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To cite this version:

Valérie V. David, Sébastien Tortajada, Olivier Philippine, Martine Bréret, Alexandre Barnett Barnett, et al.. Ecological succession and resilience of plankton recovering from an acute disturbance in freshwater marshes. Science of the Total Environment, 2020, 709, pp.135997. 10.1016/j.scitotenv.2019.135997 . hal-02490902

HAL Id: hal-02490902

https://hal.science/hal-02490902

Submitted on 25 Feb 2020

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Title: Ecological succession and resilience of plankton recovering from an acute disturbance in freshwater marshes

Short title: Ecological succession and ecosystem maturation of plankton after a storm

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Running Head: Impact on planktonic food webs in the case of marine submersion on freshwaters systems

Keywords: Acute disturbance, open system, ecosystem maturation, ecological succession, planktonic trophic pathways, phytoplankton.

Abstract

The increase in extreme events such as storms is one of the major threats that coastal ecosystems will have to face in the near future. In such a context, both maturation and ecological successions processes remain at the core of ecology to better anticipate the changes to ecosystem biodiversity and functions facing environmental stressors. However, these concepts are mainly approached through closed experimental studies that oversimplify the mechanisms. A survey was carried out on a 'natural' and open ecosystem subjected to an acute disturbance, i.e. a marine submersion of freshwater drained marshes, occurring after a storm. Plankton biomass, production and taxonomic/functional phytoplankton diversity were followed weekly at four stations over 2 months. Most of the stations were disrupted by this acute disturbance and displayed gradual growth and development, as described in the classical maturation process. The main differences between stations were attributed to the heterogeneity of the communities before the storm, the intensity of the disturbance and the different human actions performed to recover the freshwater environment. The concept of 'ecological resilience' was thus better suited than 'engineering resilience' for such open systems facing constant fluctuations in environmental drivers. With regard to ecological succession, the more impacted stations were marked by a significant change in taxonomic beta-diversity, with numerous stochastic processes, due to taxa dispersion. They first exhibited a convergence in functional traits due to the increase in nutrient availability drained from the catchment basin and then an increase in divergence when nutrients became limited.

1. Introduction

Coastal ecosystems and wetlands provide several goods and services to human populations (de Groot et al., 2012). The latter clearly depends on the 'correct' functioning of one ecosystem, which is controlled by the organisms living in it (Tilman et al. 1997; Worm et al., 2006). Compared with terrestrial biomes, coastal ecosystem function is are highly sensitive to climate change (MEA, 2005). Even if global warming is usually the main change when it comes to climate pressure, the increase in extreme events, such as storms, is also a major threat that coastal ecosystems will have to face in the near future (IPCC, 2014).

Storm flood events on coastal ecosystems are acute disturbances that disrupt biological function and species diversity by modifying the physical environment (Battisti et al., 2016). Even if such disturbances altered the trophic web organization and thus the services they provide, a system may be renewed through a maturation process, leading to an increase in total activity and system organization (Saint-Béat et al., 2015). The 'engineering resilience' is defined as the speed with which a system returns to its equilibrium state after a disturbance (Pimm, 1991; Holling, 1996) while the 'ecological resilience' supposes the existence of multiple stability domains. A distinction is made between the mean population-level resilience and the mean community-level resilience for experimental approach (Steiner et al., 2006). As they are controlled by different factors, these two kinds of resilience are not synchronized in natural environments (Zhou et al., 2014).

Biological diversity is of primary importance to the renewal and reorganization of an ecosystem following a disturbance, and acts through species composition, and functional diversity, as well as their interactions across temporal and spatial scales (Elmqvist et al., 2003). The mechanisms by which a regional species may settle and persist in a local community are set out in the community assembly theory (Kraft et al., 2015). A regional species is actually subjected to several hierarchical and interconnected filters until it becomes

established in the local community – dispersion, abiotic and biotic factors (HilleRisLambers et al., 2012). Moreover, ecological succession occurring after a disturbance describes the determinist development of community assemblages and predicts a pre-colonization of pioneer assemblage of R-strategist species followed by the establishment of K-strategist taxa (Clements, 1916). Nevertheless, recent studies show that, stochastically, such a dispersion may play an important role at several succession stages (Kreyling et al., 2011; Zhou et al., 2014). The latter is related to several biological processes, which lead to unpredictable temporal fluctuations in assemblages that may provide alternative trajectories (Prach and Walker, 2011; Zhou et al., 2014).

Plankton is commonly used as an index for climate change and disturbance (Tolotti and Thies, 2002; Beaugrand, 2005). The community recovery time was thus short (several weeks) because of its high reactivity (Vincent et al., 2002). Control experiments also highlighted that, for such a compartment, the 'community' resilience depends on the intensity of the disturbance (Steiner et al., 2006). However, none of the *in situ* studies analyze the impact of such a disturbance, or consider the concepts of ecosystem maturation and ecological succession, since they are usually approached through closed control experiments (Steiner et al., 2006; Zhou et al., 2014).

Coastal wetlands, such as marshes (e.g. drained marshes), are good models for *in situ* studies of the impact of a disturbance. They are of prime importance for moderation of disturbance (MEA, 2005) and are polder areas particularly sensitive to storm flood events causing marine submersion and thus are high risk for local economic activities and populations (Chaumillon et al., 2017). In addition, they constitute a significant artificial hydrographic network of channels and ditches, which are preserved from marine intrusion by walls punctuated with lock gates for draining the surplus water during high precipitation events.

On the night of February 27th, 2010, a storm reached the French Atlantic coast (storm Xynthia). The concordance of low atmospheric pressure, strong spring high tides and strong winds (130 to 160 km.h^{-1}) caused a rise in sea level of 7 meters. In the Charente-Maritime department, seawater passed over the sea walls and submerged a large area of freshwater drained marshes. This storm occurred two weeks after the beginning of a weekly *in situ* sampling of the plankton community in four marshes, and this survey was carried out over the 40 days following the storm (Fig. 1).

Such a survey provides an interesting *in situ* case study to prospect the concepts of ecosystem maturation and the ecological succession of nano-microphytoplankton for open systems, relating them the results obtained in closed and controlled experiments. It allowed us 1) to describe the processes involved in both themean population-level and mean community-level resilience of plankton communities facing marine submersion in a natural environment that is subject to fluctuations from external environmental factors, both in terms of climate and connectivity with other close habitats and, 2) to compare the responses of four marshes that were not subjected to the same intensity of disturbance, the heterogeneity of the initial plankton community and the human post-storm reactivity.

Our main assumptions were that 1) the concept of 'ecological resilience' would be better suited to take into account the constant fluctuations of the environmental drivers in the natural environment, since the concept of 'engineering resilience' supposes that only one equilibrium or stable state exists (Gunderson, 2000; Saint-Béat et al., 2015) and, 2) that some stochastic process systems may play significantly on ecological succession and resilience, depending on the initial population heterogeneity between stations, and local diversity provided by historical features specific to each station, as well as heterogeneous dispersion due to connectivity with upstream and downstream systems.

Ecological succession was analyzed for nano-microphytoplankon by means of both taxonomic and functional diversity, considering their common life strategies: the C (colonist species), S (nutrient stress tolerant species), R (tolerant of shear/stress forces in physically disturbed water masses) strategies (Reynolds, 2006). The functional approach provides the taxa fitness deployed by these compartments that face environmental factors and thus the importance in determinist *versus* stochastic processes in ecological succession when considering the community assembly theory (Kraft et al., 2015).

2. Material and methods

The four stations were differently impacted by the storm (Fig. 1). Seawater passed over ditches and submerged a large area of freshwater marsh, as far as 10 km inland (Fig. 1). Salinity was used as a proxy for both the intensity of the disturbance and freshwater recovery following the storm. Only the northern stations (N stations) faced a direct submersion from marine water, as testified by the significant increase in their salinities (more than 20; Fig. 1) just after the storm. By contrast, the southern stations were not located in seawater submerged areas and their lower salinity increases (a maximum of 6-9) were due to the inland draining of their catchment basins (S stations). After the storm, the freshwater recovery time was different across the stations due to their geographic positions, inland ('I') *vs* coastal ('C') stations, as well as different human controls on sea locks. Local marsh stakeholders actually applied several strategies to speed up freshwater recovery, regularly opening the sea locks during low tide to drain the salt water. NI and SC stations recovered fresh water after 15 days following a regular and rapid human control on sea locks, while salinity stabilization was attained 22 days after the storm at the NC station (Fig. 1). By contrast, the SI station was less impacted and faced a sudden salinity decrease between 15 and 21 days after the storm (Fig.

1). Finally, only NI and SC stations recovered their pre-storm freshwater level by the end of the survey.

2.1. Abiotic parameter measurements

For each marsh/date, water samples were taken from the middle of the main channel of the network to avoid the edge effect. In the field, salinity and temperature were measured using a thermosalinometer (WTW Tetracon 325). In the laboratory, nitrates (NO_3), nitrites (NO_2) and phosphate (PO_4) concentrations were analyzed according to Murphy and Ryley (1962) and ammonium (NH_4) concentration according to Koroleff (1969). Dissolved oxygen saturation was measured using the Winkler method (Carignan et al., 1998; 2000). Dissolved Organic Nitrogen (DON) and Dissolved Organic Carbon (DOC) concentrations were analysed according to the Aminot and Kerouel (2004) protocol. The sum of NO_3, NO_2 and NH_4 were used as Dissolved Inorganic Nitrogen (DIN) concentrations while PO_4 was used as Dissolved Inorganic Phosphate concentrations (DIP).

2.2. Biotic parameter measurements

From water samples, Chlorophyll *a* biomass (Chla), used as an index of the phytoplankton biomass was evaluated for three-size classes using fractioned filtration (Vargas and Gonzalez, 2004; Glé et al., 2008) using the fluorimetric method (Yentsch and Menzel, 1963). Chla biomass were then converted into carbon *via* a carbon to Chla ratio for each size-class - C= 50 Chla (Banse, 1977) and were expressed as a percentage of the total Chla biomass (%ph1, %ph2, %ph3).

Nano-microphytoplankton diversity/abundance was counted per taxa for each station/date using the Utermöhl method (Utermöhl, 1958): phytoplankton cells were identified and counted by inverse microscopy (magnification of ×400 or ×600), at least at the genus level. Biovolume estimations and related carbon biomass were obtained using to cell measurements and according to their specific forms (Hillebrand et al., 1999). Taxa were

classified as ‘present before the storm’, ‘marine’, ‘euryhaline’ or ‘freshwater’ species based on several surveys undertaken in Marennes-Oleron Bay a few days before the storm (REPHY survey, Ifremer – marine taxa) and in marshes the year before the survey (euryhaline *vs* freshwater taxa). Each of the taxonomic units were classified according to the C-S-R strategy of Reynolds (Reynolds, 2006) adapted from Grime (1977). The strategy of each taxa was assigned according to literature (Smayda et al., 2001; Smayda and Reynolds, 2003; Reynolds, 2006; Alves-de-Souza et al., 2008) and completed for the taxa for which the strategy was not available based on i) the trophic knowledge of each species and ii) the global strategy recognized for some taxonomic groups (Litchman and Klausmeier, 2008). Species displaying tyckopelagic or benthic life mode were also considered separately and recorded according to literature. Finally, a total of 4 functional groups were obtained: benthic taxa, C, S and R strategists.

Primary production was measured using the Steeman Nielsen method (Steeman Nielsen, 1952) based on the DIN assimilation by phytoplankton using a radioactive tracer between day -5 and day 32 and by oxygen measurement following the Winkler method throughout the survey (Bender et al., 1999). The primary production estimated by the Winkler method (Bender et al., 1999) corresponded to the quantification of the net primary production (NPP) of the plankton community, since oxygen losses by respiration take into account the other non-autotrophic plankton organisms (Reeder and Binion, 2001). A correlation was applied between the results of the two methods and applied to correct the values obtained by the Winkler method at the end of the survey.

Heterotrophic prokaryote and picophytoplankton abundance was estimated according to Lee and Fuhrman (Lee and Furhman, 1987). Bacterial production was estimated by quantifying of the incorporation rate of [^{3}H] thymidine by bacteria according Riemann et al. (Riemann et al., 1982). Rates of ^{3}H-thymidine incorporation were transformed to cell

production using a conversion factor of 2.7×10^{17} cells produced per mole of thymidine incorporated. This conversion factor was experimentally determined in batch experiments where the increase of bacteria abundance and ^{3}H-Thy incorporation were simultaneously followed.

With regard to protozoans, ciliate abundance was evaluated from a sample of in *situ* water preserved in alkaline lugol iodine (2% final concentration) and stored at 4°C. Protozoa diversity/abundance was estimated by microscopy (magnification of ×200 or X 400) after a 24-hour sedimentation using the Utermöhl method (Utermöhl, 1958). Heterotrophic nanoflagellate abundance was estimated according to Bloem et al. (1986). Biovolumes were estimated by applying standard geometric formulae to each taxon (Hillebrand et al., 1999). Cell carbon was computed per taxon/functional group with conversion factors of 0.19 and 0.15 pgC μm^{-3} for ciliates and nanoflagellates, respectively (Sakka Hlaili et al., 2008).

In the field, metazoans were sampled at 1 m depth with a portable pump-based zooplankton sampler equipped with a microprocessor-controlled flow sensor for precise determination of the volume of water processed by the sampler (Nayar et al., 2002): two-hundred liters were pumped for each station/date and filtered on a 200 µm-mesh-size sieve. Metazoans were fixed at 5% (final concentration) water/buffered formalin. In the laboratory, metazoans were sorted and identified to the highest taxonomic level under a dissecting stereomicroscope (×63). The determination and measurements were performed according to Frontier (Frontier, 1972). Conversion in carbon biomass per taxa was carried out according to Masclaux et al. (2015) and allowed the estimation of the total metazoan carbon biomass.

The zooplankton grazing on phytoplankton was estimated for the three producer size-classes and both protozoans and mesozooplankton according to David et al. (2016). The grazing rates were calculated according to the Frost equations (Frost, 1972) when chlo a biomass were significantly lower after a 24-hour incubation than at the beginning of the

experiment. The differences between B200µm and B63µm were used to estimate the protozoan community grazing while the differences between BPred and B200µm enabled metazoan community grazing to be quantified.

Four emergent properties were approached based on previous data (Fath et al., 2007; Legendre and Niquil, 2013). The connectance is a measure of the level of complexity of the planktonic trophic web and was estimated as the number of significant grazing links between zooplankton and phytoplankton (among Gmic1, Gmic2, Gmic3, Gmes1, Gmes2 and Gmes3). The ecological efficiency is an index of the efficiency with which the energy is transferred from the first to the last trophic level in the PTPs and was approached as the ratio between metazoan and phytoplankton biomass. The Primary Production/Phytoplankton biomass (PP/B) ratio was used as an index of primary productivity and the Primary Production/Respiration (PP/R) ratio as an index of the imbalance between gross production and respiration of the water column.

Taxonomic/functional richness and functional dispersion based on the 4 functional groups for nano-microphytoplankton were also considered (Villéger et al., 2008; Laliberte and Legendre, 2010).

2.3. Statistical analysis

Beta-diversity, measured as the Bray-Curtis dissimilarity between two consecutive dates, was analyzed over time: the more significant the dissimilarities were, the greater the difference in diversity between the previous and subsequent date. The BAS framework had been used to isolate, within the dissimilarity, the variation in species (or functional groups) assemblages due to species replacement from the one derived from nested patterns, that is to say, an evolution through a subset of species smaller than the original one (Baselga, 2010; Baselga and Leprieur, 2015). Moreover, the null model was used to assess if beta-diversity was different that it would have been by chance by holding alpha diversity constant at each

time point and across all time points (gamma diversity; 9999 permutations) (Zhou et al., 2014). The relative importance of determinist *vs* stochastic processes in shaping both structural and functional communities was tested based on the confrontation of the observed similarity value and the one expected by chance and obtained by the null models through the formula of Zhou et al. (2014). Null models were used in order to estimate if functional richness and dispersion were significantly different from the one that would be obtained by chance. For functional richness, the Gotelli and Entsminger (Gotelli and Entsminger, 2003) swap null model was used by randomly reallocated species' presence/absence within the community at each station/date while keeping the marginal sums constant and functional richness computed for each station/date simulated. For functional dispersion, the Mason et al. (2008) abuswap null model was used by randomly reallocating species biomass within the community at each station/date while keeping the marginal sums constant and functional dispersion computed for each station/date simulated. The Standardized Effect Size was computed on 9999 permutations and tested according to Hardy (2008).

All numerical analyzes were performed with the R software (R-Core-Team, 2014) using the package [vegan],[cluster],[ade4], [FD],[caret], [e1071] and [rpart].

3. Results

3.1. Environmental context

The four stations displayed a similar change in water temperature throughout the survey (Fig. 2A). The week before the storm was marked by a sensitive warming from 2 to 9°C. No water temperature fluctuations were recorded just after the storm, while the following ten days were marked first by a cooling phase (from 9 to 5°C) followed by a warming phase until the 25th day after the storm.

Marine submersion implied a drastic fall in DIN (dissolved inorganic nitrogen) concentrations (<10 mg L^{-1}, Fig. 2B) except at the SI station, for which concentrations were already low before the storm compared to the other three stations (10 *versus* 25-50 mg L^{-1}; Fig. 2B). The later three stations exhibited an overall DIN increase from 10 days after marine submersion, despite broad fluctuations over time, while DIN concentrations remained low over the period at the SI stations.

SPM (suspended particulate matter) concentrations fluctuated greatly between 0.01 and 0.07 g L^{-1} during the survey and were marked by high concentrations over the days preceding the storm at the NC station – 0.14 g L^{-1} (Fig. 2C).

3.2. Spatio-temporal evolution of the Planktonic Trophic Pathways (PTPs) and their emergent properties

The main Planktonic Trophic Pathways (PTPs) were determined by a Fuzzy c-means clustering based on the Euclidean distance matrix of the different plankton compartments biomass (heterotrophic prokaryotes, phytoplankton, protozoans and metazoans), the bacterial and phytoplankton productions, the percentage of pico-, nano, microphytoplankton and the four emergent properties of the system - connectance, ecological efficiency, productivity (PP/B) and production to respiration ratio (PP/R) (Borcard et al., 2011; David, 2017). Data was previously scaled and the number of clusters (i.e. PTPs) optimized by the Calinsky-Harabasz index. Three distinct PTPs were highlighted as corresponding to significant differences in plankton biomass, production, grazing and emergent properties (Fig. 3).

The first, one providing a 'low active' PTP ('LA'), was characterized by the lowest heterotrophic prokaryotes and phytoplankton biomass, the lowest bacterial and phytoplankton production, the lowest metazoan biomass and grazing on the phytoplankton as well as the lowest connectance, ecological efficiency and PP/R ratio (Kruskal-Wallis test and pairwise

Wilcoxon Post Hoc tests with Bonferroni corrections $p<0.05$; Figs. 3 and 4). By contrast, a second PTP, the 'herbivorous' pathway, presented among the highest primary production *vs* the lowest bacterial production, the highest contribution of the microphytoplankton (ph3) in phytoplankton biomass and trophic efficiency, and a high connectance (Kruskal-Wallis test and post Hoc $p<0.05$; Figs. 3 and 4). A final PTP, 'Multivorous' pathway, displayed the highest biomass and production, the highest connectance,and the lowest contribution of microphytoplankton (ph3) among the phytoplankton biomass (Kruskal-Wallis test and post Hoc $p<0.05$; Figs. 3 and 4).

All of the stations displayed 'herbivorous' pathways before the storm, except the NC station. Moreover, they all displayed 'low active' pathways just after the storm except the SC station. The temporal chronology finished by setting up a 'Multivorous' pathway 4 weeks later for the NI station (30 days) and 15 days after the storm for three others stations (Fig. 5).

Southern stations displayed the highest productivity (PP/B) in the days following the storm, contrasting with the northern stations, which exhibited higher values of this emergent property. However, a one-week delay was noted for the Northern stations (Fig. 5). Moreover, a second peak in productivity occurred three weeks after the storm for all stations. The increase in primary production began quickly and reached its maximum 20 days after the storm, except for the NI station, for which production was low throughout the survey. Moreover, a peak in bacterial production occurred systematically 15 days before the peak in primary production. Both production peaks were higher in the Southern stations than in the Northern stations. Total phytoplankton biomass (three size-classes) increased during the survey, up to a maximum of 30 days after the storm, except at the SC station, for which maximum values occurred 15 days after the disturbance. Metazoan and heterotrophic prokaryotes biomass exhibited very dissimilar and high fluctuations throughout the survey for and between the four stations. Connectance increased during the survey following the storm

with the maximum attained at 9 days, 20 days, 30 days and 36 days after the storm for the SI, NC, SC and NI stations, respectively. Ecological efficiency displayed an unclear and very different evolution over time between stations, as with the biomass (Fig. 5). The highest production, productivity and biomass attained after the storm were higher than the ones recorded before the storm, except for the NI station.

3.3. Ecological succession for nano-microphytoplankton

64 taxonomic units belonging to 7 taxonomic groups were identified - diatoms, Euglena, Chlorophyta, Chrysophyta, Haptophyta, Dinoflagellates and Cyanophyta. Nano-microphytoplankton taxonomic diversity displayed different trajectories during the sampling period even if they seemed closer to each other in terms of geographic area – Northern *vs* Southern stations (non-metric, multidimensional scaling on Bray-Curtis dissimilarities and log-transformed data, Fig. 6). The taxonomic diversity was significantly different before and after the storm (multiple response permutation procedure MRPP, p-value < 0.05; Figs. 6, 8). New taxa compared with the ones recorded during the pre-storm period occurred just after the storm or with a one-week delay at the SC station (Fig. 8). Their contribution increased during the following period except at the NI station, which was quickly dominated by pre-storm taxa. By contrast, other stations presented high contributions of marine taxa in biomass after ten days. Moreover, the contributions of marine species increased over time at SI stations (Fig. 8). This taxonomic diversity structure was significantly explained by water temperature (permutation test of the chemical and physical parameters to the NMDS axis, p<0.01, Figs. 6, 7).

Contrasting with taxonomic diversity, nano-microphytoplankton functional diversity was not significantly different between the pre-storm date and the last date of the survey (MRPP, p-value > 0.05), even if each station displayed its own trajectory during the period

following the storm (distance based redundancy analysis –dbRDA- based on Bray-Curtis dissimilarities, Fig. 7A). While the pre-storm period was characterized by very different dominances of functional groups between stations, the last date was characterized by the co-dominance of S and R strategists. Environmental parameters, which are mainly driven by temperature, salinity and DIN concentrations (dbRDA and permutation tests on the first two axis, Fig. 7B) significantly explained 29% of the functional structure: the temperature increase and O_2 saturation increase were related to the dominance of R-strategists, while the lower DIN concentrations were characterized by the presence of S-strategists.

To combine taxonomic and functional diversity, all stations displayed broad changes in taxonomic diversity (wide beta-diversity) mainly due to significant taxa replacements the week before the storm (Fig. 8). This period coincided not only with a high importance of stochastic processes that explained diversity changes but also a sensitive increase in specific and functional richness. While the Northern stations displayed a decreasing dispersion, the Southern stations presented an increasing dispersion. During this period, the community evolved from a dominance of mixotrophs and even benthic cells (for NI station) to large pelagic autotroph cells in the Southern stations (data not shown). After the storm, changes in taxonomic diversity were mainly due to species replacement, except at the SC station, for which the great diversity change occurred one week later when the temperature decreased (Fig. 8). Related to the stochastic process, this change lasted 3 weeks for the NI station *versus* one week for the NC and SI stations and one week after the cooling phase at the SC station. By contrast, functional beta-diversity was lower and mainly explained by nested patterns. NC and SC stations were marked by a decrease in functional dispersion and an increase of functional richness during the two to three weeks following the storm,compared to the SI station, which was characterized by a decrease in functional dispersion. The last phase was contrastingly marked by decreasing functional dispersion.

4. Discussion

The acute disturbance, which impacted the drained marshes of Charente-Maritime, consisted of a marine submersion into freshwater masses.

4.1. Maturation of the ecosystems after the disturbance

As a 'living' and 'open' system, an ecosystem exchanges both matter and energy with its environment (Meysman and Bruers, 2010). It evolves and matures with increasing complexity (Saint-Béat et al., 2015). The maturation of an ecosystem involves structural changes that are orderly, directional and predictable (Odum, 1969), classically decomposed into successional phases (Jørgensen and Fath, 2004).

The first step consisted of the entry of 'external' biomass and energy that progressively increases the 'internal' biomass of several biological compartments within the system. In this study, increasing biomass and production of phyto-, metazoan and heterotrophic prokaryotes (e.g. bacteria) were recorded at all stations during at least the first weeks after the storm. Secondly, trophic connections increase, leading to the introduction of matter and energy cycles, and thus a progressive rise of energy flows inside and through the ecosystem. At all the stations, a decrease in productivity (PP/B) matched with the peak of bacterial production 30 days after the storm. All of the marshes displayed an overall increase in PP/R ratio, confirming the progressive maturation of drained marshes in the few weeks following the storm since Odum (1969) suggests that the PP/R ratio could be a good functional index for the maturity of an ecosystem with a lower food webs ratio that is facing disturbance, and a higher ratio for more mature systems. Finally, the ecosystem evolved through a more efficient organization to perform its energy accumulation. However, the ecological efficiency measured during this study did not display such a clear evolution at all

the stations: only the Northern stations presented an increase in this emergent property at the beginning of the survey following the storm.

The storm flood event disrupted the food web structure and functioning for at least three stations (Northern and SI stations). Consequently, they moved from an 'herbivorous' to a 'low active' pathway functioning a few days after being subjected to marine submersion. Only the SC station was an exception and was still characterized by a 'low active' pathway before the storm, probably due to the greater turbidity, which may imply lesser availability of light, thereby limiting phytoplankton production (Irigoien and Castel, 1997; David et al. 2016). The 'herbivorous' pathway recorded at three stations before the storm is characteristic of a non-limiting environment (Legendre and Rassoulzadegan, 1995; Sakka Hlaili et al., 2014) since it displayed large phytoplankton production and biomass mainly dominated by large cells and a dominance of metazoans versus protozoans, which attest to a good ecological efficiency and connectance due to the large plankton biomass and the wide diversity of phytoplankton size-class used by the protozoans. In contrast, the 'low active' pathway is characterized by very low phytoplankton biomass and production and a greater biomass of protozoans *versus* metazoans. It may be considered an immature food web since it is characterized by i) its low connectance due to the poor diversification of prey for the metazoans, ii) its low ecological efficiency, explained by the very low metazoan biomass and iii) its low PP/R ratio due to low primary production, contrasting with the relatively large protozoan biomass sustained by other trophic ways (Fig. 1).

In contrast to the Northern and SI stations, the SC station seemed to be more affected by the cooling phase recorded one week after the storm than by the storm itself. Sensitive decreases in plankton production, productivity, ecological efficiency and maturation (lower PP/R ratio) were actually highlighted only nine days after the storm while it exhibited the same connectance value, PP/R ratio and displayed a greater ecological efficiency despite the

lower phytoplankton biomass and production in the few days following the disturbance. This station was one of the lesser impacted stations with a weak salinity increase due to an indirect input of saltwater. Moreover, it is located near to a marine system and is thus more likely to be subjected to recurrent inputs of marine water, which may imply a greater adaptability to such stress compared to the SI station. Indeed, an annual survey conducted at the same stations during the year preceding the storm highlighted that coastal stations displayed greater taxonomic richness than inland stations due to their vicinity to marine habitats and the lack of completely watertight sea locks (112 vs 100 phytoplankton species for coastal and inland stations, respectively; data not published).

All of the stations evolved towards a 'multivorous' pathway, which displayed the highest connectance and PP/R ratio, creating a greater level of system maturation than the 'herbivorous' pathway that was observed before the storm (Fig. 1). The 'multivorous' pathway was recorded at the end of the survey at all of the stations, and for the same season and system as Masclaux et al. (2015). It displayed both the highest bacterial and phytoplankton production and heterotrophic prokaryote and phytoplankton biomass. It corresponds to the coexistence of both an 'herbivorous' and a 'microbial' pathway when favorable conditions (temperature, nutrients) are maintained and when metazoan activities involve dissolved organic carbon production that may sustain heterotrophic prokaryote development (Legendre and Rassoulzadegan, 1995; Sakka Hlaili et al., 2014). However, the 'multivorous' pathway (two maturity indices: PP/R and connectance) did not occur simultaneously between the stations: sooner for the coastal stations (weeks 2 and 3 at the SC and the NC station, respectively) and later for the inland stations. While inland stations probably displayed a lesser adaptability to such stress compared to coastal ones due to a lesser local diversity (lower tolerance to brackish water and species probably less euryhaline than in coastal stations), it was also subjected to more human action on sea locks in order to shorten

the freshwater recovery time. Such human action may have disturbed and delayed the maturation process at these stations. The NI station displayed the lowest biomass, production and productivity throughout the survey.

Moreover, the chronology of maturation that is controlled by the seasonal fluctuations of local meteorological factors, such as warming (Masclaux et al., 2015), added to the classical resilience process following a storm that would be described in a closed environment.

4.2. Ecological succession along the resilience process

An acute disturbance involving an abrupt loss of biological biomass and/or structure and ecological succession is historically defined as the sequential replacement of taxonomic units (Cléments, 1916; Odum, 1969). The warming that took place just before the storm led to the introduction of an 'herbivorous' pathway for most of the stations. This period was marked by an increase in taxonomic and functional phytoplankton diversity, with large numbers of species and functional groups being replaced, and the dominance of large pelagic autotrophs cells. R-strategist and tychopelagic taxa were dominant at the northern stations, testifying to a large hydrodynamic due to flood draining, with high nutrient loads from the catchment basin, i.e. DIN concentrations (Tortajada et al., 2011). By contrast, the SC station was dominated by C-strategists, providing a less current environment. The dominance of S-strategists at the NI station may be explained by lower DIN concentrations favoring taxa, which are capable of deploying alternative nutrition methods, such as mixotrophy (Reynolds et al., 2002).

But a 40-day survey after the storm is clearly not sufficient to obtain an entire taxonomic-level resilience as described by Steiner et al. (2006) using a controlled experiment of the same duration. Zhou et al. (2014) almost obtained taxonomic-level resilience but only after 269 days for a microbial community. Functional diversity exhibited a closer relationship

to environmental factors than taxonomic diversity, suggesting a clearer response to environmental factors that highlights the importance of determinist processes using the community assembly theory (Kraft et al., 2015). Therefore, phytoplankton diversity might likely never have reached the population-level resilience it could in closed experiments in which environmental parameters are controlled by the response of each taxa to the increasing temperature (Steiner et al., 2006; Zhou et al., 2014).

Our results clearly illustrate the different trajectories taken by either the taxonomic or functional diversity of nano-microphytoplankton assemblages at several stations. Ecological succession is usually described firstly as a colonization of pioneer assemblage of r-strategists characterized by high productivity and low trophic specialization, followed by the establishment of a more stable community dominated by K-strategist taxa with lower productivity but a greater specialization (Cléments, 1916; Odum, 1969). However, stochastic processes may play an important role at several stages of these successions, leading to unpredictable, idiosyncratic temporal fluctuations in assemblages that may lead to alternative trajectories due to context-dependent and open systems (Loreau et al., 2002). Stochastic processes generate assemblages that are not distinguishable from those obtained by chance, such as speciation, drift, dispersion and initial population heterogeneity (Chase, 2007; Kreyling et al., 2011; Zhou et al., 2014). Speciation can be excluded from this study because of the short duration of the survey. Dispersion and drift are contrastingly important factors to consider due to the open status of these 'natural systems', which areconnected to both upstream and downstream habitats through hydraulic conductivity. By contrast, determinist processes involve non-random mechanisms based on niche differentiation for which species assemblages present in a system are the ones able to adapt to local environmental factors according to the Niche-based theory – selection process (Grinnell, 1917). Downstream taxa contributions occurred through marine submersion from the Pertuis-Charentais, at the

Northern stations in particular, for which marine taxa were recorded just after the storm, while hydraulic movements, specifically through sea lock management following the storm, contributed to taxa contribution upstream from the catchment basin. Moreover, the four stations did not display the same taxonomic and functional diversities in the few days before the storm and this initial population heterogeneity may also have played a significant role, along with dispersion and drift, to the different trajectories observed.

In addition, it is clear that considering a 'natural' system makes it difficult to disentangle and interpret the importance of stochastic *vs* determinist processes as observed in closed experiments by Zhou et al. (2014). To better understand the relative importance of such processes involved in the ecological succession in a natural environment, we approached the mechanisms by which a regional species may settle and persist in a local community using the community assembly theory (Kraft et al., 2015) combined with null-models on beta-diversity and functional richness and dispersion. A regional species subjected to several hierarchical factors until itbecomes etablished in the local community: i) the dispersal filter depending on connectivity with closer habitats, ii) the environmental filter depending on tolerance to local abiotic factors and iii) the biotic filter that includes competition and/or prey-predator relationships, which may act retroactively on both previous filters during the succession. Moreover, the last filter may provide to several functional diversity patterns: divergence, i.e. functional traits dispersion in the community *vs* convergence, or homogenization through several functional traits (HilleRisLambers et al., 2012).

The SC station appeared not to be impacted by the storm, as seen by the low taxonomic beta-diversity following the storm, while it was highly impacted by the subsequent cooling phase since it was dominated by S strategists at this time. However, it presented a wide phytoplankton taxonomic and functional beta-dissimilarities in the following two weeks. This wide dispersion may correspond to stochastic processes in population resilience that could be

attributed to taxa dispersion from upstream areas, as there was intense human action on sea locks.

Moreover, the consequent hydrodynamic features may explain the large contribution of tychopelagic taxa. The increase in functional dispersion, which usually takes place when available resources are diverse (HilleRisLambers et al., 2012), may be due to the rise in nutrient loads drained from the catchment basin. This station attained maturation, only 15 days after the storm ('multivorous' pathways). The following period is characterized by a dominance of determinist processes, explaining plankton diversity. It actually corresponded to a stabilization of nano-microphytoplankton taxa and functional groups, with a dominance of freshwater species, present before the storm, or other species recorded in the same system during the year preceding the disturbance. An increase in functional richness with a co-dominance of R, C and S strategists and a functional dispersion may show that food resources were limited: even if DIN concentrations increased, other nutrients, such as DIP, may be limited for primary production. Multivorous pathways may actually be characterized by unbalanced nutrient ratios that lead to the development of S-strategists such as N_2 fixators or mixotrophs.

The northern stations were greatly impacted by direct marine submersion. The first weeks were marked by a large taxonomic beta-diversity change, mainly due to biomass gradients. This phase was thus marked by many stochastic processes due to taxa dispersion linked to both the input of marine species from the downstream Pertuis Charentais and the freshwater taxa linked to the human action on sea locks. However, this period is also characterized by determinist processes with a functional divergence, i.e. an increasing functional richness and dispersion and thus a biotic filter that may be explained by increasing nutrient availability. The main difference between the stations concerned the duration of the 'LA' pathways after the disturbance that coincided with great changes in taxonomic diversity

and dispersion. The NI station faced intense human action to recover a freshwater environment within 2 weeks. However, this implied a high stressor environment for local species dominated by S-strategists before the increasing in R-strategists, providing a turbulent and nutrient-rich environment. By contrast, the SC station faced a more progressive freshwater recovery that allowed for quicker stabilization of taxonomic diversity dominated by R-strategists. The NC station then displayed a functional convergence, with the dominance of S strategists showing limited food resources for phytoplankton as the multivorous pathways persisted. Nevertheless, neither station displayed full system maturation with regard to ecological succession.

Despite it being subjected to the indirect impact of the storm, the SI station displayed the same evolution as the NC station, with a short phase dominated by stochastic processes, i.e. dispersion/drift from the upstream area and a quick stabilization of taxonomic diversity. By contrast, the NC station was marked by nano-microphytoplankton diversity evolving toward S-strategist dominance due to the low availability of nutrients. The rapid decrease in salinity between the second and the third weeks implied a species renewal leading to R-strategist taxa providing a nutrient-rich and dynamic environment and finished with S-strategist dominance due to a lower availability of nutrients at the end of the survey. The brackish environment implied a dominance of marine species at the end of the survey for both the NC and SI stations.

5. Conclusions

This survey provided an interesting ‘case study’ of the processes involved in ‘natural’ systems facing an acute disturbance and related them to maturation and ecological succession theories. Stations displayed progressive growth and development, providing their progressive community-level resilience with respect to the overall features describing the classical

maturation of an ecosystem. After the disturbance, the stations most impacted by the marine submersion were marked by a high taxonomic beta-diversity change mainly due to biomass gradients and high stochastic processes caused by taxa dispersion. They first exhibited decreasing functional dispersion due to the increase in nutrient availability drained from the catchment basin and then an increase of functional richness leading to increased divergence when nutrients became limited.

The lowest resilience rates were observed for the greatest disturbance intensity, as well as the most intense human management to speed freshwater recovery. Consequently, both natural and human pressures act in synergy in the resilience process for 'natural' systems.

ACKNOWLEDGMENTS. This study was supported by the « Ministère de l'Enseignement Supérieur et de la Recherche », the water agencies Loire-Bretagne and Adour-Garonne, conseil général de Charente-Maritime, European Union. Thanks are extended to the UNIMA (Union des Marais de Charente-Maritime) for their expertises on the Charente-Maritime marshes and to Céline Lavergne, Alicia Shuman and Laurie Charrieau for their help during laboratory experiments. We are grateful "Version internationale" compagny and especially Grace Mc Carroll for English correction and helpful comments.

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Legends of Figures:

Fig. 1. Location of the 4 sampling stations and their corresponding marshes. The inland areas submerged by marine waters following the storm are indicated (shadow areas). Northern stations were localized in sea submerged areas while southern stations were attained by marine water after the draining of their catchment basins.

Fig. 2. Temporal evolution of temperature (A), dissolved inorganic nitrogen (B) and suspended particulate matter (C) concentrations at the four stations along the temporal survey.

Fig. 3. Schematic representation of the three Planktonic Trophic Pathways obtained in the Charente Maritime drained marshes. Bac= bacteria, ph1, 2 and 3: several size classes of phytoplankton, proto: protozoans and meta: metazoans. The size of the compartment corresponds to qualitative importance in biomass and the arrow widths the importance of the flows: The relative importance of emergent properties is displayed per PTPs. The main phytoplankton class size consumed by protozoan and metazoans are also reported.

Fig. 4. Dispersion of the main planktonic biomass, fluxes and emergent properties per Planktonic Trophic Pathways established by c-mean clustering. Zooplankton grazing have been estimated on phytoplankton biomass only. Letters highlight the significant differences established by pairwise post Hoc displayed after Kruskal-Wallis tests.

Fig. 5. Evolution of the production, productivity, biomass, connectance, ecological efficiency and PP/R ratio at all station over the survey. The several parameters traducing the attributes of the ecosystems (biomass, production, emergent properties) were rearranged between 0 and 1

in order to analyse their temporal evolution along the survey and compare them between the four stations.

Fig. 6. Trajectories of phytoplankton taxonomic diversity per station illustrated through a non-metric multidimensional scaling during the survey according to the date from the storm (D=day): Light shadow surrounds the dispersion and location of pre-storm date and dark shadow the last date of the survey. The significant environmental variable (water temperature) highlighted by permutation test is reported as an arrow.

Fig. 7. Distance based Redundancy analysis based on Bray-curtis dissimilarities and log-transformed data conducted on biomass of nano-microphytoplankton functional groups related to environmental parameters. Phytoplankton functional groups and correlation circle on the plane Axis 2 *vs* Axis 1 (A) and corresponding trajectories per station (B); Light grey and dark grey shadows surrounded the pre-storm period and the last dates of the survey, respectively.

Fig. 8. Taxonomic and functional beta-diversity, richness and dispersion for nano-microphytoplankton. For beta-diversity: shadow bars indicated the part due to biomass gradient and white bars the part related to nested gradient in the Bray-Curtis dissimilarity. Stars reported the date for which beta-diversity is lesser than the one expected by chance or the date for which functional richness or dispersion are significantly different that the one recorded by chance (null model, $p<0.05$). The importance of stochastic factors in taxonomic diversity changes is reported by a black line above the beta-diversity. The percentage of taxa of each origin and strategists in biomass were also reported per station/dates.

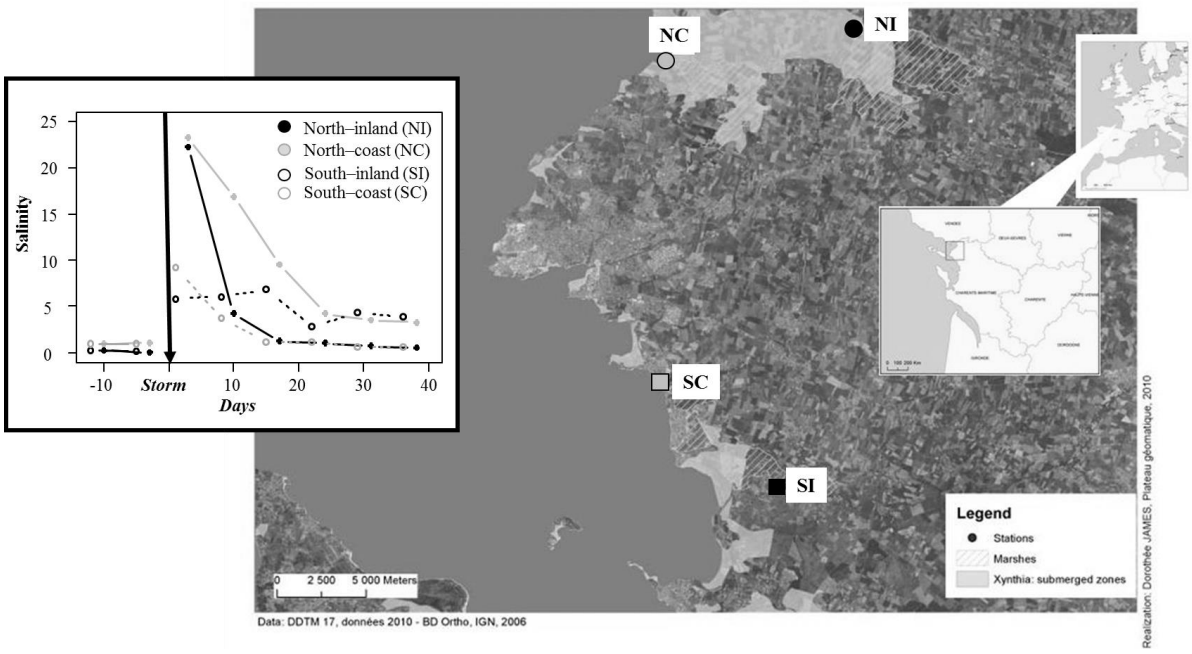
NC
NI
SC
SI
North–inland (NI)
North–coast (NC)
South–inland (SI)
South–coast (SC)
Salinity
Days
Storm
Legend
Stations
Marshes
Xynthia: submerged zones
0 2 500 5 000 Meters
Data: DDTM 17, données 2010 - BD Ortho, IGN, 2006
Realization: Dorothée JAMES, Plateau géomatique, 2010

Fig. 1.

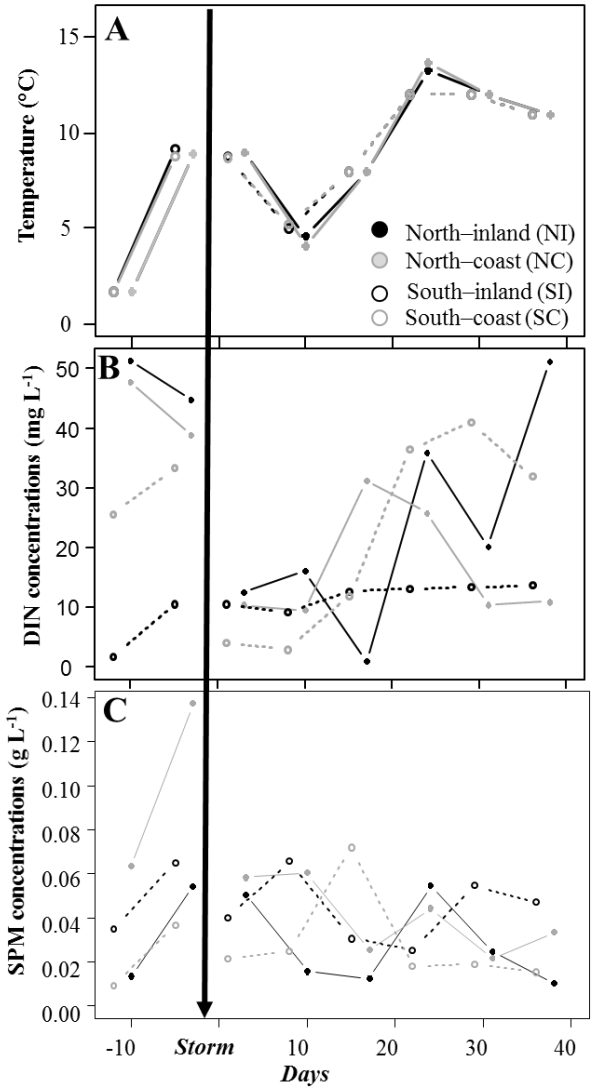
A
B
C
Temperature (°C)
DIN concentrations (mg L-1)
SPM concentrations (g L-1)
North–inland (NI)
North–coast (NC)
South–inland (SI)
South–coast (SC)
Storm
Days

Fig. 2.

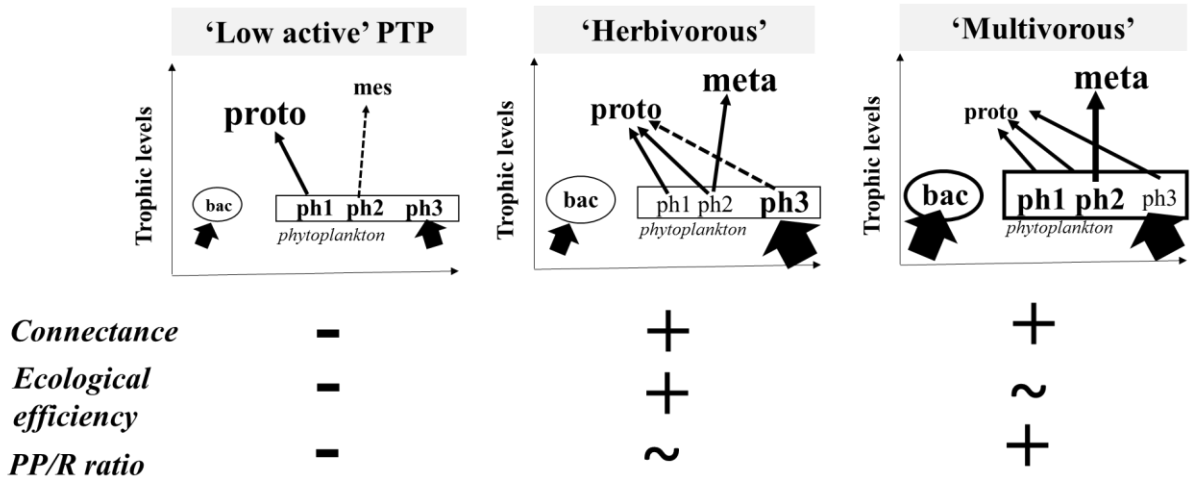
'Low active' PTP
'Herbivorous'
'Multivorous'
Trophic levels
proto
mes
meta
bac
ph1 ph2 ph3
phytoplankton
Connectance
Ecological efficiency
PP/R ratio
-
+
~

Fig. 3.

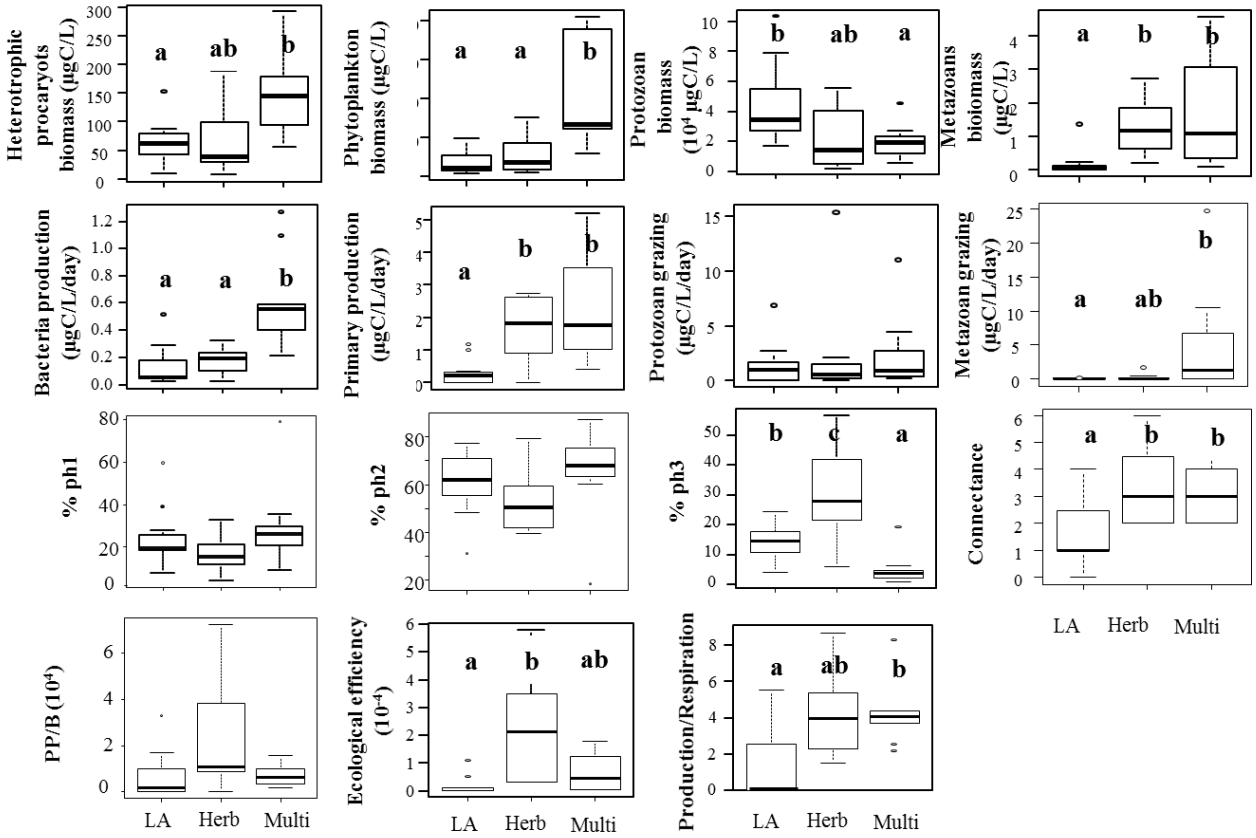
Heterotrophic procaryots biomass (µgC/L)
Phytoplankton biomass (µgC/L)
Protozoan biomass (10⁴ µgC/L)
Metazoans biomass (µgC/L)
Bacteria production (µgC/L/day)
Primary production (µgC/L/day)
Protozoan grazing (µgC/L/day)
Metazoan grazing (µgC/L/day)
% ph1
% ph2
% ph3
Connectance
PP/B (10⁴)
Ecological efficiency (10⁻⁴)
Production/Respiration
LA
Herb
Multi

Fig. 4.

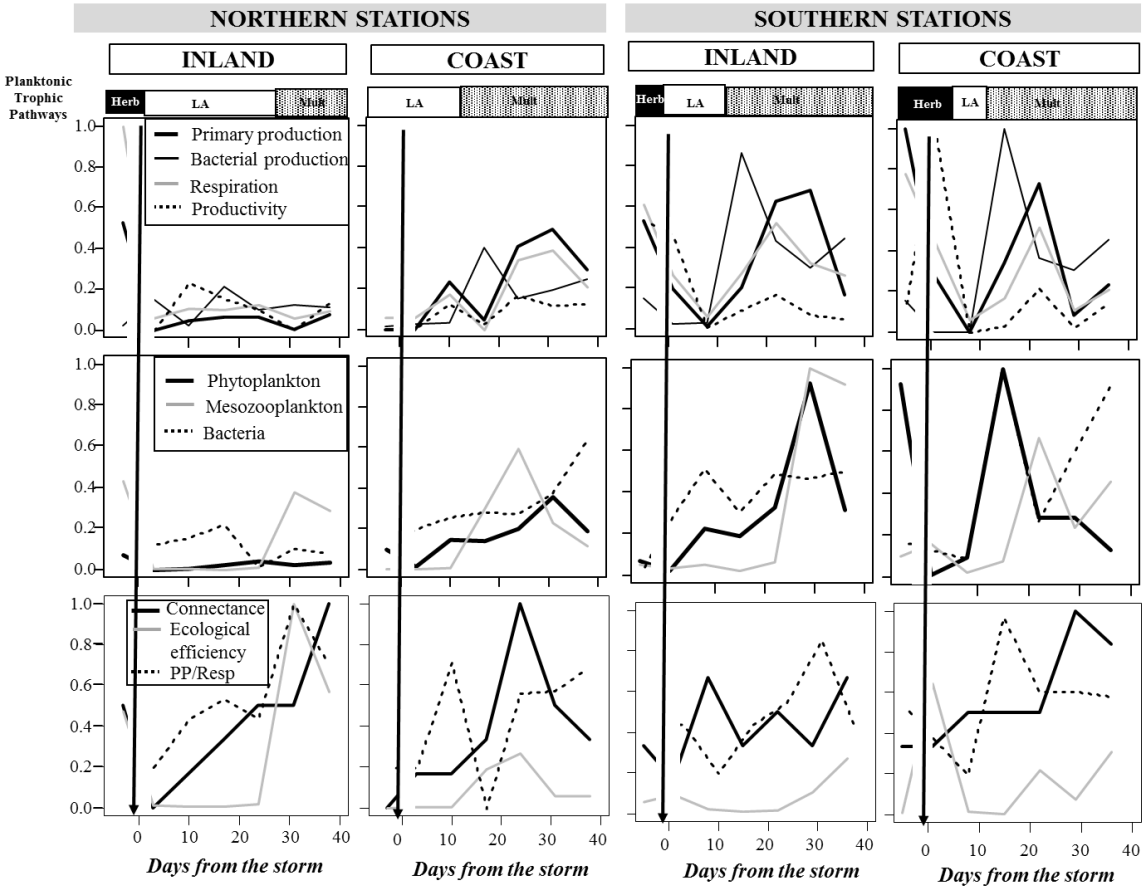
NORTHERN STATIONS
SOUTHERN STATIONS
INLAND
COAST
INLAND
COAST
Planktonic Trophic Pathways
Herb
LA
Mixt
Primary production
Bacterial production
Respiration
Productivity
Phytoplankton
Mesozooplankton
Bacteria
Connectance
Ecological efficiency
PP/Resp
Days from the storm

Fig. 5.

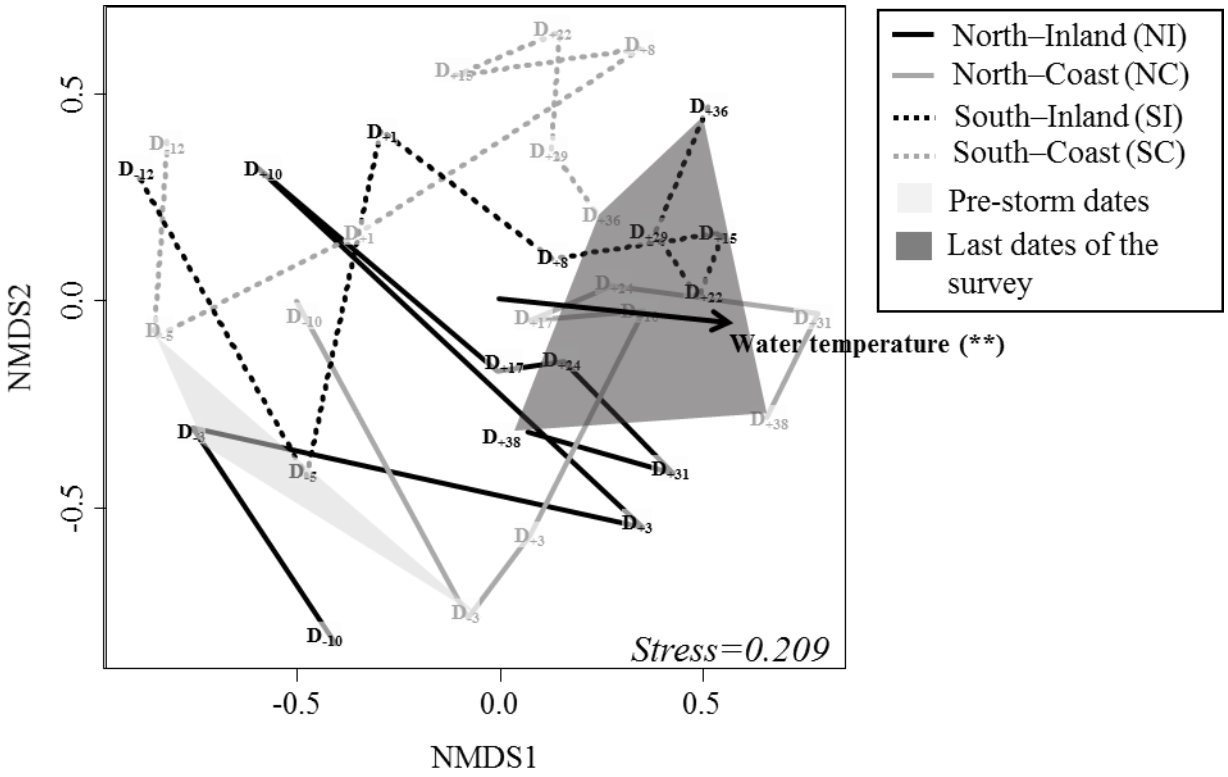
North–Inland (NI)
North–Coast (NC)
South–Inland (SI)
South–Coast (SC)
Pre-storm dates
Last dates of the survey
Water temperature (**)
Stress=0.209
NMDS1
NMDS2
-0.5
0.0
0.5

Fig. 6.

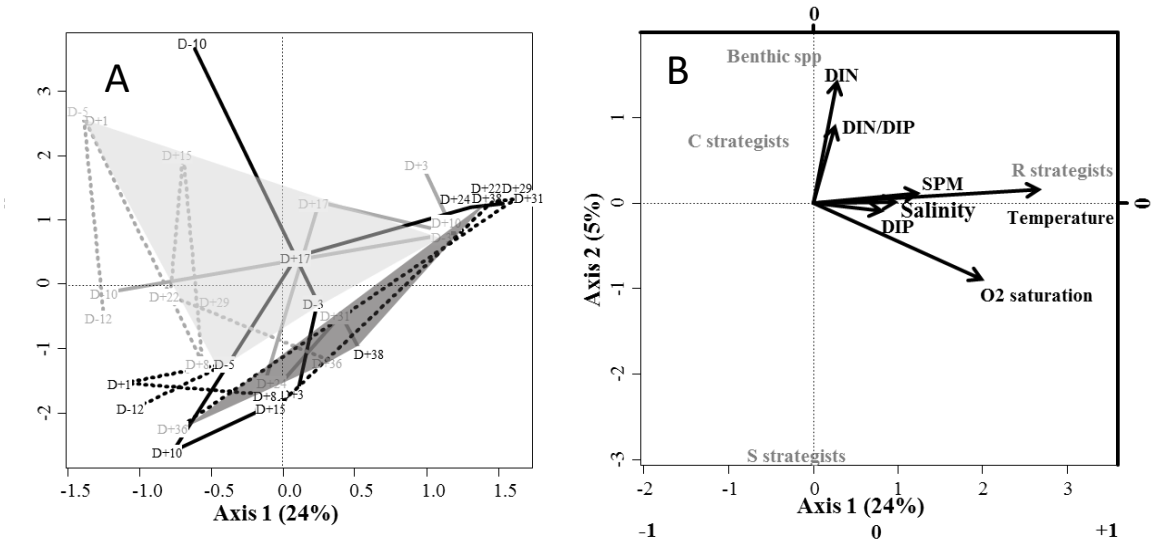
A
Axis 1 (24%)
B
Benthic spp
DIN
DIN/DIP
C strategists
R strategists
SPM
Salinity
Temperature
DIP
O2 saturation
S strategists
Axis 1 (24%)
Axis 2 (5%)

Fig. 7.

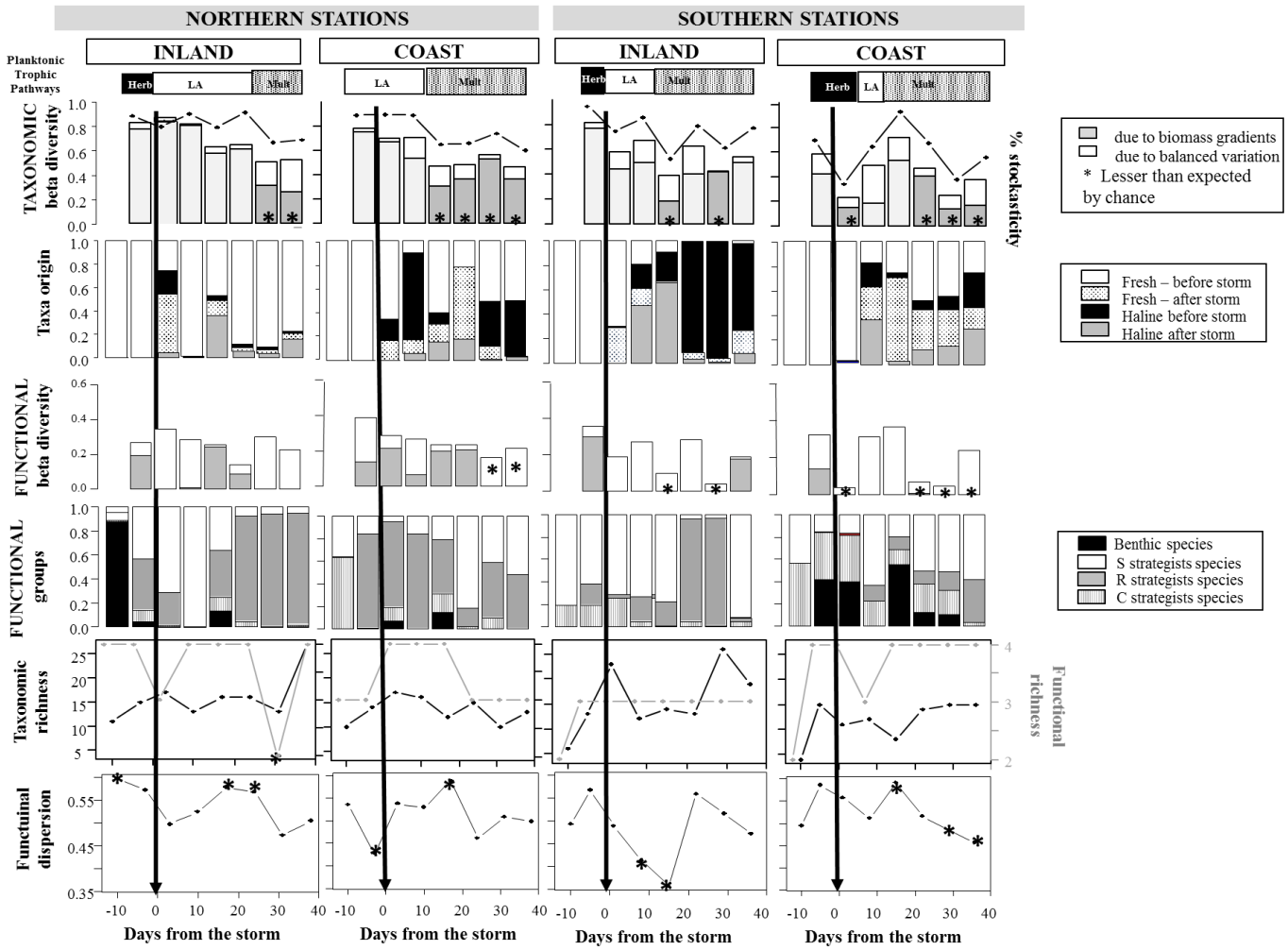
NORTHERN STATIONS
SOUTHERN STATIONS
INLAND
COAST
INLAND
COAST
Planktonic Trophic Pathways
Herb
LA
Mult
TAXONOMIC beta diversity
% stochasticity
Taxa origin
FUNCTIONAL beta diversity
FUNCTIONAL groups
Taxonomic richness
Functional richness
Functuinal dispersion
Days from the storm
due to biomass gradients
due to balanced variation
* Lesser than expected by chance
Fresh – before storm
Fresh – after storm
Haline before storm
Haline after storm
Benthic species
S strategists species
R strategists species
C strategists species

Fig. 8.