroid* (CD): Average Euclidean distance of each species to the $\delta^{13}C$-$\delta^{15}N$ centroid, where the centroid is the mean $\delta^{13}C$ and ^{15}N value for all species in the food web. This metric provides a measure of the average degree of trophic diversity within a food web;
- *Mean nearest neighbor distance* (NND): Mean of the Euclidean distances to each species' nearest neighbor in bi-plot space, and thus a measure of the overall density of species packing.

Three other indices from Cucherousset and Villéger (2015) were also calculated to analyse the similarity between March and September and among assemblages:

- *Isotopic similarity* (ISim): Overlap in the total isotopic niches as the ratio between the isotopic niche of the intersection and of the union off the two groups considered. It ranges from 0 when there is no isotopic overlap to 1 when the group with the lowest isotopic richness fills a subset of the isotopic space filled by the group with the highest isotopic richness;
- *Isotopic divergence* (IDiv): Distribution of points (close to the centroid or edges) within the convexhull. IDiv is minimal (i.e. tends to 0) when most of the points are close to the centre of gravity of the convex hull, and organisms with the most extreme stable isotope values are rare in a community. IDiv tends to 1 when all the points are located on the edges of the convex hull and organisms with the most extreme stable isotope value(s) dominate the foodweb;
- *Isotopic Eveness* (IEve): Regularity in the distribution of organisms along the shortest tree that links all the points. IEve tends to 0 when most of organisms are packed within a small region of the stable isotope space while a few others are far from this cluster. IEve tends to 1 when organisms are evenly distributed in the stable isotope space.

The new Stable isotope trajectory analysis (SITA) framework was used to measure shifts in stable isotope values for sources and trophic groups (Sturbois et al., 2021b). The quantitative analysis of stable isotope dynamics in response to ecological and environmental changes has been explored in the past through the comparative analysis of temporal trajectories in a two-dimensional (usually $\delta^{13}C$ and ^{15}N) isotopic space (δ space). For instance, Schmidt et al. (2007) and Wantzen et al. (2002) quantified the direction and magnitude of temporal changes in food web structure based on the geometric properties of trajectories in the δ space. Schmidt et al. (2007) used specifically circular statistics and charts to represent and test direction shifts in the δ space. Turner et al. (2010) characterized attributes of path trajectories (size, direction and shape) over data sets containing more than two temporal samples to provide a quantitative description and tested changes in stable isotope compositions change in response to spatial and temporal gradients. Building on these previous works and on the recent Community trajectory analysis framework (De Cáceres et al., 2019; Sturbois et al., 2021c), the SITA framework goes further in the explicit quantitative description, analysis and representation of the magnitude and the nature of changes in stable isotope composition.

Length- and direction-based SITA metrics were calculated. The net change (Euclidian distance between March and September for a given group) and the angle α (0–360° direction in the δ-space considering the Y axis, $\delta^{15}N$, as the North, i.e. 0°) were calculated to assess the magnitude and the nature of change in the $\delta^{13}C/\delta^{15}N$-space, respectively. Net changes and angle α were represented through trajectory diagrams and trajectory roses (Sturbois et al., 2021b) and temporal differences in $\delta^{13}C$ and $\delta^{15}N$ mean values for sources and trophic groups were represented through bar plots and tested with permutation Student's t-tests (package '*RVAAideMemoire*', '*perm.t.test*' function, 999 permutations).

3. Results

3.1. Primary food sources

3.1.1. Bay scale

Contrasts were observed in primary food sources stable isotope values (Fig. 2, Table 1). Values of $\delta^{13}C$ were lower for terrestrial POM (−30.13 ± 0.98‰). Salt marsh plants exhibited among the lowest $\delta^{13}C$ values, excepted the common cord-grass *Spartina anglica* characterised by the highest $\delta^{13}C$ (−12.89 ± 0.20‰) typical of C4 plants (Currin et al., 1995). Higher $\delta^{15}N$ values were observed for the sea purslane *Halimione portulacoides* in March (12.98 ± 1.74‰), and September (11.94 ± 0.44‰).

3.1.2. Temporal variability

The SOM samples of all assemblages were characterized by the lowest variability in $\delta^{13}C$ and $\delta^{15}N$ values (Fig. 3, Table 1). The stable isotope composition of *Ulva* spp. was characterized by an increase in both isotopes in September (angle α: 50.57°, trajectory length: 6.49), although this variation was not significant for $\delta^{13}C$ ($p = 0.094$, Supplementary material, Appendix C). POMs followed an inverse pattern (243.49°, 7.41). Significant $\delta^{13}C$ shifts between March and September were observed, with a decrease for POM_SEA ($p = 0.004$), and an increase for terrestrial POM ($p = 0.032$).

3.2. Consumers

3.2.1. Bay scale

Benthic consumers displayed a wide range of stable isotope compositions in both months (Table 2). In March, mean $\delta^{13}C$ values ranged from −21.90 ± 0.30‰ in the grazer *O. gammarellus* to −12.58 ± 0.94‰ in the deposit-feeder *P. ulvae* (Fig. 2, A.). Mean $\delta^{15}N$ values ranged from 8.81 ± 0.50‰ in the deposit-feeder *Bathyporeia sarsi* to 13.46 ± 0.73‰ in the carnivore *Sigalion mathildae*. In September, $\delta^{13}C$ mean values ranged from −21.39 ± 0.93‰ still for *O. gammarellus,* to −11.88 ± 0.94‰ in the deposit-feeder *Bathyporeia pilosa* (Fig. 2, B.). $\delta^{15}N$ mean values ranged from 9.08 ± 0.50‰ in the deposit-feeder *Bathyporeia pilosa,* 14.37 ± 0.29‰ in the omnivore *Hediste diversicolor*. Omnivores and carnivores exhibited among the highest $\delta^{15}N$ values, while deposit-feeders and suspension-feeders among the lowest with an important variability (Fig. 2).

Shifts in the stable isotope compositions of sources helped with the identification of potential food sources for different consumers. POM_SEA was characterised by an important depletion in $\delta^{13}C$ values between March and September, as observed in the suspension-feeders (Fig. 2). SOM $\delta^{13}C$ values were quite similar among assemblages in March, while a ^{13}C-depletion was observed in the SOM measured from muddy salt marsh creeks. SOM collected in fine and medium sands also were likely to support deposit-feeders in these assemblages (Fig. 2).

Total areas were similar in March (43.46‰^{2}) and September (46.64‰^{2}) (Table 3, Fig. 4). The food web centroid was characterized by a $\delta^{13}C$ decrease (−0.95‰) but the food web still strongly overlapped in March and September (Isotopic Similarity = 0.728). CD remained similar over time (1.99 vs 2.02) revealing a stable trophic diversity. In September, species were more evenly distributed, decreasing the trophic

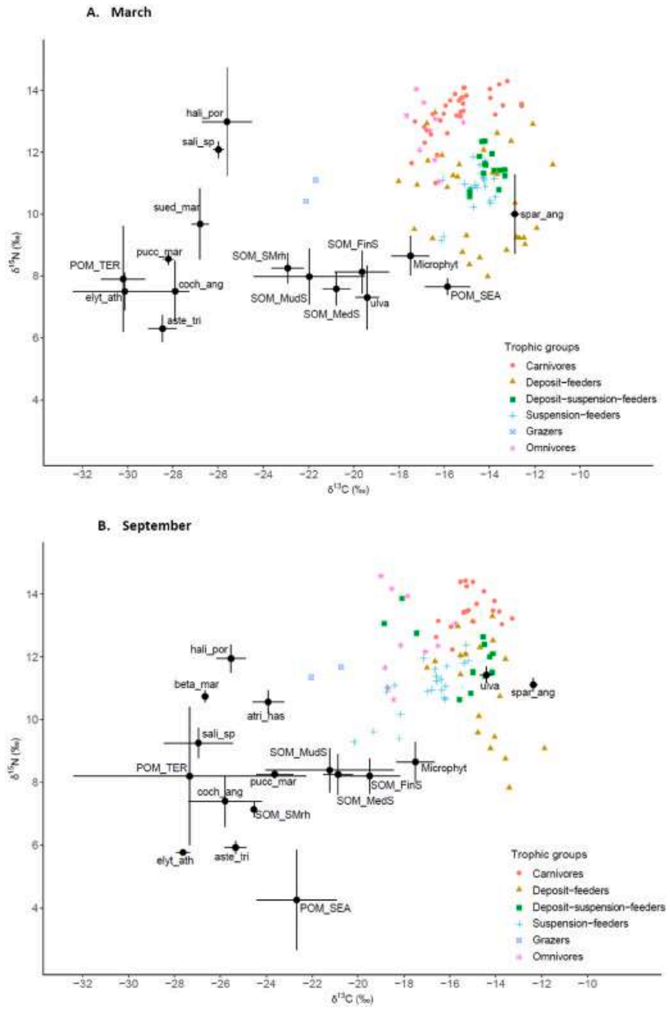

Fig. 2. Stable isotope composition ($\delta^{13}C$ and $\delta^{15}N$) of consumers and potential dietary sources of organic matter in March (A) and September (B) from intertidal soft-bottom sediments of the bay of Saint-Brieuc. $\delta^{13}C$ and $\delta^{15}N$ values are plotted for each individual consumer. Colors and shapes represent trophic groups. Mean $\delta^{13}C$ and $\delta^{15}N$ values of potential dietary sources are represented with black dots with error bars (size proportional to sd values). Marine and terrestrial particulate organic matter (POM_SEA, POM_TER). Sedimentary organic matter in the different habitat from salt marsh to muddy, fine and medium sands (SOM_SMrh, SOM_MudS, SOM_FinS, SOM_MedS). Microphytobenthos (Microphyt). C3 plants: *Halimione protulacoides* (hali_por), *Beta maritima* (beta_mar), *Atriplex hastata* (atri_has), *Salicornia* sp. (salic), *Puccinelia maritima* (pucc_mar), *Cochlearia anglica* (coch_ang), *Elytrigia atherica* (Elyt_ath), *Aster Tripol*ium (aste_tri). C4 plant: *Spartina anglica* (spar_ang). Algae: *Ulva* sp. (ulva).

redundancy as shown by the increase in NND (0.28 vs 0.36), SDNND (0.24 vs 0.31), and IEve (0.61 vs 0.80).

3.2.2. *Assemblage scale*

3.2.2.1. Stable isotope composition. Species sampled in the salt marsh were characterised by the lowest $\delta^{13}C$ values at both months and were excluded to fulfil the normality assumption and perform ANOVA across the three sands assemblages. Excluding salt marshes, $\delta^{13}C$ values showed significant spatio-temporal variability characterised by a $\delta^{13}C$ depletion gradient from muddy to medium sands (F: 54.38, p-value $<$ 0.0001) which was consistent over time (Supplementary material, Appendix D), and followed the previously mentioned emersion time gradient. CR increased between March and September (2.74 vs 5.20) in medium sands and remained stable in other assemblages (Table 3). $\delta^{15}N$ were significantly different between assemblages (F: 5.16, p-value $<$ 0.01).

Some spatial patterns in the stable isotope composition of trophic groups were also identified at the scale of trophic groups and correlated with emersion time. Deposit-suspension-feeder $\delta^{13}C$ values were negatively correlated with emersion time in March (−0.674, $p < 0.01$, Pearson), while suspension-feeders (0.720, $p < 0.001$), deposit-feeders (0.635, $p < 0.01$), and carnivores (0.588, $p < 0.01$) showed a positive correlation in September.

3.2.2.2. Structure. TA was higher in March for muddy (21.92‰^{2}) and fine sands (23.16‰^{2}) compared to medium sands (9.12‰^{2}) and salt marsh (9.59‰^{2}) (Table 3, Fig. 5). In September, the TA of the different sand assemblages were equivalent, following a decrease in muddy and fine sands and an increase in medium sands.

Little convex hull overlap was observed between the salt marsh and other assemblages. An overall decreasing $\delta^{13}C$ gradient from muddy ($\delta^{13}C$ centroids in March: −13.93‰, September: −14.46‰), to fine (−15.01‰, −15.08‰) and medium (−16.41‰, −17.34‰) sands assemblages led to a partial convex hull overlap. The lowest isotopic similarity among sand assemblages were observed between muddy and medium sands in both months (March: 0.139, September: 0.149). In March, fine sands were more similar to muddy sands (0.607) than medium sands (0.351). In September, overlap became more balanced (0.401 vs 0.441, respectively), revealing more similarity in isotopic niche between assemblages. More specifically, dissimilarity at the lower levels of the food web increased in September between muddy and medium sands indicating some differences in stables isotopes values mainly implying suspension-feeders (Fig. 5B).

In sand assemblages, CD ranged from 1.40 to 1.76 in March, and from 1.50 to 1.91 in September. Species sampled in muddy and medium sands were more evenly distributed in the δ-space in September as shown by the increase in NND, SDNND, IDiv and IEve values (Table 3).

3.2.2.3. Trajectories of trophic groups. Significant decreases in $\delta^{13}C$ value between March and September were observed in muddy sands in suspension-feeders ($p = 0.012$, Supplementary material, Appendix C) and deposit-suspension-feeders ($p = 0.020$), and for suspension-feeders from fine ($p = 0.002$) and medium sands ($p = 0.002$) (Figs. 3 and 6, A & B). A moderate increase in $\delta^{13}C$ value was observed in carnivores from medium sands ($p = 0.022$). Contrasts among assemblages were observed in trophic groups stable isotope compositions between March and September. Medium sands suspension-feeders exhibited the longest trajectory (Euclidean distance = 3.12), while muddy sand deposit-feeders were characterized by the lower shift (0.16) (Table 4, Fig. 6A and B). Trophic groups stable isotope compositions of consumers remained contrasted between assemblages but the temporal shifts of both $\delta^{13}C$ and $\delta^{15}N$, were similar for some trophic groups among assemblages. Suspension-feeders exhibited very similar directions (283.90 ± 3.70°) and among the highest changes (2.27 ± 0.68, Euclidean distance), characterized by a^{13}C-depletion and a moderate increase in $\delta^{15}N$. Similar temporal patterns across assemblages were also observed in deposit/suspension-feeders from muddy (0.95, 297.24°) and fine (0.81, 294.95°) sands, and in omnivores and carnivores from fine and medium sands respectively. Inversely, deposit-feeders exhibited contrasting trajectories in muddy (0.16, 221.10°), fine (1.19, 359.20°) and medium sands (0.63, 182.00°) mainly influenced by shifts in $\delta^{15}N$. In salt marsh creeks, omnivores and grazers both exhibited singular trajectories.

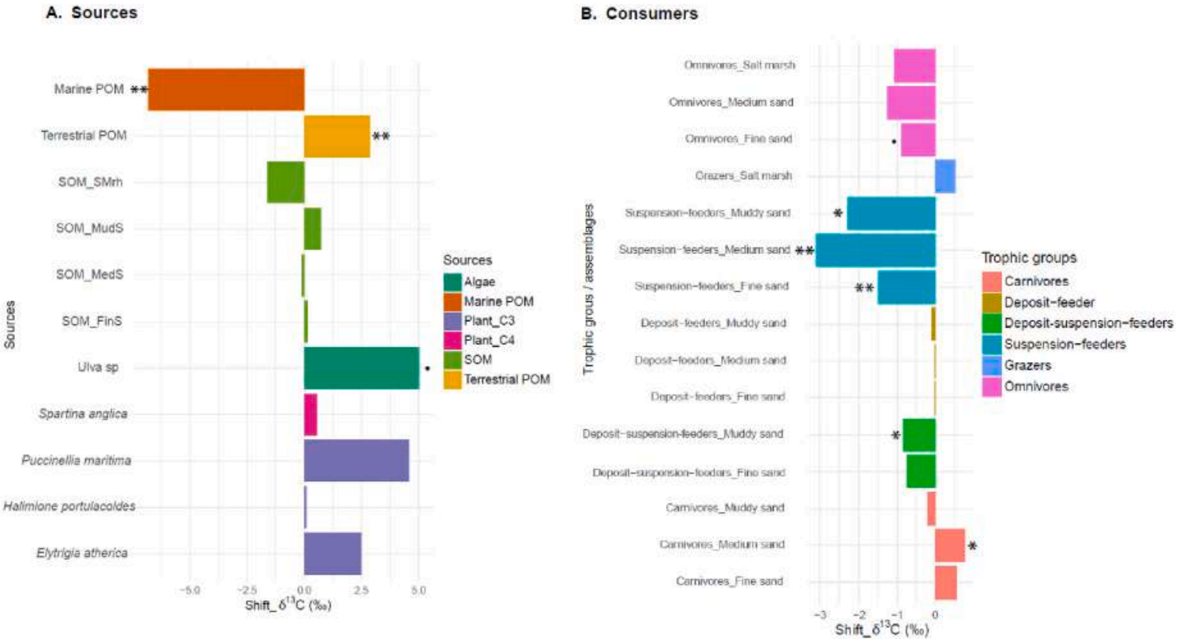

Fig. 3. Temporal variation of $\delta^{13}C$ between March and September. Sources (A): main primary food sources are represented by colors: marine POM, terrestrial POM, SOM for the four assemblages (Salt marsh creeks (SOM_SMrh), and muddy (SOM_MudS), fine (SOM_FinS), and medium (SOM_MedS) sands), *Ulva* sp, and the four main C3 (*Puccinellia maritima, Halimione portulacoides, Elytrigia atherica*) and C4 salt marsh plants (*Spartina anglica*). Consumers (B): consumers are represented by colors and temporal shift in $\delta^{13}C$ values is provided for each habitat. Mean significant differences tested with Permutation Student's t-tests are summarized as *** ($P < 0.001$), ** ($P < 0.01$), * ($P < 0.05$). Mean differences near the significant level are also represented (·, $P < 0.1$).

Table 1
Values of $\delta^{13}C$ and $\delta^{15}N$ (mean ± sd) of the various food sources collected in March and September 2019. n: number of samples. Marine and terrestrial particulate organic matter (POM_SEA, POM_TER). Sedimentary organic matter in the different assemblages from salt marsh to muddy, fine and medium sands (SOM_SMrh, SOM_MudS, SOM_FinS, SOM_MedS).

Sources	Types	March			September		
		n	$\delta^{13}C$	$\delta^{15}N$	n	$\delta^{13}C$	$\delta^{15}N$
Atriplex hastata	Plant C3				3	−23.92 ± 0.68	10.56 ± 0.36
Beta maritima	Plant C3				3	−26.66 ± 0.11	10.74 ± 0.19
Elytrigia atherica	Plant C3	3	−30.13 ± 2.28	7.50 ± 0.62	3	−27.63 ± 0.29	5.77 ± 0.08
Cochlaearia anglica	Plant C3	3	−27.90 ± 0.60	7.51 ± 0.97	3	−25.80 ± 1.59	7.40 ± 0.86
Halimione portulacoides	Plant C3	3	−25.61 ± 1.08	12.98 ± 1.74	3	−25.53 ± 0.63	11.94 ± 0.44
Puccinellia maritima	Plant C3	3	−28.20 ± 0.23	8.55 ± 0.19	3	−23.63 ± 0.79	8.26 ± 0.14
Salicornia sp.	Plant C3	3	−25.98 ± 0.23	12.08 ± 0.27	3	−26.96 ± 1.50	9.25 ± 0.47
Sueda maritima	Plant C3	3	−26.80 ± 0.37	9.67 ± 1.15			
Spartina anglica	Plant C4	3	−12.89 ± 0.20	10,00 ± 1.28	3	−12.36 ± 0.16	11.11 ± 0.21
Ulva spp.	Algae	3	−19.41 ± 0.52	7.30 ± 1.03	3	−14.40 ± 0.27	11.42 ± 0.26
POM_TER	Terrestrial POM	15	−30.20 ± 0.98	7.90 ± 1.71	15	−27.34 ± 5.06	8.20 ± 2.20
POM_SEA	Marine POM	6	−15.86 ± 0.99	7.65 ± 0.27	5	−22.68 ± 1.73	4.26 ± 1.59
SOM_INTER_FinS	SOM	10	−19.64 ± 1.19	8.13 ± 0.68	10	−19.49 ± 1.31	8.20 ± 0.56
SOM_INTER_MedS	SOM	4	−20.78 ± 0.61	7.58 ± 0.54	6	−20.87 ± 0.64	8.25 ± 0.64
SOM_INTER_MudS	SOM	5	−21.97 ± 2.44	7.97 ± 0.90	7	−21.24 ± 2.79	8.39 ± 0.70
SOM_SMrh	SOM	2	−22.93 ± 0.69	8.25 ± 0.49	3	−24.54 ± 0.12	7.14 ± 0.25
Microphythobenthos	MPB (mean June 2019 and July 2020)	5	−17.50 ± 0.83	8.65 ± 0.63	5	−17.50 ± 0.83	8.65 ± 0.63

4. Discussion

4.1. Spatio-temporal patterns as a potential alternative to track trophic links

Consumers and their food sources stable isotope compositions are commonly used to determine the composition diet. The use of isotopic mixing models is a way to convert isotopic data into estimates of food source contributions from the various components of a consumer's diet (Phillips et al., 2014). The use of source pools characterized by distinct isotope values allows for the full exploitation of the mixing model analysis. Inversely, a multiplicity of sources or strong similarity in their stable isotope composition may decrease the relevance of mixing models in answering questions about trophic relationships (Fry, 2013; Layman et al., 2012). When mixing models are not correctly applied or when the data sets do not allow their proper application (Fry, 2013; Phillips et al., 2014), conclusions may lead to an incomplete picture. It may mislead the description of functioning and dynamics with potential overstating conservation progress or misdirecting conservation actions.

The source pools described in this study were highly diversified and characterised by strong overlap and high dynamics, potentially limiting the relevance of mixing models and claiming for an alternative approach. The present study therefore focused on stable isotope trajectories of sources and consumers to infer trophic relationships. Spatial and temporal covariation of stable isotope composition between sources and consumers has previously proven to be very useful in identifying the

Table 2

Values of $\delta^{13}C$ and $\delta^{15}N$ (mean ± sd) of consumers in March and September. n: number of samples.

Species	Trophic groups	March			September		
		n	$\delta^{13}C$	$\delta^{15}N$	*n*	$\delta^{13}C$	$\delta^{15}N$
Euspira catena	Carnivores	2	−16.50 ± 0.15	11.79 ± 1.11			
Nephtys hombergii	Carnivores	17	−14.68 ± 1.40	13.39 ± 0.68	10	−14.71 ± 0.92	13.19 ± 0.65
Sigalion mathildae	Carnivores	9	−15.56 ± 0.76	13.46 ± 0.73	9	−15.09 ± 0.50	13.81 ± 0.53
Tritia reticulata	Carnivores	6	−16.40 ± 0.65	13.08 ± 0.17	2	−16.56 ± 0.07	12.88 ± 0.36
Arenicola marina	Deposit-feeders	4	−13.91 ± 1.38	11.88 ± 0.78	4	−14.50 ± 0.44	12.81 ± 0.48
Bathyporeia sarsi	Deposit-feeders	7	−13.41 ± 1.03	8.81 ± 0.50			
Bathyporeia pilosa	Deposit-feeders				1	−11.88	9.09
Corophium arenarium	Deposit-feeders	5	−15.39 ± 1.70	9.43 ± 0.59	3	−13.60 ± 0.21	9.11 ± 1.49
Maldanidae sp.	Deposit-feeders				1	−14.74	10.10
Peringia ulvae	Deposit-feeders	2	−12.58 ± 0.94	9.19 ± 0.50	3	−14.35 ± 0.38	9.37 ± 0.26
Scoloplos armiger	Deposit-feeders	9	−16.46 ± 0.84	11.73 ± 0.86	6	−15.95 ± 0.70	12.00 ± 0.53
Urothoe poseidonis	Deposit-feeders	4	−12.90 ± 1.17	11.96 ± 0.62	1	−13.57	11.93±
Limecola balthica	Deposit-Suspension-feeders	7	−13.91 ± 0.46	11.79 ± 0.46	4	−14.36 ± 0.20	12.28 ± 0.29
Macomangulus tenuis	Deposit-Suspension-feeders	4	−14.05 ± 0.62	11.13 ± 0.44	5	−14.84 ± 0.55	11.31 ± 0.38
Scrobicularia plana	Deposit-Suspension-feeders	3	−14.46 ± 0.36	11.17 ± 0.55	4	−17.37 ± 1.62	12.63 ± 1.28
Cerastoderma edule	Suspension-feeders	19	−14.50 ± 0.54	10.98 ± 0.44	16	−16.23 ± 0.60	11.40 ± 0.52
Pecten maximus	Suspension-feeders	2	−16.09 ± 0.07	9.27 ± 0.08	2	−18.77 ± 0.79	9.50 ± 0.15
Donax vittatus	Suspension-feeders				1	−18.14	10.16
Mactra stultorum	Suspension-feeders				3	−18.63 ± 0.20	10.99 ± 0.11
Crepidula fornicata	Suspension-feeders				1	−20.17	9.29
Orchestia gammarellus	Grazers	2	−21.92 ± 0.30	10.76 ± 0.49	2	−21.39 ± 0.93	11.51 ± 0.23
Hediste diversicolor	Omnivores	3	−16.05 ± 1.41	13.10 ± 0.12	2	−18.77 ± 0.34	14.37 ± 0.29
Acrocnida spatulispina	Omnivores	7	−16.70 ± 0.38	12.60 ± 1.06	8	−17.66 ± 1.10	12.14 ± 1.07

Table 3

Food web structure properties at site (whole bay) and assemblage scale in March and September. $\delta^{13}C$_rg and $\delta^{15}N$_rg: range in $\delta^{13}C$ and $\delta^{15}N$ values (‰). $\delta^{13}C$_ctr and $\delta^{15}N$_ctr: $\delta^{13}C$ and $\delta^{15}N$ centroids values (‰). CD: Mean distance to centroid. NND: Mean of the Euclidean distances to each species to the $\delta^{13}C$ and $\delta^{15}N$ centroids. SDNND: Standard deviation of nearest neighbor distance. TA: Total area. IDiv: Isotopic divergence. IEve: Isotopic Evenness.

		$\delta^{13}C$_rg	$\delta^{15}N$_rg	$\delta^{13}C$_ctr	$\delta^{15}N$_ctr	CD	NND	SDNND	TA	IDiv	IEve
March	**Whole bay**	10.92	6.31	−15.30	11.41	1.99	0.284	0.24	43.46	0.73	0.61
	Muddy sand	5.32	6.31	−13.93	11.21	1.58	0.416	0.36	21.92	0.67	0.67
	Fine sand	5.59	5.71	−15.01	11.79	1.76	0.34	0.39	23.16	0.82	0.81
	Medium sand	2.74	4.87	−16.41	12.07	1.40	0.492	0.27	9.12	0.66	0.52
	Salt marsh	4.80	3.67	−18.97	11.15	2.57	2.25	1.66	9.59	0.91	0.87
September	**Whole bay**	10.16	6.74	−16.25	11.42	2.02	0.36	0.32	46.64	0.73	0.80
	Muddy sand	5.58	5.95	−14.46	11.28	1.80	0.53	0.42	16.25	0.78	0.73
	Fine sand	5.40	4.31	−15.08	12.16	1.50	0.36	0.25	15.08	0.74	0.90
	Medium sand	5.21	5.09	−17.34	11.38	1.91	0.622	0.38	15.80	0.73	0.89
	Salt marsh	3.96	3.23	−19.54	13.11	1.71	0.92	0.39	3.79	0.77	0.43

sources at the base of food webs (Leclerc et al., 2013; Melville and Connolly, 2003; Vanderklift and Wernberg, 2010).

4.2. Saltmarsh influence on the sandflat food web

The productivity of salt marshes during summer is high, reaching 30 tonnes of dry matter per ha per year (Lefeuvre et al., 2000). The outwelling hypothesis states that salt marshes export organic matter, dissolved carbon and nutrients to tidal adjacent habitats from tidal channels to estuaries and coastal ocean (Odum, 1968; Teal, 1962). The influence of salt marsh vegetation on food webs is highly variable, ranging from almost insignificant (Christianen et al., 2017), to very important, and reflected in the stable isotope composition of marshes inhabiting consumers (Nordström et al., 2014; Riera et al., 1999), or adjacent habitats assemblages (Conway-Cranos et al., 2015).

In the study area, salt marshes are characterised by good conservation status but only cover a limited area [125 ha, Sturbois and Bioret (2019)], compared to other comparable coastal bays of the French Atlantic coast, such as the bay of Mont-Saint-Michel [4000 ha, Lafage et al. (2021)], the bay of Seine [1200 ha, Lafage et al., 2021)], or the bay of Aiguillon [1100 ha, Joyeux et al. (2017)]. Trophic connectivity relies on the relative proportion of allochthonous and autochthonous resources rather than only on asymmetric production among habitats, especially when the nutritional value of allochthonous sources (i.e. salt marsh detritus) is lower than local, fresh sources (Mann, 1982). Differences in the proportion of resources result from interaction among productivity, permeability, and transport vectors that lead to many states of trophic connectivity (Domingos and Lana, 2017).

The influence of C3 plants was limited to the grazer *O. gammarellus*, the omnivore *H. diversicolor* and the deposit-suspension-feeder *Scrobicularia plana* inhabiting the muddy salt marsh creeks. *O. gammarellus* is a known consumer of salt marsh detritus [*H. portulacoides* in particular (Joyeux et al., 2017; Laffaille et al., 2001)]. *H. diversicolor* is a very generalistic omnivore able to: feed on sediment, microphytobenthos, macroalgae, detritus and plant material; predates small invertebrates; suspension feed by secreting and using a mucobag as a filter when drawing down particles in its burrow; and garden by sprouting seeds (Durou et al., 2007; Scaps, 2002; Zhu et al., 2016).

Only a few evidences have been reported in the use of salt marsh vegetation in the study area: juveniles of *Dicentrachus labrax* were proven to feed on ^{13}C-depleted preys inhabiting salt marshes (Sturbois et al., 2016), or *Branta bernicla*, on *Puccinellia maritima* (Ponsero et al., 2009b). As no benthic species displayed such a ^{13}C depletion, which would be consistent with the significant assimilation of such sources further on the shore, no evidence was found that salt marsh plants support the benthic food webs in unvegetated sandy habitats. The influence of the C4 plant *S. anglica* was also discarded according to its ^{13}C enriched values. The capacity of salt marsh plants to fuel intertidal

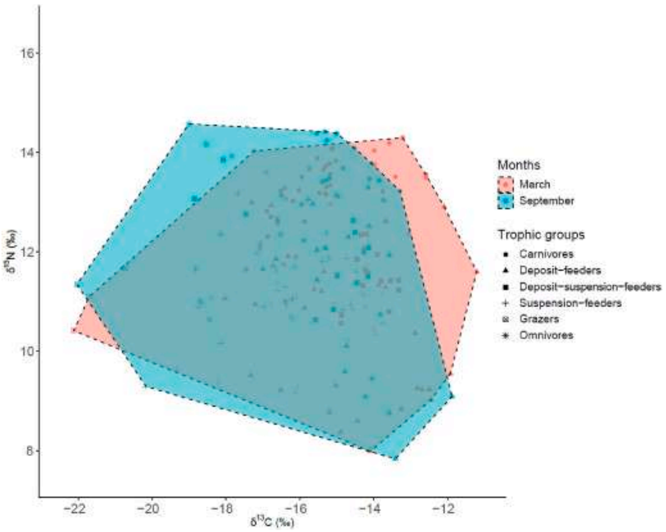

Fig. 4. δ^{13}C and δ^{15}N of the sampled species in March (red) and September (green) in intertidal soft-bottom sediments of the bay of Saint-Brieuc. δ^{13}C and δ^{15}N values are plotted for each individual consumer. Shapes represent trophic groups. Isotopic niche (total area) is represented by convex hull polygons for March (green) and September (red).

benthic habitat seems limited, especially for macrofauna species which exhibit limited mobility in a large flat characterised by megatidal and dispersive conditions.

Consequently, we believe that salt marsh organic matter is either transferred into coastal food webs through highly mobile consumers (fish, shorebirds), thereby overpassing the intertidal benthic food web, or exported over spatial scales which exceed the bay, contributing to the overall detrital pool. It results in a strong dilution and the impossibility to assess its influence through stable isotopes. In further studies, fatty acid analysis might be useful in this regard.

Salt marsh muddy creeks are characterized by a large production of benthic diatoms. Mullets (*Chelon* spp.) feeding on biofilm and associated meiofauna contribute to the exportation pathway of the biofilm (Carpentier et al., 2014). Regularly reach by the tide at high tide, salt marshes are submerged when water height exceeds 10.70 m, which represents 45% of the tide cycles (76% for associated creeks) (Sturbois et al., 2016). Megatidal conditions associated with strong currents may also contribute to the effective resuspension of sediments and microphytobenthos (personal observation), exporting benthic diatoms in the water column and further away in the bay. The importance of resuspended microphytobenthos as a major food source for macrobenthos in mudflat environments is a long known mechanism (De Jonge and Van Beuselom, 1992; Riera and Richard, 1996).

4.3. Sources supporting the food web: limited influence of seasonal *Ulva* spp. Blooms

The year 2019 was characterised by important *Ulva* spp. biomass which progressively accumulated during summer (Supplementary materials, Appendix A). In the close bay of Douarnenez, Quillien et al. (2016) found evidence of a direct consumption of *Ulva* spp. fragments by a few species (*Owenia fusiformis, Acrocnida spatulispina*), and an indirect influence on the whole food web through the isotopic modification of SOM and POM due to *Ulva* spp. presence. On the western coast of Korea, Park et al. (2016) showed that blooming green macroalgae support an intertidal macrobenthic food web with a certain variability depending on both feeding strategies of consumers and resource availability. From field experiments with varying macroalgal mat thickness (0.5, 1.5 and 4 cm) over eight weeks, Green and Fong (2016) quantified the effects on macrofauna on a Californian lagoon mudflat. They found that the predominant mechanism triggering negative effects on macrofauna for the highest macroalgal biomasses was the development of anoxic conditions. Sulfide accumulation for the 4 cm treatment reduced ecosystem functioning, favouring subsurface deposit feeding such as capitellids.

Ulva spp. was ^{13}C- and ^{15}N-enriched in September compared to March, which provided an opportunity to investigate the potential role of *Ulva* spp. in the food web. Our results reveal that the influence of *Ulva* spp. on the entire food web can be considered as low, regarding the limited area concerned by stranded *Ulva* spp. in February (12 ha), and the absence of such isotopic enrichment at the community scale in September. For example, *A. spatulispina* sampled in September were ^{13}C-depleted, suggesting no *Ulva* spp. influence and contrasting with the results of Quillien et al. (2016). The moderate ^{13}C- and ^{15}N-enrichment observed for carnivores may reveal accidental ingestion of *Ulva* spp. fragments when hunting and feeding on preys, but the low magnitude of the trophic trajectory suggest a very limited influence. Such a low

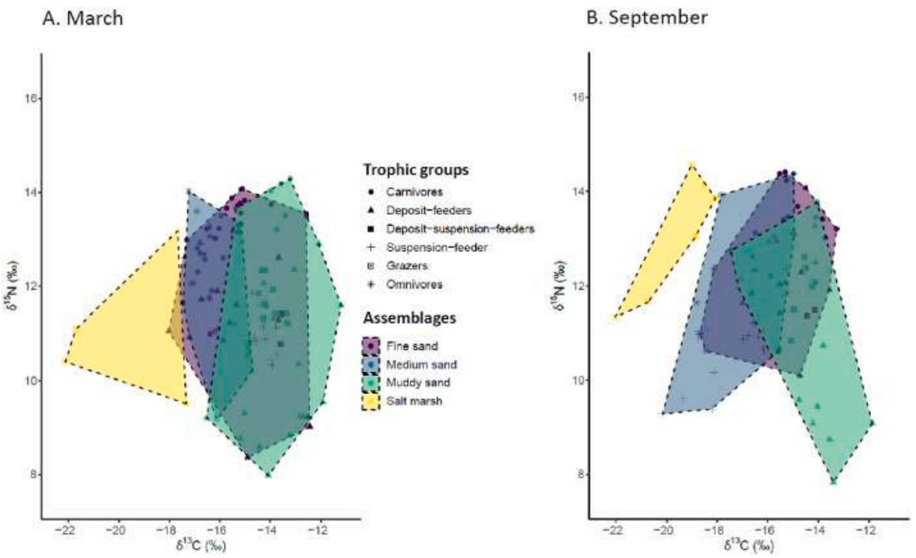

Fig. 5. δ^{13}C and δ^{15}N stable isotope composition of the sampled species in March (A) and September (B) in the four assemblages. δ^{13}C and δ^{15}N are plotted for each individual of consumers. Shapes represent trophic groups. Isotopic niche (Total area) is represented by convex hull polygons for each habitat: salt marsh creeks (yellow), muddy sands (green), fine sands (purple) and medium sands (blue).

Table 4
$\delta^{13}C$ and $\delta^{15}N$ (mean ± sd) of trophic groups in March and September. n: number of samples.

	Assemblages	March			September			Trajectory metrics	
Trophic groups		**n**	**$\delta^{13}C$**	**$\delta^{15}N$**	**N**	**$\delta^{13}C$**	**$\delta^{15}N$**	**N. changes**	**Angle α**
Grazers	Salt marsh creeks	2	−21.92 ± 0.30	10.75 ± 0.49	2	−21.39 ± 0.93	11.51 ± 0.23	0.92	35.13
Omnivores	Salt marsh creeks	1	−17.68±	13.18	2	−18.77 ± 0.34	14.37 ± 0.29	1.61	317.46
Carnivores	Muddy sands	6	−13.88 ± 0.77	13.82 ± 0.42	2	−14.09 ± 0.04	13.62 ± 0.22	0.28	225.93
Deposit-feeders	Muddy sands	16	−13.67 ± 1.44	10.16 ± 1.53	9	−13.78 ± 0.81	10.04 ± 1.81	0.16	221.11
Deposit-Suspension-feeders	Muddy sands	12	−14.15 ± 0.50	11.53 ± 0.56	8	−15.00 ± 1.06	11.97 ± 0.65	0.95	297.24
Suspension-feeders	Muddy sands	6	−14.16 ± 0.26	11.13 ± 0.53	3	−16.44 ± 0.82	11.87 ± 0.22	2.40	287.95
Carnivores	Fine sands	19	−15.25 ± 1.18	13.40 ± 0.67	10	−14.69 ± 0.80	13.74 ± 0.50	0.66	58.44
Deposit-feeders	Fine sands	11	−14.99 ± 1.76	10.81 ± 1.34	8	−15.01 ± 0.69	12.00 ± 0.94	1.19	359.18
Deposit-Suspension-feeders	Fine sands	2	−13.57 ± 0.02	11.10 ± 0.44	2	−14.31 ± 0.21	11.44 ± 0.09	0.81	294.95
Suspension-feeders	Fine sands	11	−14.61 ± 0.61	10.98 ± 0.37	12	−16.11 ± 0.53	11.32 ± 0.52	1.54	283.07
Omnivores	Fine sands	5	−16.55 ± 0.33	12.12 ± 0.79	6	−17.44 ± 1.17	11.92 ± 0.92	0.91	257.49
Carnivores	Medium sands	9	−16.43 ± 0.69	12.60 ± 0.60	9	−15.66 ± 0.61	13.04 ± 0.69	0.90	60.48
Deposit-feeders	Medium sands	3	−16.80 ± 0.40	12.38 ± 1.26	2	−16.82 ± 0.25	11.75 ± 0.14	0.63	181.99
Suspension-feeders	Medium sands	4	−15.50 ± 0.70	9.91 ± 0.85	8	−18.59 ± 0.93	10.29 ± 0.77	3.12	277.06
Omnivores	Medium sands	2	−17.08 ± 0.23	13.81 ± 0.30	2	−18.33 ± 0.69	12.79 ± 1.61	1.62	230.79

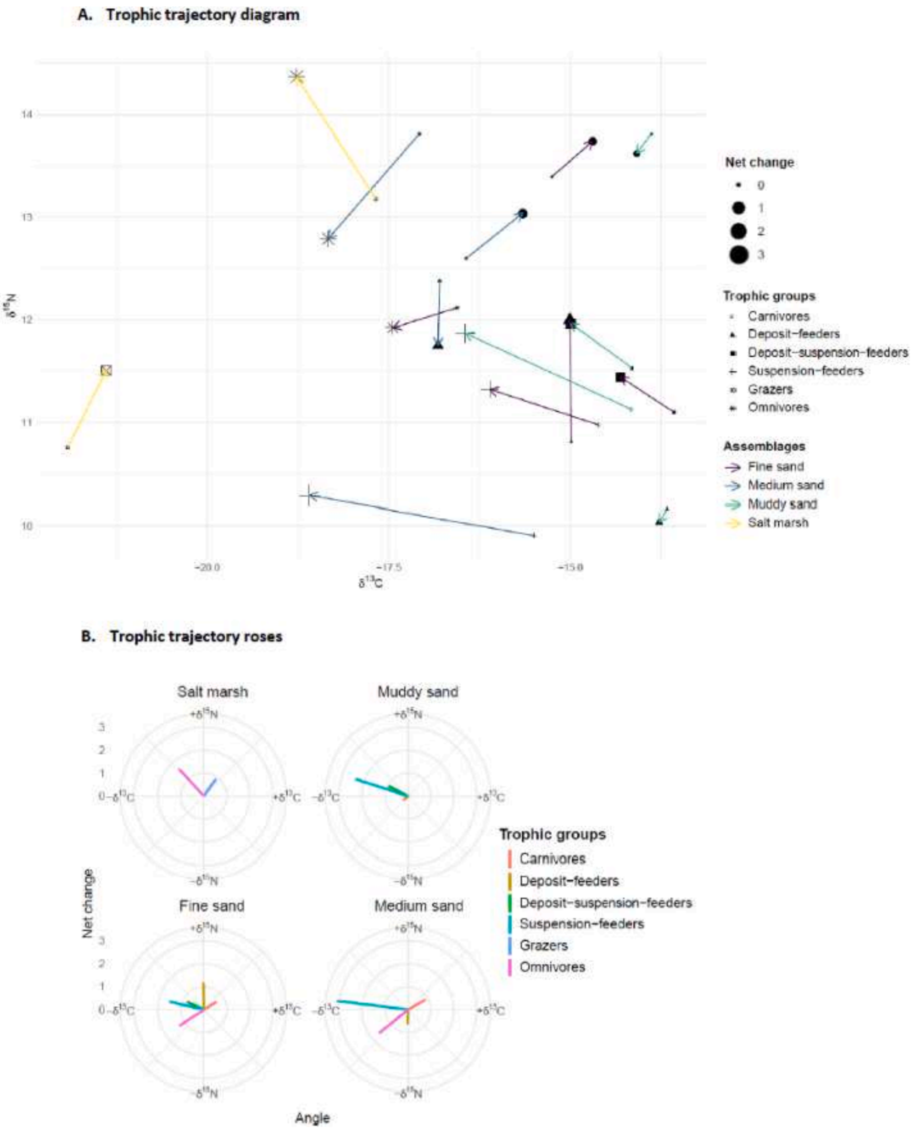

Fig. 6. Temporal trajectories of trophic groups between March and September. Stable Trophic trajectory diagram (A): Arrows represent trophic trajectory in the $\delta^{13}C/\delta^{15}N$ space between March and September for each trophic group in each assemblage (color). Length of arrows and size of dots corresponds to the net change (Euclidean distance) and inform about the magnitude of change. Different symbols correspond to trophic groups. Trophic trajectory roses (B): Angles α and net changes are represented in trophic trajectory rose for each trophic group (color) in each habitat (panel). Angle α values (0–360°) represent the nature of change in the δ-space (0–90°: + $\delta^{13}C$ and + $\delta^{15}N$; 90–180°: + $\delta^{13}C$ and - $\delta^{15}N$; 180–270°: $\delta^{13}C$ and - $\delta^{15}N$; 270°–360°: $\delta^{13}C$ and + $\delta^{15}N$).

influence of *Ulva* spp. in the diet and stable isotope composition of marine crustaceans has also been demonstrated by experimental (Karez et al., 2000; Salathé and Riera, 2012) and *in situ* (Adin and Riera, 2003) studies. The contrast with the results obtained by Quillien et al. (2016), Park et al. (2016) and Green and Fong (2016), may be explained by the mega-tidal conditions which characterize the study area. In the bay of Saint-Brieuc, tides are a strong driving factor. Daily resuspension and redistribution of algal mats and limited long-term static accumulation of algae make potential anoxic episodes restricted to very limited zones (i.e. beaches on the upper shore), where *Ulva* spp. are all the more collected by local authorities as part of precautionary sanitary measures (e.g. 12 682 tons has been collected in 2021). This phenomenon potentially limits the integration of *Ulva* spp. in the food web. Furthermore, the bay of Saint-Brieuc shelters benthic producers on muddy and muddy sand habitats, which contrasts from the sandy beaches located in the bay of Douarnenez.

Marine POM and MPB displayed stable isotope compositions which were the most likely to represent the actual basis of food webs within the different habitats, regarding $\delta^{13}C$ ranges displayed by the benthic communities. Marine POM was the only source exhibiting a significant ^{13}C-depletion between March and September, which was also observed for suspension-feeders from all habitats, as well as by mixed deposit/suspension-feeders and some omnivores. In contrast, the low shift in $\delta^{13}C$ values of deposit-feeders between March and September suggests a low temporal variability in the composition of benthic producers. This is also in accordance with the low shift observed for SOM values, especially in fine and medium sands. Deposit-feeders are often quite, or even very, selective with regard to the total SOM (Levinton, 1989), which is a composite source by definition, so they only use a portion of it, and benthic diatoms represent a particularly easy-to-use source with a high food quality within the SOM.

Christianen et al. (2017) reported that energy in the Wadden sea ecosystem is mainly provided by locally produced organic matter and in a lesser extent by pelagic producers. Such contribution of MPB has also been highlighted, at lower geographic scales in salt marsh consumers in the Mont Saint-Michel bay (Créach et al., 1997), 1997), and for cockles in Marennes-Oléron Bay (Kang et al., 1999). Other intertidal studies also revealed the fuelling of higher trophic levels by MPB and pelagic primary production (van Oevelen et al., 2006). In the bay of Saint-Brieuc, where muddy habitats are limited (64 ha), our results suggest that the food web is mainly fuelled by pelagic producers and, to a lesser extent, by benthic producers. However, salt marsh muddy creeks could also support a part of the MPB production, in addition with muddy sands. Such assumption will require further investigations to be accurately quantified (Méléder et al., 2020; Morelle et al., 2020).

These overall considerations and assumptions do not exclude contributions from other food sources at finer local scale in this highly dynamic system as already observed in the Roscoff Aber bay (Ouisse et al., 2011), in the Wadden Sea (Christianen et al., 2017), or in this study for the macrofauna inhabiting salt marsh creeks.

4.4. *Spatial patterns in benthic-pelagic coupling*

Large scale spatial heterogeneity in the carbon stable isotope composition of consumers has been observed by Christianen et al. (2017) in the Wadden Sea for species that forage either on benthic or pelagic sources. In a large part of the Wadden sea, a dominant use of pelagic food sources was observed for the common cockle suspension-feeder *Cerastoderma edule,* while the use of benthic producer was suggested for some spatially limited areas. Conversely, for the Baltic clam *Limecola balthica*, which is a facultative deposit and suspension-feeder, $\delta^{13}C$ indicated a high benthic contribution to its diet in most of the flat, contrasting with a dominant pelagic contribution in some limited areas.

In our study, spatial patterns have been revealed at the scale of trophic groups, with higher $\delta^{13}C$ values for suspension-feeders, deposit-suspension-feeders and carnivores in muddy and fine sands compared to medium sands. They were maintained between March and September and confirmed by the correlation between $\delta^{13}C$ values and emersion time for some trophic groups. In addition, some contrasted temporal trophic trajectories among habitat were evidenced. Trajectory metrics (net changes and angle α) revealed a congruent negative shift in marine POM and suspension-feeders $\delta^{13}C$ values between March and September. However, while direction in the δ space was similar suspension-feeders at assemblage scale, differences were observed in net changes values. This contrasting pattern in the magnitude of change suggests a decreasing influence of pelagic sources in the diet of suspension-feeders from muddy and sandy habitats compared to medium sands. Deposit-suspension-feeders showed similar direction but lower net changes than suspension-feeders, confirming both their higher dependence to benthic primary producers and their ability to feed on pelagic producers. The low variability of deposit-feeder $\delta^{13}C$ values was in accordance with the temporal stability observed for sedimentary organic matter in medium sands and suggested a low temporal variability in the stable isotope composition of MPB.

Lower net changes exhibited by suspension-feeders in muddy and fine sand habitats suggest a major resuspension of MPB in the water column as already shown in different intertidal areas (De Jonge and Van Beuselom, 1992; Liénart et al., 2017; Riera and Richard, 1996; Sauriau and Kang, 2000; Underwood and Chapman, 1998). Suspended particulate organic matter corresponds to a dynamic mixture of pelagic and benthic algae due to the resuspension of MPB. Microphytobenthos growth is favoured in muddy and muddy sands habitats (Morelle et al., 2020), and its spatio-temporal distribution is driven by highly variable physical and biological factors (Méléder et al., 2020). MPB resuspension is known to be favoured by hydrodynamics and bioturbation activities of some macrofauna species such as *C. edule* (Rakotomalala et al., 2015). The bay of Saint-Brieuc is characterized by megatidal conditions and high density of *C. edule*, reaching 2000 ind.m^2 in muddy sands. MPB can be easily resuspended at relatively low current velocities (~10 cm s−1) on silty sediment (Blanchard et al., 1997; Kang et al., 2015; Ubertini et al., 2015). Resuspension is increased by the coverage and the important dynamics of tidal channels (Sturbois et al., 2021a), which may contribute to organic matter fluxes. Emersion time regulates the trophic availability of MPB for some consumers (suspension and surface deposit feeders). Hydrodynamics and tides favour the trophic connectivity between muddy sand and fine sand habitats located at lower levels through the exportation of microphytobenthos in the water column. However, the exportation of the tidally resuspended MPB seems limited to fine sand habitats and suggests spatial contrast in benthic-pelagic coupling. De Jonge and Van Beuselom (1992) and Riera and Richard (1996) found similar results, demonstrating that the influence of the MPB exported in the water column is limited to close adjacent habitats.

4.5. *Small spatial scale variability in food web structure*

Despite a slight increase in IEve in relation to the ^{13}C-depletion of suspension and deposit-suspension-feeders, the stability of structural properties and the strong overlap observed at site scale between March and September highlight the temporal stability of the system. Dissimilarity among assemblages was strongly influenced by the $\delta^{13}C$ decreasing gradient of consumers from muddy to fine and medium sands assemblages, while no such pattern was observed for $\delta^{15}N$. This gradient illustrates the spatial variability in the benthic pelagic coupling, with a higher influence of MPB in the upper level compared to low shore habitats. The decrease in the similarity between the low levels of the muddy and medium sands observed between March and September (in relation with the trophic trajectory of suspension-feeders in medium sands) highlights the two main energy pathways supported by pelagic and benthic producers.

Quillien et al. (2016) showed an overall simplification of community-wide food web structure and functioning in sandy beach harbouring green tides. They notably highlighted a significant community-wide shift in $\delta^{13}C$ over time progressively splitting up into two distinct isotopic niches. A linear arrangement of trophic web components indicated a single carbon pathway where *Ulva* spp. mats were present on the shore. No such simplification was observed at site or assemblages scale in the study area. Conversely, the selected indices of trophic structure and functioning were stable or increased during the year. Assemblages still overlapped over time and no overall ^{13}C

enrichment of consumers was observed in accordance with $\delta^{13}C$ composition of *Ulva.* Overall, the temporal consistency observed in the food web structure in the different habitats confirm that the summer *Ulva* bloom did not play a major role in the trophic functioning off the bay of Saint-Brieuc.

4.6. Implications of food web dynamics for sampling strategy

The trajectories of trophic groups can occurs, notably: 1) if shift occurs in stable isotope compositions of the consumed sources; 2) if they change their diets (i.e. use different sources depending on the availability of these sources or the same sources in different proportions); 3) if within groups the dominant species vary and as species within groups have different diets, this inevitably leads to a group average isotopic deviation (in this case some species may have faster growth rates and different tissue turnover and hence an impact on the average of the trophic group); and 4) isotopic variations due to ontogenetic variations within a species.

In the Wadden sea, Christianen et al. (2017) suggested that different factors are potentially involved in the spatial heterogeneity of food web $\delta^{13}C$ values: spatial variability in benthic production; differential consumption of benthic and pelagic producers; and/or the differential contribution of resuspended benthic primary producers for consumers feeding entirely on pelagic producers. Fine scale variations in the local environment may also influence food web properties (Ouisse et al., 2011). Our study highlights these spatio-temporal variations in the stable isotope compositions of sources and consumers. The different degrees of trophic connectivity with a low influence of salt marshes and variations in benthic-pelagic coupling in relation with the distribution and the resuspension of MPB confirm the importance of sampling food webs at large spatial and temporal scales for a better integration of dynamics.

Similarly, differences in the influence of *Ulva* spp. on benthic food web properties between the Bay of Saint-Brieuc and the sandy beaches of Douarnenez indicate that effects on ecosystems are not spatially consistent at regional scale, and claims for local studies integrating local physical and biological driven factors.

4.7. Food webs studies: a baseline for conservation process

As the first attempt to characterize intertidal benthic food webs of the bay of Saint-Brieuc, this study provides valuable information for managers about the functioning and energy pathways supporting the specific benthic communities. First, the influence of salt-marsh plants on benthic macrofauna is limited. Such result remains fundamental for the consideration of trophic functioning at larger scale in the bay, but does not question the value of salt marsh already shown for juveniles of some fish species (Carpentier et al., 2014; Joyeux et al., 2017; Lafage et al., 2021; Sturbois et al., 2016) or birds (Ponsero et al., 2009b, 2019). Second, the seasonal increase in biomass of *Ulva* spp. does not influence the functioning of the local benthic food webs. This result was unexpected given that two local bird species, *Mareca penelope* and *Branta bernicla*, feed on this algae (Ponsero et al., 2009b). These results pointed that green tides may represent a trophic cul-de-sac for the benthic macrofauna inhabiting the bay of Saint-Brieuc.

Users and stakeholders do not give due consideration to muddy habitats and regularly ask for managements in these habitats (sands deposits, harbour management or dredging). As shown by our results, they now have to consider that MPB partially supports the food web in muddy sands, and that resuspended MPB is exported in fine sands habitat. This process may also be supported by benthic producers of the salt marsh muddy creeks.

Despite all habitats are used by birds, muddy and fine sand assemblages are the most available due to low emersion time of medium sands (Ponsero et al., 2016; Sturbois et al., 2015). Our study highlights that waders trophic resource (i.e. benthic invertebrates) is supported by pelagic and benthic producers with a decreasing inshore/offshore gradient of MPB influence. The bay of Saint-Brieuc is characterized by *C. edule* fishing grounds exploited by professional and recreational fishers and muddy habitats, where young cockles can feed on MPB (Sauriau and Kang, 2000), are known to be favourable areas for settlement (Ponsero et al., 2009a).

In this context, governance processes of the bay of Saint-Brieuc must integrates the conservation of muddy habitats to inform and sensitize stakeholders, users and managers about the importance of muddy habitats for waders populations and fishing activities, and to avoid cascading effect further up the food webs leading to potential ecological and economical consequences.

5. Conclusion

Results highlighted that the benthic trophic network is, most likely, based on phytoplankton, microphytobenthos and SOM. The trophic connectivity between salt marsh and benthic habitats within the bay was limited to some macrofauna species inhabiting muddy creeks within the salt marsh. Unexpectedly, the influence of *Ulva* spp. in the trophic functioning of the different assemblages appeared quite limited. Spatial patterns illustrates the constancy of the spatial variability in the benthic pelagic coupling, with a higher influence of microphytobenthos in the upper level compared to low shore assemblages. This first attempt to characterize intertidal benthic food web constitutes a relevant baseline for the conservation of the bay of Saint-Brieuc where a National nature reserve has been created in 1998 for the conservation of overwintering birds. The spatio-temporal patterns of the benthic food web also confirms the importance to consider food web variability at spatial and temporal scales from sampling designs to data analysis. The ability of the stable isotope trajectory analysis framework to highlight spatio-temporal patterns was also demonstrated.

CrediT authorship contribution statement

Anthony Sturbois: Conceptualization, Methodology, Validation, Formal analysis, Data curation, Writing - original draft, Visualization, Project administration, Funding acquisition, Investigation. **Pascal Riera:** Conceptualization, Methodology, Validation, Writing -review & editing, Investigation, Supervision. **Nicolas Desroy:** Conceptualization, Methodology, Validation, Writing -review & editing, Investigation, Supervision. **Titouan Brébant:** Investigation, Writing - review & editing. **Alexandre Carpentier:** Methodology, Validation, Writing - review & editing. **A. Ponsero:** Writing -review & editing. **Gauthier Schaal:** Conceptualization, Methodology, Validation, Writing -review & editing, Investigation, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2022.105572.

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ECOLOGICAL TRAJECTORIES: METHODS AND APPLICATIONS.
A case study on the conservation and taxonomic/functional/trophic dynamics of soft bottom benthic assemblages in the bay of Saint-Brieuc (Western English Channel, France).

Mots clés: Ecological Trajectory Analysis, Metrics, Data visualisation, Dynamics, Temporal changes, Conservation, Bay of Saint-Brieuc.

Abstract: The objective of this thesis was to analyse taxonomic and functional dynamics of soft bottom benthic assemblages in the bay of Saint-Brieuc (Western English Channel, France) during the last decades, and to track spatio-temporal patterns in the intertidal benthic food web. To this end, considering that evolution and functioning of intertidal and subtidal benthic assemblages in the bay of Saint-Brieuc did resonate into broader ecological questions relative to the stability and variability of ecosystems, methodological developments in the field of trajectory analyses have been proposed to quantify, qualify and visualise ecological dynamics in different fields of ecology. These developments, resulting from cross-pollination between marine and terrestrial ecology fields, served local analysis in marine habitats and underlined contrasted results in intertidal and subtidal areas. In the intertidal zone, observed changes mainly reflect random population changes of structuring species in habitat under strong natural pressures, rather than specific changes of the community. Dynamics of only few species look under influence of green tides in some assemblages. On the opposite, in subtidal habitats, trajectory analyses indicate changes in the structure and distribution of benthic assemblages, with a homogenization of assemblages, and significant functional shifts. As in many comparable ecosystems, phytoplankton and microphytobenthos support the food webs within the different habitats. Results are discussed regarding their potential determinism and implications in conservative management and governance processes. Some potential directions are proposed, as the use of trajectory analysis for the reporting of ecological quality status, which imply implies to deal with the double challenge of the theoretical and practical definition of reference conditions and of conservation targets.

TRAJECTOIRES ECOLOGIQUES: METHODES ET APPLICATIONS.
Un cas d'étude sur la conservation et les dynamiques taxonomique/fonctionnelle/trophique des assemblages benthiques de substrats meubles dans la baie de Saint-Brieuc (Manche occidentale, France)

Mots clés: Ecological Trajectory Analysis, Métriques, Représentation des données, Dynamique, Changements temporels, Conservation, Baie de Saint-Brieuc.

Résumé: L'objectif de cette thèse était d'analyser la dynamique taxonomique, fonctionnelle et trophique des assemblages benthiques des fonds meubles de la baie de Saint-Brieuc (Manche occidentale, France) au cours des dernières décennies, et de caractériser les patrons spatio-temporels du réseau trophique benthique intertidal. L'évolution et le fonctionnement des assemblages benthiques intertidaux et subtidaux de la baie de Saint-Brieuc intégraient des questions écologiques plus larges relatives à la stabilité et à la variabilité des écosystèmes. Des développements méthodologiques dans le domaine des analyses de trajectoires ont été proposés pour quantifier, qualifier et visualiser les dynamiques écologiques dans différents domaines de l'écologie. Ces développements, issus d'une pollinisation croisée entre les domaines de l'écologie marine et terrestre, ont servi l'analyse locale des habitats marins révélant des résultats contrastés dans les zones intertidales et subtidales. Dans la zone intertidale, les changements observés reflètent principalement des changements aléatoires de populations d'espèces structurantes de l'habitat soumis à de fortes pressions naturelles, plutôt que des changements spécifiques de la communauté. Seules les dynamiques de quelques espèces semblent sous l'influence des marées vertes dans certains assemblages. A l'inverse, dans les habitats subtidaux, les analyses de trajectoires indiquent des changements dans la structure et la distribution des assemblages benthiques, avec une homogénéisation des assemblages, et des changements fonctionnels significatifs. Comme dans de nombreux écosystèmes comparables, le phytoplancton et le microphytobenthos soutiennent les réseaux trophiques dans les différents habitats. Les résultats sont discutés quant à leur déterminisme potentiel et leurs implications dans les processus de conservation, de gestion et de gouvernance. Certaines perspectives sont proposées, comme l'utilisation de l'analyse de trajectoire pour le rapport de la qualité des états écologiques, ce qui implique de traiter le double défi de la définition théorique et pratique des conditions de référence et des objectifs de conservation.

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