



Sources, quality and transfers of organic matter in a highly-stratified sub-Arctic coastal system (Saint-Pierre-et-Miquelon, NW Atlantic)

Guillaume Bridier^{a,*}, Tarik Meziane^b, Jacques Grall^{a,c}, Laurent Chauvaud^a, Sébastien Donnet^d, Pascal Lazure^e, Frédéric Olivier^{b,f}

^a Laboratoire des Sciences de l'Environnement Marin (LEMAR) UMR 6539 UBO/CNRS/IRD/Ifremer, Rue Dumont D'Urville, 29280 Plouzané, France

^b Biologie des Organismes et Écosystèmes Aquatiques (BOREA) UMR 7208 MNHN/SU/UNICAEN/UA/CNRS/IRD, 61 Rue Buffon CP53, 75005 Paris, France

^c Observatoire Marin, UMS 3113, Institut Universitaire Européen de la Mer, Rue Dumont D'Urville, 29280 Plouzané, France

^d Fisheries and Oceans Canada, Northwest Atlantic Fisheries Centre, 80 East White Hills Rd, St. John's NL, A1C 5X1, Canada

^e Ifremer, Univ. Brest, CNRS, IRD, Laboratoire d'Océanographie Physique et Spatiale (LOPS), IUEM, 29280 Plouzané, France

^f Station Marine de Concarneau, Muséum National d'Histoire Naturelle, Place de la Croix, 29900 Concarneau, France

ARTICLE INFO

Keywords:

Pelagic-benthic coupling
Seasonal stratification
Organic matter
Fatty acids
Stable isotopes
Subarctic ecosystems
Saint-Pierre et Miquelon archipelago
Newfoundland shelf

ABSTRACT

In response to ongoing global climate change, marine ecosystems in the northwest Atlantic are experiencing one of the most drastic increases in sea surface temperatures in the world. This warming can increase water column stratification and decrease surface nutrient concentrations, in turn impacting primary productivity and phytoplankton assemblages. However, the exact impacts of these changes on sources and quality of organic matter as well as its transfers to the benthic compartment remain uncertain. This survey characterized organic matter sources and quality within a highly-stratified sub-Arctic coastal system (Saint-Pierre and Miquelon) and described its transfer towards a biomass-dominant primary consumer, the sand dollar *Echinarachnius parma*. This study analyzed fatty acid and stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) composition of surface and bottom Particulate Organic Matter (s-POM and b-POM, respectively), Sedimentary Organic Matter (SOM) and sand dollar tissue along a near shore to offshore gradient during two contrasting seasons associated either with sharp or weak water column stratification (i.e. High vs Low Stratification Periods). Results revealed high relative abundances of polyunsaturated fatty acids (notably macro- and microalgae markers) in POM during the Low Stratification Period while the High Stratification Period was characterized by elevated relative abundance of saturated fatty acids indicating a higher organic matter degradation state. In addition, strong seasonal differences were also observed in food availability with four-fold higher concentrations in total suspended solids during Low vs High Stratification Periods. These results suggested thus multiple negative effects of stratification on pelagic-benthic coupling and POM quality. Lower nutrient repletion of surface waters during period of sharp stratification diminishes pelagic-benthic coupling by reducing food availability, POM quality and vertical transfer of organic matter. By contrast, the sediment-based diet of *E. parma* showed a low spatiotemporal variability reflecting the homogenous composition of the SOM. This study suggests that intensified water column stratification due to increasing sea surface temperatures may modify the pelagic-benthic coupling and future quality and composition of POM pools.

1. Introduction

Coastal benthic ecosystems are highly productive areas (e.g. Clavier et al. 2014) that provide essential ecosystem services such as seafood production and carbon sequestration (Barbier et al. 2011, Pendleton et al. 2012). However, their functioning and services can strongly depend on the quality and quantity of organic matter made available in

the ecosystem through processes like bioturbation, nutrient cycling and secondary production (Müller-Navarra et al. 2004, Wiekling and Kröncke 2005, Snelgrove et al. 2014, Campaña-Llovet et al. 2017). Decreases in the Particulate Organic Matter (POM) quality and quantity for example can reduce the efficiency of organic matter transfers to higher trophic levels. Benthic food webs may suffer subsequent impacts (e.g. shift from fresh matter-based to detritus-based food webs) including a decline in

* Corresponding author.

E-mail address: guillaume.bridier@live.ie (G. Bridier).

<https://doi.org/10.1016/j.pocean.2020.102483>

Received 19 May 2020; Received in revised form 13 November 2020; Accepted 16 November 2020

Available online 21 November 2020

0079-6611/© 2020 Elsevier Ltd. All rights reserved.

benthic secondary/tertiary production (e.g. Iken et al. 2010). The dependence of benthic ecosystems on organic matter quality and quantity suggests that perturbations to organic matter sources and fluxes induced by rising sea surface temperatures may also perturb pelagic-benthic coupling (defined here as the vertical flow of organic matter from the surface to the seafloor) (Campanyà-Llovet et al. 2017, Griffiths et al. 2017).

Numerous studies have investigated how pelagic-benthic coupling may evolve with declining surface water nutrient concentrations expected from rising sea surface temperatures and enhanced water column stratification (e.g. Wassmann & Reigstad 2011, Harrison et al. 2013, Randelhoff et al. 2020). A decrease in surface water nutrient concentrations may lead to a drop in phytoplankton production (Riebesell et al. 2009, Turner, 2015, D'Alelio et al. 2020) associated with pronounced shifts in the composition of phytoplankton communities (from large diatoms to smaller cells as flagellates; Kiørboe 1993, Finkel et al. 2010). In addition, warmer surface temperatures in thermally-stratified waters can enhance POM degradation by increasing heterotrophic bacteria metabolic activity (Piontek et al. 2009, Wohlers et al. 2009). These reduce carbon fluxes towards bottom waters (Bopp, 2005, Turner, 2015, Griffiths et al. 2017). In contrast, the impacts of increased stratification on the quality and composition of the organic matter exported towards the seafloor as well as their consequences on the benthic food webs remain unknown.

This research investigated the quality and sources of organic matter (i.e. surface and bottom Particulate Organic Matter, or s-POM and b-POM, respectively, and Sedimentary Organic Matter, or SOM) and their transfers towards a dominant secondary producer, the sand dollar *Echinarachnius parma* in a highly stratified coastal marine ecosystem of the sub-Arctic archipelago Saint-Pierre and Miquelon (SPM) in the NW Atlantic. SPM is an ideal study area due to an exceptionally sharp vertical water column stratification in late-August/mid-September, when temperatures drop abruptly from 18 °C at the surface to 0–2 °C at 80 m depth (Lazure et al. 2018, Poitevin et al. 2018). Climate change is expected to intensify this stratification. The Newfoundland-Labrador continental shelf is experiencing one of the highest increase in sea surface temperature in the world (i.e. + 1 °C between 1982 and 2006, Belkin, 2009). A recent study also detected diurnal internal waves along SPM's shallow continental shelf (30–60 m depth) during the stratified season (Lazure et al. 2018). Although these waves remain poorly studied, they play a critical role in near shore ecosystem functioning by stimulating nutrient replenishment and primary production in surface waters through increased turbulence and mixing through the pycnocline (Wang et al. 2007, Jantzen et al. 2013, Woodson 2018). Increased water stratification will make the thermocline less responsive to perturbations generated by internal waves (i.e. less turbulence and thermocline vertical motion, Woodson 2018). Given these oceanographic factors, climate change is likely to modify the quality and sources of organic matter available around SPM through increased stratification, with potentially cascading effects on benthic food-webs.

In order to better understand these impacts, we conducted two sampling surveys around SPM during periods of either pronounced (August 2017) or weak (July 2018) stratification along a near shore to offshore gradient (i.e. pelagic-benthic coupling strength gradient; four stations). Quality, sources and transfers of organic matter were assessed through fatty acid and stable isotope analyses since these tools can identify the origin and quality of organic matter at different trophic levels in aquatic ecosystems (e.g. Søreide et al. 2013, Connelly et al. 2015, Mathieu-Resuge et al. 2019). The main goals of this study were to (1) describe spatial variability and seasonality (i.e. periods of strong vs weak stratification) in POM and SOM from a poorly studied sub-Arctic ecosystem, (2) assess the potential impact of seasonal sea surface temperature increases on quality and sources of POM and SOM, and their transfers to a dominant primary consumer (i.e. *E. parma*).

2. Materials and methods

2.1. Study site

The study was conducted in SPM (46°50'N, 56°20'W), a sub-Arctic archipelago located about 20 km south of Newfoundland (Fig. 1). Sea surface temperatures usually show large seasonal variations (from sub-zero temperatures in March – April to 18 °C in August – September) while bottom water temperatures (i.e. below 80 m) remain stable throughout the year (0–2 °C; Lazure et al. 2018, Poitevin et al. 2018). The annual primary production occurs mainly during the phytoplankton bloom in April (Harrison et al. 2013, Pepin et al. 2017). Aqua MODIS satellite data (OCI algorithm) over the last two decades have revealed inter-annual variations in which a second phytoplankton bloom may occur in September/October (Figure S1). SPM is a coastal oligotrophic environment deprived of major surface nutrient inputs from local rivers (C. Jauzein pers. com., Doré et al. 2020). Although the Saint-Lawrence River is a major source of freshwater for the NW Atlantic, its outflows are deflected toward the western part of Cabot Strait and do not influence SPM waters (e.g. Wu et al. 2012). The absence of river influence on SPM environments has been further confirmed by two recent paleoecology studies using primary production proxies (Poitevin et al. 2019, Doré et al. 2020).

Considering the physical characteristics, SPM is located within the contiguous part of the coastal branch of the Labrador Current flowing through the Avalon channel towards the NW, south of Newfoundland (De Young and Hay 1987, White and Hay 1994, Wu et al., 2012, Lazure et al., 2018). This current speed varies seasonally (strongest in fall/winter, weakest in summer; Wu et al., 2012) with an annual mean value of 10 cm s⁻¹ in the middle of Saint-Pierre's Channel (Hay and De Young, 1989). Although mean currents were not measured within our study area, they are probably weaker than average due to higher bottom friction in shallow water areas. Sedimentation rates have not been estimated for SPM but global estimates (usually ranging from 1 to 150 m d⁻¹, Turner, 2015) suggest POM sedimentation time is much shorter than one season (e.g. minimum estimates of 1 m d⁻¹ implying that POM would settle in 80 days at the deepest station).

Lazure et al. (2018) reported remarkably large near-daily oscillations of near-bottom temperatures around SPM. During the stratification period (July–September), the interaction of surface tides with local bathymetric features generates diurnal internal waves, which propagate around the archipelago guided by bathymetry. The large amplitude of these internal waves (40–60 m) and the sharp thermocline can generate temperature gradients along the seafloor of as much as 11 °C over a period of hours in mid-September. The 15–25 m depth of the thermocline and internal wave amplitudes lead to strong perturbations between 30 and 60 m depth (respective depths of thermocline elevations and depressions). Water column zones above 30 m and below 60 m do not appear to experience the direct effects of these internal waves.

2.2. Sampling strategy

Sampling was conducted in late August 2017 and early July 2018. These timeframes respectively correspond to a “High Stratification Period” and a “Low Stratification Period” observed for the study area (see Lazure et al. 2018). During both sampling campaigns, four stations were sampled along a bathymetric gradient labeled L1 (10 m) to L4 (80 m) and spanning contrasted zones of pelagic-benthic coupling (Fig. 1, Table 1). At each station, 10 L of seawater per replicate were collected by Niskin bottles at one meter below the surface for surface POM samples (s-POM) and one meter above the seafloor for bottom POM samples (b-POM). CTD probes (Seabird 911plus, coupled to a Wetlab ECO FL chlorophyll-a fluorescence sensor in 2017; RBR concerto in 2018) were deployed during sampling at each station to record depth profiles of temperature, salinity and fluorescence. Salinity was not measured from station L4 in July 2018 due to logistical reasons and fluorescence was

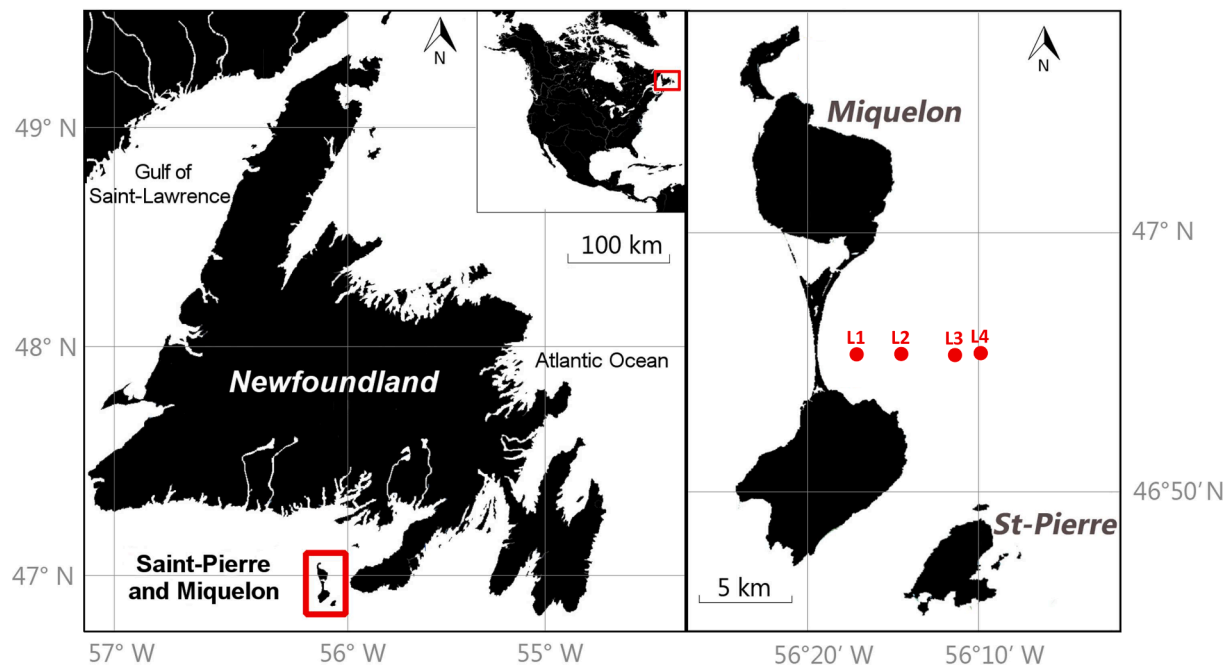


Fig. 1. Map of the Saint-Pierre and Miquelon's archipelago (SPM) showing station F3B14 and the four Langlade's stations (L1, L2, L3 and L4; modified from Poitevin et al. 2018).

Table 1

Site coordinates, date and biological material sampled in August 2017 and July 2018 around Saint-Pierre and Miquelon.

Station	Latitude	Longitude	Sampling dates	Depth (m)	Biological material / Physical parameters
L1	46°55.514' N	56°17.279' W	29/08/2017 & 04/07/2018	11	s-POM, b-POM, SOM (only in 2017), <i>E. parma</i> , macroalgae, CTD
L2	46°55.678' N	56°14.654' W	30/08/2017 & 02/07/2018	25	s-POM, b-POM, SOM, <i>E. parma</i> , macroalgae, CTD
L3	46°55.468' N	56°11.549' W	28/08/2017 & 05/07/2018	60	s-POM, b-POM, <i>E. parma</i> (only in 2018), CTD
L4	46°55.909' N	56°09.936' W	28/08/2017 & 07/07/2018	88	s-POM, b-POM, <i>E. parma</i> (only in 2017), CTD (only in 2017)
F3B14	46°48' N	56°05' W	01/07/2017 to 31/08/2017	125	CTD

not measured in July 2018 due to the absence of a fluorescence sensor. An oceanographic mooring (composed of 28 Onset HOBO TidbiT temperature sensors ranging from 15 m below the surface to 120 m) was deployed from May 2017 to May 2018 to assess water circulation as well as water column stratification seasonality and short-term variability around SPM (i.e. down to hourly timescales). Temperature profiles sampled at 10 min intervals were then averaged on a weekly basis for the first week of July and the last week of August 2017. The mooring was deployed to the northeast of Saint-Pierre island at 125 m depth (F3B14 in Fig. 1). Scuba divers collected SOM samples at stations L1 and L2 in 2017 and only at L2 in 2018 (Table 1). SOM was collected using a 450 ml

syringe sucking the upper millimeters of the sediment surface (i.e. 0–3 mm, surface area $\approx 625 \text{ cm}^2$). The upper few millimeters of the sediment are expected to be highly-responsive to particle fluxes (e.g. Danovaro et al. 1999) and are more likely to be resuspended and thus assimilated by benthic invertebrates than deeper sediment layers. In order to track organic matter transfers to primary consumers, several sand dollar individuals (i.e. 3–9) were collected at each station by either scuba divers or using a “Rallier du Baty” dredge. *E. parma* was selected in our study as a model species for two reasons: (1) *E. parma* is a biomass-dominant species in SPM benthic habitat (i.e. this species has therefore a preponderant role on the organic matter flowing through the benthic food web) and (2) *E. parma* was the only species found at every stations from 10 to 80 m (J. Grall per. obs.). Five macroalgae species (*Agarum clathratum*, *Desmarestia viridis*, *Halosiphon tomentosus*, *Porphyra* spp., *Saccharina latissima*) were also collected in 2017 to assess their potential contribution to POM, SOM and sand dollar diet (Table 1). These five palatable macroalgae represent a major part of the seaweed biomass around SPM and are known to be potentially major food sources for benthic invertebrates (Perez et al. 2013, Renaud et al. 2015, Gaillard et al. 2017).

2.3. Sample analyses

2.3.1. Preliminary information

We decided to investigate seasonal variations in quality, composition and transfers of organic matter between High and Low Stratification Periods by analyzing fatty acid and stable isotope composition of *E. parma* as well as various sources of organic matter (i.e. POM, SOM and macroalgae). Fatty acids have been shown to constitute powerful tools to identify the origin of the organic matter in aquatic ecosystems (e.g. Meziane & Tsuchiya 2000) since fatty acid profiles (i.e. the list and relative contributions [%] of all fatty acids contained in one lipid sample) of primary producers are usually characteristics of specific taxonomic groups (see Table 2). Moreover, some fatty acids as PolyUnsaturated Fatty Acids (PUFAs) can be used to describe the diet of secondary consumers since they are generally transferred conservatively (Dalsgaard et al. 2003, Gaillard et al. 2017, Thyrring et al. 2017). Stable isotopes are a useful complementary tools to study organic matter

Table 2

List of fatty acids used in this study as tracer and descriptor of the organic matter origin and quality (modified from Bridier et al. 2019). SFA, PUFA and EFA refer to Saturated, PolyUnsaturated and Essential Fatty Acid, respectively.

Descriptor of	Fatty acids	References
Organic matter origin		
Diatoms	16:1 ω 7, 16:4 ω 1, 20:5 ω 3	Reuss & Poulsen (2002), Dalsgaard et al. (2003), Kelly & Scheibling (2012)
Dinoflagellates	18:4 ω 3, 22:6 ω 3	Napolitano et al. (1997), Kelly & Scheibling (2012)
Macroalgae (Phaeophyceae)	18:2 ω 6, 18:3 ω 3, 18:4 ω 3, 20:5 ω 3	Kelly & Scheibling (2012), De Cesare et al. (2017), Gaillard et al. (2017)
Organic matter quality		
Degraded organic matter	Dominance of SFA (e.g., 14:0, 16:0, 18:0)	Rhead et al. (1971), Connelly et al. (2015), Connelly et al. (2016)
Labile and nutritionally rich organic matter	Dominance of PUFA and EFA (here, sum of 20:4 ω 6, 20:5 ω 3, and 22:6 ω 3)	Soudant et al. (1996), Parrish et al. (2005), Parrish (2009)

transfers in secondary producers (Fry 2006, Perez et al. 2013, De Cesare et al. 2017, Gaillard et al. 2017). Their high sensitivity to biological and physical processes allow also to distinguish organic matter sources according to their compartment (pelagic vs benthic), freshness (fresh vs refractory) or origin (phytoplankton, microphytobenthos, macroalgae, seagrass, Kharlamenko et al. 2001, McTigue et al. 2015, Mathieu-Resuge et al. 2019). Although POM and SOM pools are inherently highly variable and relate on environmental variations occurring in the ecosystem (e.g. variations in primary production or river inputs), fatty acid and stable isotope analyses are generally adapted to track high temporal variations within 1–2 weeks (Riera and Richard 1997, Lorrain et al. 2002, Leu et al. 2006, Mayzaud et al. 2013). Similarly, turnover rates of animal organs (e.g. digestive gland, stomach) are usually sufficiently high to identify monthly variations of diets of benthic invertebrates (e.g. Pazos et al. 2003, Paulet et al. 2006). Therefore, such a high response of organic matter fatty acid profiles and stable isotope signatures to environmental fluctuations should allow us to track high-frequency variations in organic matter quality and composition related to seasonal changes in stratification conditions. Conversely, the short temporal resolution of these trophic markers eliminates any influences of the spring phytoplankton bloom on our results (occurring usually in April; Pepin et al. 2017, Maillet et al. 2019).

2.3.2. Preliminary treatments

POM samples were obtained by filtering seawater samples on pre-combusted GF/F Whatman® microfiber filters (diameter: 47 mm; pore: 0.7 μ m) until clogging when possible (mean filtered volume = 8.9 ± 1.4 l; range: 4.2–10.0 l max). SOM samples represented a mixture of organic matter (including microphytobenthos and detritus), inorganic particles and seawater. SOM samples were agitated and allowed to settle for one hour before filtration on GF/F filters (mean filtered volume = 0.450 ml). All filters and biological samples (i.e. urchins and macroalgae) were stored at -20 °C in the field laboratory (Ifremer/DTAM, Saint-Pierre) and transferred frozen by boat and train (-20 °C) to the MNHN-Paris where they were stored at -80 °C until further analyses. Prior to analysis, all samples were freeze-dried at -50 °C for at least 5 h (48 h for animal and macroalgae tissues) and then immediately weighed. Urchin stomachs (i.e. intestinal tissues and gut content) were dissected and ground prior to stable isotope and fatty acid analyses. POM and SOM GF/F filters were divided into two fractions for stable isotope and fatty acid analyses. The mass of organic matter on each half-filter was estimated using the equation given in Bridier et al. (2019):

$$M(X) = \frac{W_{\text{Half filter}}}{W_{\text{Whole filter}}} X (W_{\text{Whole filter}} - W_{\text{Precombusted filter}})$$

Where M (X) is the mass (mg) of POM or SOM used for the fatty acid or stable isotope analysis, and W is the dry weight of half, whole or pre-combusted filters.

2.3.3. Fatty acid analyses

Fatty acid extraction followed the Bligh and Dyer method (1959) as modified in Meziane & Tsuchiya (2002). Samples were sonicated in a distilled water-chloroform-methanol solution (1:1:2, v:v:v) for 20 min. After this extraction, samples were dissolved in a 1:1 (v:v) distilled water-chloroform solution and then centrifuged (1409 X g, 5 min). After this physical separation, the solution containing lipid phases (i.e. 2 ml) was transferred into separate tubes, and subjected to additional rounds of phase transfer, sonication and centrifugation. Lipid were then dried under a dinitrogen (N_2), diluted in a sodium hydroxide-methanol solution (1:2, v:v, [NaOH] = 2 mol.l⁻¹) and heated at 90 °C for 90 min for fatty acid saponification. This reaction was stopped by the addition of 500 μ l of hydrochloric acid (37%). Lipid fractions were then dissolved in 3 ml chloroform, transferred in separate tubes and dried under a dinitrogen (N_2) gas. Finally, lipid extracts were heated at 90 °C for 10 min with 1 ml of a methanolic boron trifluoride solution (BF₃-CH₃OH, 14%) in order to convert fatty acids into Fatty Acid Methyl Esters (FAMES). At the end of the reaction, lipids were retrieved in 2 ml of chloroform and stored at -20 °C.

Fatty acid quantification was performed using a Varian CP-3800 gas chromatograph equipped with a Supelco® Omegawax® Capillary GC 320 column and He carrier gas. Fatty acid identifications were validated using retention times and mass spectra measured from a commercial reference standard (Supelco® 37 Component FAME Mix). Mass spectra were measured with a Varian 220-MS coupled to a Varian 450-GC using a He carrier gas. Fatty acid nomenclature is defined as X:Y ω Z where X is the number of carbon atoms, Y the number of double bonds and Z the position of the last double bond relative to the methyl group. Concentration of each fatty acid peak was determined using an internal commercial standard (23:0, 5 mg.l⁻¹) and the equation given in Schomburg (1987):

$$C_{FA} = \left(\frac{A_{FA}}{A_{C23}} \times \frac{C_{23}}{M_f} \right)$$

Where C_{FA} is the fatty acid concentration (μ g.g⁻¹), A_{FA} is the fatty acid peak area, A_{C23} is the 23:0 peak area, C_{23} is the 23:0 quantity (μ g) added to each sample and M_f is the mass of organic matter measured from the half-filter.

2.3.4. Stable isotope analyses

Half-filters and sand dollar guts were fumigated over 4 and 48 h, respectively, with 37% HCl to remove inorganic carbon (Lorrain et al. 2003, Søreide et al. 2006). The surface layer of POM and SOM filters were scraped into 10–30 mg fragments which were then transferred to tin capsules. Macroalgae and gut samples were first ground into a fine powder using a ball mill. Fractions of about 1 mg were then transferred to tin capsules.

Samples were analyzed at the University of California Davis Stable Isotope Facility (UC Davis SIF) using two different elemental analyzers (PDZ Europa ANCA-GSL, Sercon macroalgae/animal tissues and an Elementar Vario EL Cube elemental analyzer for filters) interfaced with an isotope ratio mass spectrometer (PDZ Europa 20–20, Sercon). Isotopic ratios are expressed using δ notation corresponding to deviation (‰) in ¹³C/¹²C and ¹⁵N/¹⁴N ratios from the international standards (Vienna PeeDee Belemnite and Air, respectively). The δ notation from Peterson & Fry (1987) is as follows:

$$\delta X = \left[\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] \times 1000$$

Where δX is $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ and R is the corresponding $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ ratio.

2.4. Statistical analyses

Detecting meaningful covariation in the different datasets collected required the application of PERMANOVA statistical tests frequently used in marine ecological surveys. Statistical analyses were performed using the R software (R Core Team 2017) and “vegan” package (Oksanen et al. 2019). In contrast to ANOVAs, well designed PERMANOVA analyses do not depend on assumptions of normality and homoscedasticity

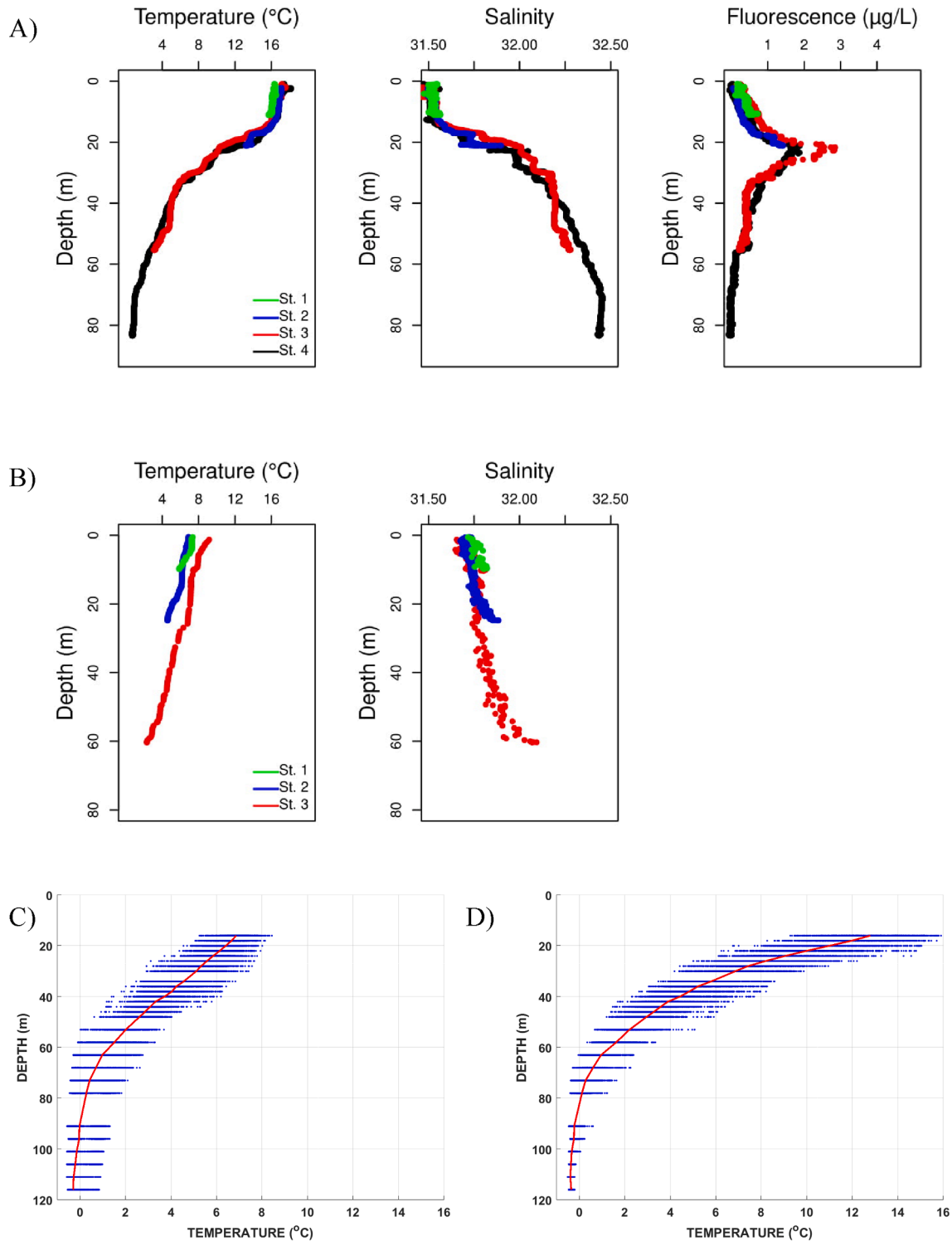


Fig. 2. Temperature (°C), Salinity and Fluorescence (µg.l⁻¹) depth profiles at sample stations in either August 2017 (L1 to L4, A) or July 2018 (L1 to L3, B). Averaged (red lines) and raw temperatures (blue dots) at station F3B14 from 1 to 7th July 2017 (C) and from 25th to 31th August 2017 (D).

(Anderson & Walsh 2013). Three-factor PERMANOVA was not appropriate given strong interactions among factors. We applied one-way PERMANOVA to test the seasonal variability of POM fatty acid profiles. A two-way PERMANOVA procedure was applied to test the effects of station and depth on POM fatty acid profiles for both seasons. We also

used pairwise PERMANOVA to test for interactions between station and depth factors for both seasons. The effect of season on SOM fatty acid profiles could not be tested due to the low number of replicates (i.e. only 2 replicates in July 2018). Spatial variability of SOM fatty profiles was tested through one one-way PERMANOVA. Similar to fatty acid profiles,

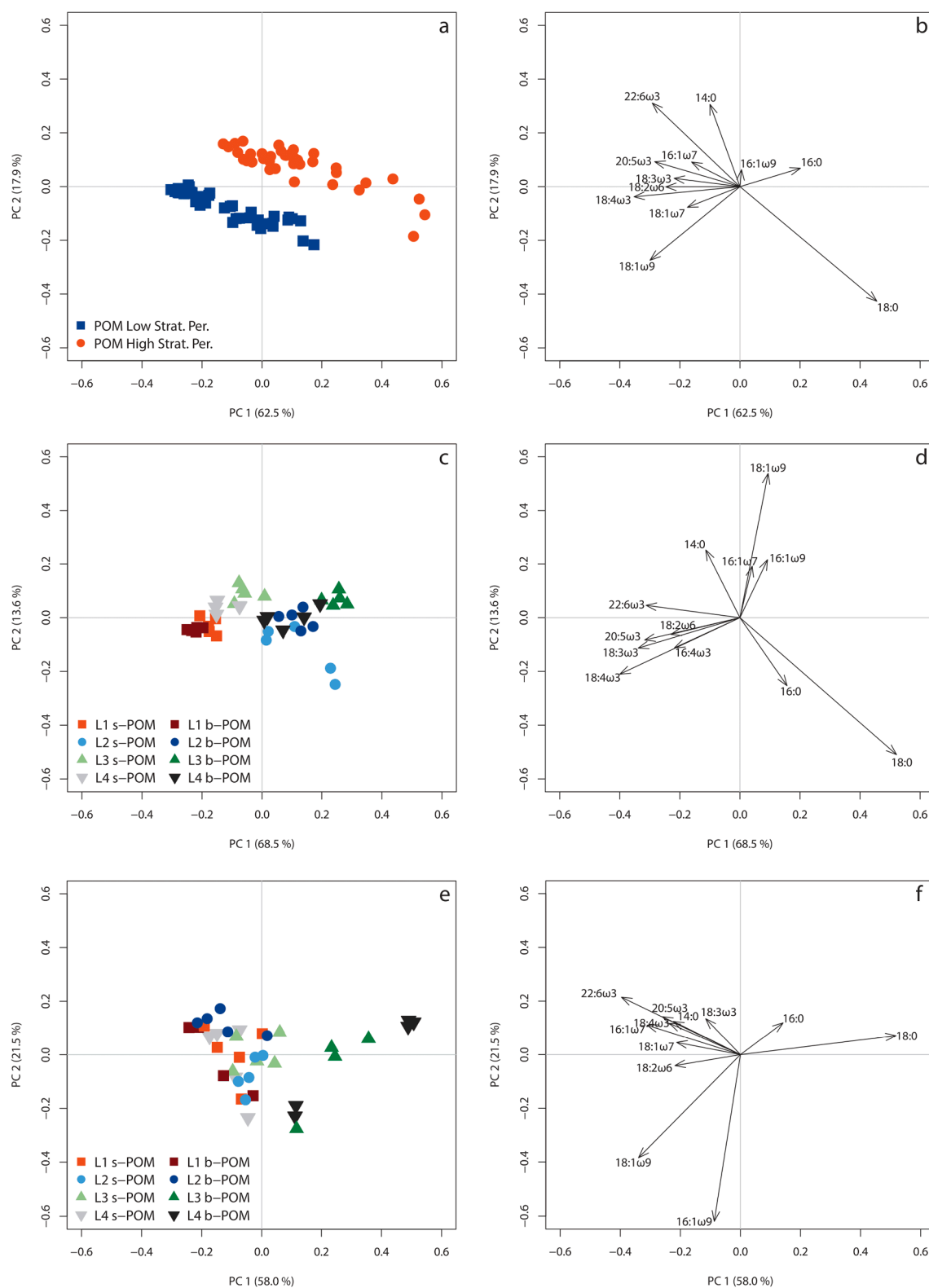


Fig. 3. Principal Component Analyses (PCA) based on Hellinger-transformed POM fatty acid percentages from both High and Low Stratification Periods (a, b) as well as from separate Low (c, d) and High (e, f) Stratification Periods. Individual factor maps are represented in left plots (a, c, e) while variables factor maps are showed and right plots, respectively (b, d, f). Variable factor maps include only the 12 most discriminant fatty acids.

effects of seasons and stations-depth on POM stable isotope signatures were tested by one-way and two-way PERMANOVAs, respectively. Station effects on SOM stable isotope signatures during the High Stratification Period and station-depth effects influencing stable isotope signatures from sand dollars were also tested by one-way and two-way PERMANOVAs, respectively.

Finally, one Principal Component Analysis (PCA) was computed on the entire POM fatty acid data set to identify POM seasonal variation. In addition, two others PCAs were realized separately on POM fatty acid profiles from High and Low Stratification Periods in order to highlight spatial and depth variations. The PCA procedure used a Hellinger similarity matrix in order to reduce the influence of rare fatty acids in the ordination (Legendre and Gallagher 2001).

3. Results

3.1. Environmental measurements

During the High Stratification Period, CTD profiles showed pronounced water column stratification characterized by temperatures above 16 °C in surface waters and below 4 °C in bottom waters (i.e. below 50 m, Fig. 2A). The thermocline occurred at around 15–25 m, where temperature decreases from 15 °C to 9 °C. This zone also exhibits a peak in fluorescence (Fig. 2A). During the Low Stratification Period, datasets showed more gradual declines in temperature. These decreased continuously from about 10 °C or less at the surface to 4 °C at the bottom (Fig. 2B). Fig. 2 shows averaged temperature profiles for the first week of July and the last week of August 2017 (Fig. 2C and 2D, respectively). These profiles show a clear increase in stratification in which the temperature gradient increases from about 5 °C to 10 °C between 15 and 60 m. This shift matches that observed in CTD profiles taken during Low and High Stratification Periods. Consistency across sampled years (2017–2018) suggests that inter-annual variation is negligible compared to seasonal variation in terms of their relative influence on water column stratification.

3.2. Fatty acids profiles of POM and SOM samples

3.2.1. Particulate organic matter

Sixty fatty acids were identified in POM and SOM samples (51 and 52 fatty acids during High and Low Stratification Periods, respectively). Only fatty acids with a relative abundance higher than 0.2% in all samples were represented in Table S1 (Supplementary material). POM fatty acid profiles varied considerably between High and Low Stratification Periods ($p < 0.001$, Table S1). Seasonal differences in POM composition were mainly observed for PUFAs. Relative to those collected during the High Stratification Period, samples collected during the Low Stratification Period contained higher levels of PUFAs, especially 18:2 ω 6, 18:3 ω 3, 18:4 ω 3 and 20:5 ω 3 (Fig. 3a, b, Σ PUFA range = 5.3–36.7% and 3.0–19.7% for Low and High Stratification Periods, respectively). Samples collected during the High Stratification Period contained larger levels of saturated Fatty Acids (SFA) relative to those collected during the Low Stratification Period (Σ SFA range = 53.7–80.6% and 38.2–61.5% for High and Low Stratification Periods, respectively). POM quantity showed strong temporal variation with four-fold higher concentrations of total suspended solids (TSS) during the Low Stratification Period (mean [TSS] = 4.0 ± 1.0 mg l⁻¹) compared to the High Stratification Period (mean [TSS] = 1.5 ± 1.1 mg l⁻¹). TSS samples exhibited similar fatty acid concentrations for both seasons (mean [FA] = 4.4 ± 2.8 μ g mg⁻¹ TSS for High Stratification vs 5.0 ± 4.0 μ g mg⁻¹ TSS for Low Stratification Period).

During the Low Stratification Period, all stations showed statistically distinctive POM fatty acid profiles ($p < 0.05$). Spatial variation was particularly pronounced between L1 and the other stations sampled since both s-POM and b-POM samples from L1 displayed the highest relative contributions of PUFAs (especially 18:2 ω 6, 18:3 ω 3, 18:4 ω 3 and

20:5 ω 3; Fig. 3 c, d). Samples collected during the High Stratification Period showed high spatial variation in b-POM fatty acid profiles (Table S3). The High Stratification b-POM samples also varied considerably between L1-L2 and L3-L4 stations ($p < 0.01$; Table S3). This variation appeared primarily as higher relative contributions of PUFAs (especially 18:2 ω 6, 18:4 ω 3, 20:5 ω 3 and 22:6 ω 3) at L1-L2 relative to those measured from L3-L4 (Fig. 3e, f).

3.2.2. Sedimentary organic matter

Table 3 and Figure S2 show seasonal differences in SOM fatty acid profiles between High and Low Stratification Periods. SOM samples from the Low Stratification Period displayed higher levels of PUFAs (especially for 18:4 ω 3 and 20:5 ω 3) compared with samples collected during the High Stratification Period (Σ PUFA = 12.9% vs 5.7% for Low and High Stratification Periods, respectively). By contrast, SFA (16:0 and 18:0 in particular) contributions were lower in samples from the Low Stratification Period relative to those collected during the High Stratification Period (Σ SFA = 39% vs 77.4%). MonoUnsaturated Fatty Acid (MUFA) contributions differed significantly between both seasons (Σ MUFA = 9.3 vs 44.8% for High and Low Stratification Periods, respectively), especially for 16:1 ω 7 (3.4 vs 23.8%) and 18:1 ω 9 (1.6 vs 9.4%). However, no spatial variations were observed between L1 and L2 stations during the High Stratification Period ($p > 0.05$).

3.3. Stable isotopes signatures of POM and SOM samples

POM samples showed a general decrease in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from High to Low Stratification Periods ($p < 0.001$, Fig. 4). Two-way PERMANOVA detected significant station, depth and station-depth interaction effects on POM's $\delta^{13}\text{C}$ values ($p < 0.01$) but not $\delta^{15}\text{N}$ values ($p > 0.05$) during the High Stratification Period. During the Low Stratification Period, station and depth factors exerted influence on POM $\delta^{13}\text{C}$ values ($p < 0.01$), while only depth factors and station-depth interactions exerted effects on $\delta^{15}\text{N}$ values ($p < 0.05$). Supplementary materials list pairwise PERMANOVA results (Table S3).

The SOM samples collected during the Low Stratification Period showed more depleted $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values than samples collected during the High Stratification Period ($\approx$ depletion of -1.6 and -1.4 ‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively). During the High Stratification Period, SOM from L2 displayed significantly higher $\delta^{15}\text{N}$ and lower $\delta^{13}\text{C}$ values than L1 ($p < 0.05$).

3.4. Fatty acids profiles and stable isotopes signatures from sand dollars

Overall, fatty acid profiles from *E. parma* stomachs showed relatively low variation between years and stations. All samples contained relatively high proportions of PUFAs (range = 46–49.8%), especially 20:5 ω 3 (range = 26.7–29.2%). Presence of 16:4 ω 1, 18:4 ω 3, 20:4 ω 6 and 22:6 ω 3 were also noticed in fatty acid profiles (Table 3). Samples contained lower proportions of SFAs (Σ SFA range = 18–23.4%), which consisted primarily of 14:0, 16:0 and 18:0. Proportions of MUFAs ranged between 27.9 and 31.2% and were dominated by 16:1 ω 7 (range = 7.7–12.5%) and 20:1 ω 15 (range = 5.2–8.8%).

Although *E. parma* samples showed significant different fatty acid profiles between High and Low Stratification Periods ($p < 0.01$), lipid profiles from these two years were highly similar (83.14% of similarity, Table 3). *E. parma* fatty acid profiles showed significant differences among stations during the High Stratification Period ($p < 0.01$) but not during the Low Stratification Period ($p > 0.05$).

The *E. parma* samples collected during the Low Stratification Period gave slightly enriched carbon isotopic values relative to those collected during the High Stratification Period ($p < 0.01$, Fig. 5a, b). *E. parma* samples collected from different stations did not show significant differences in carbon isotopic values ($p > 0.05$). Nitrogen isotopic values from *E. parma* samples differed between L3 and L1-L2 stations ($p < 0.01$) but not between seasons ($p > 0.05$). During the High Stratification

Table 3

Fatty acid (FA) composition from sand dollar and Sedimentary Organic Matter (SOM) samples collected in August 2017 and July 2018. Values correspond to mean percentages from 3 to 9 samples with standard deviation in brackets. SFA, MUFA, PUFA, BrFA and EFA refer to Saturated, MonoUnsaturated, PolyUnsaturated, Branched and Essential fatty acids, respectively. EPA: Eicopensaconoic acid (i.e. 20:5 ω 3); DHA: Docohexaconoic acid (i.e. 22:6 ω 3), nd: not detected. Fatty acid percentages < 2% in all samples are not shown. The entire table is provided in the appendix Supplementary material (see Table S2).

	High Stratification Period (August 2017)				Low Stratification Period (July 2018)			
	<i>Echinarachnius parma</i>			SOM	<i>Echinarachnius parma</i>			SOM
	Station 1	Station 2	Station 4	Stations 1 & 2	Station 1	Station 2	Station 3	Station 2
	N = 3	N = 3	N = 4	N = 7	N = 6	N = 5	N = 9	N = 2
14:0	5.2 (1.2)	4.8 (0.4)	4.9 (0.6)	6.7 (1.3)	4.8 (1.2)	5 (0.4)	4.9 (0.7)	6 (0.6)
15:0	0.9 (0.2)	0.9 (0.2)	0.8 (0.1)	2.6 (0.5)	0.8 (0.1)	0.9 (0.3)	0.7 (0.1)	2.2 (0.2)
16:0	9.8 (2.3)	10.8 (1.2)	7.2 (0.8)	43.7 (4.1)	9.6 (1.8)	10.8 (1.4)	8.2 (1.0)	23.5 (1.0)
18:0	5.6 (0.9)	5.2 (0.7)	3.9 (0.3)	17.7 (3.8)	5.3 (1.1)	5.2 (0.8)	4.9 (0.7)	4.7 (0.1)
Σ SFA	23.0 (4.1)	23.4 (2.8)	18.0 (1.2)	77.4 (8.2)	22.1 (3)	23.1 (2.2)	20 (1.4)	39 (0.2)
16:1 ω 7	7.7 (2.9)	8.1 (0.4)	12.5 (2.5)	3.4 (3.5)	8 (3)	10.9 (3.5)	9.7 (2.4)	23.8 (1.5)
16:1 ω 9	tr	0.2 (0.0)	0.3 (0.0)	0.5 (0.2)	0.2 (0.1)	0.4 (0.5)	0.2 (0.1)	4.6 (2.2)
18:1 ω 7	2.5 (0.2)	3.1 (0.6)	3.0 (0.2)	1.2 (1.1)	2.6 (0.3)	2.8 (0.4)	3.2 (0.2)	2.5 (0.1)
18:1 ω 9	1.9 (0.9)	2.3 (0.3)	1.8 (0.3)	1.6 (1.4)	5.1 (2.3)	4.7 (1.6)	4.2 (1.9)	9.4 (2.2)
20:1 ω 7	2.6 (0.4)	2.4 (0.1)	2.4 (0.5)	0.4 (0.2)	2.6 (0.4)	2.4 (0.1)	2.4 (0.5)	0.3 (0.0)
20:1 ω 9	1.2 (0.1)	1.3 (0.1)	1.2 (0.3)	0.3 (0.2)	2.4 (0.9)	1.9 (0.2)	2.3 (0.5)	0.3 (0.0)
20:1 ω 15	8.8 (2.0)	6.5 (1.5)	5.9 (1.7)	nd	7.4 (1.5)	5.2 (1.2)	6.8 (1.0)	nd
21:1 ω 9	2.3 (0.6)	1.6 (0.4)	1.5 (0.2)	0.5 (0.5)	2.3 (0.6)	1.6 (0.4)	1.5 (0.2)	nd
Σ MUFA	29.4 (1.2)	27.9 (1.6)	31.2 (1.1)	9.3 (6.7)	30.4 (1.5)	29.9 (1.3)	30.8 (1.3)	44.8 (1.4)
16:4 ω 1	1.4 (0.7)	1.3 (0.3)	2.2 (0.5)	nd	1.6 (1)	1.9 (1)	1.7 (0.7)	0.6 (0.0)
18:4 ω 3	2.1 (0.1)	2.5 (0.5)	2.7 (0.2)	0.4 (0.2)	2.5 (0.5)	2.9 (0.3)	3.2 (0.5)	1.4 (0.4)
20:2 Δ 5, 13	2.2 (0.5)	2.0 (0.1)	2.0 (0.5)	nd	1.8 (0.5)	2 (0.5)	2.2 (0.3)	nd
20:2 Δ 5, 11	5.1 (1.3)	4.1 (0.3)	3.6 (0.8)	nd	4.5 (1.5)	3.5 (0.8)	3.7 (0.5)	nd
20:4 ω 6	1.8 (0.4)	2.0 (0.2)	2.9 (0.8)	0.4 (0.3)	1.3 (0.4)	1.8 (0.6)	1.6 (0.2)	0.5 (0.0)
20:5 ω 3	28.5 (4.0)	26.7 (2.2)	28.5 (1.1)	1.3 (1.0)	29.2 (3.4)	26.9 (2.2)	28.7 (2.2)	4.2 (0.5)
22:6 ω 3	1.7 (0.0)	4.1 (1.8)	2.3 (0.3)	0.4 (0.2)	1.4 (0.3)	1.8 (0.2)	2.1 (0.1)	0.5 (0.1)
Σ PUFA	47.1 (5.4)	47.8 (4.2)	49.8 (2.3)	5.7 (1.7)	47 (3.3)	46 (2.3)	48.3 (2.3)	12.9 (1.0)
Σ BrFA	0.5 (0.1)	0.9 (0.0)	1.0 (0.1)	6.7 (0.7)	0.6 (0.1)	0.9 (0.1)	0.9 (0.2)	3.3 (0.2)
Σ EFA	32.1 (4.3)	32.8 (3.7)	33.8 (2.0)	2.2 (1.3)	32 (3.5)	30.6 (1.9)	32.4 (2.2)	5.2 (0.7)
Σ PUFA/ Σ SFA	2.1 (0.6)	2.1 (0.4)	2.8 (0.3)	0.1 (0.0)	2.2 (0.4)	2 (0.3)	2.4 (0.3)	0.3 (0.0)
EPA/DHA	16.9 (2.6)	7.1 (2.4)	12.7 (1.6)	2.9 (1.7)	20.8 (3.2)	15 (1.3)	13.9 (1)	8.3 (1.3)
[FA] (mg/g)	31.7 (23.0)	22.8 (19.7)	52.5 (38.5)	0.2 (0.1)	78.0 (43.0)	63.9 (33.7)	90.3 (23.1)	1.8 (1.1)

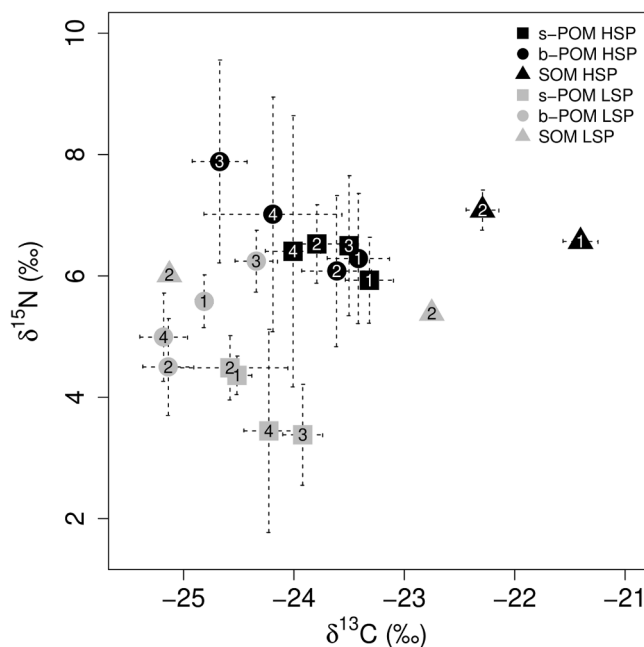


Fig. 4. Mean ($\pm$ SD) stable isotope signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of surface and bottom Particulate Organic Matter (s-POM and b-POM, respectively) and Sedimentary Organic Matter (SOM) samples collected during High Stratification (August 2017, black symbols) and Low Stratification (July 2018, grey symbols) periods (HSP and LSP, respectively). Numbers within symbols refer to sampled stations.

Period, *E. parma* and SOM samples gave similar respective $\delta^{13}\text{C}$ values of $-21.4 \pm 0.1\text{‰}$ vs $-21.4 \pm 0.2\text{‰}$ for L1 and $-22.2 \pm 0.3\text{‰}$ vs $-22.3 \pm 0.1\text{‰}$ for L2 (Fig. 5a).

4. Discussion

4.1. Spatiotemporal variations in POM sources

During both seasons, microalgal fatty acids represented significant proportions of POM fatty acid profiles. Dinoflagellate (22:6 ω 3, 18:4 ω 3) and diatom markers (20:5 ω 3, 16:1 ω 7) were notably present (Fig. 4, Table S1). Macroalgae also made significantly apparent contributions to the organic matter pool as indicated by the presence of 18:2 ω 6 and 18:3 ω 3 PUFAs (range Σ (18:2 ω 6 + 18:3 ω 3) = 1.4–13.5%, Table S1). Stable isotope signatures were consistent with a contribution from the macroalgae *A. clathratum* and possibly several other mixed species (e.g. *D. aculeata* and *S. latissima*). Higher relative percentages of 18:2 ω 6 and 18:3 ω 3 indicated that macroalgal contributions to POM were much higher during the Low Stratification Period relative to the High Stratification Period conditions. On the whole, the Low Stratification Period was characterized by fresh and high quality organic matter as indicated by high levels of EFAs (Essential Fatty Acids) and PUFAs (especially 18:2 ω 6, 18:4 ω 3, 20:5 ω 3). Higher TSS concentrations observed during this season may also indicate higher food availability compared to that available during the High Stratification Period (Table S1).

Our results revealed also major variations along the cross-shore transect. Strong spatial variations were observed in both surface and bottom waters during the Low Stratification Period due to a predominance of macroalgal sources for POM collected from near shore environments while POM from more distal environments (i.e. depth > 20 m) appeared to originate from a mixture of microalgal and macroalgal sources. In contrast, POM sources and quality were homogenous in

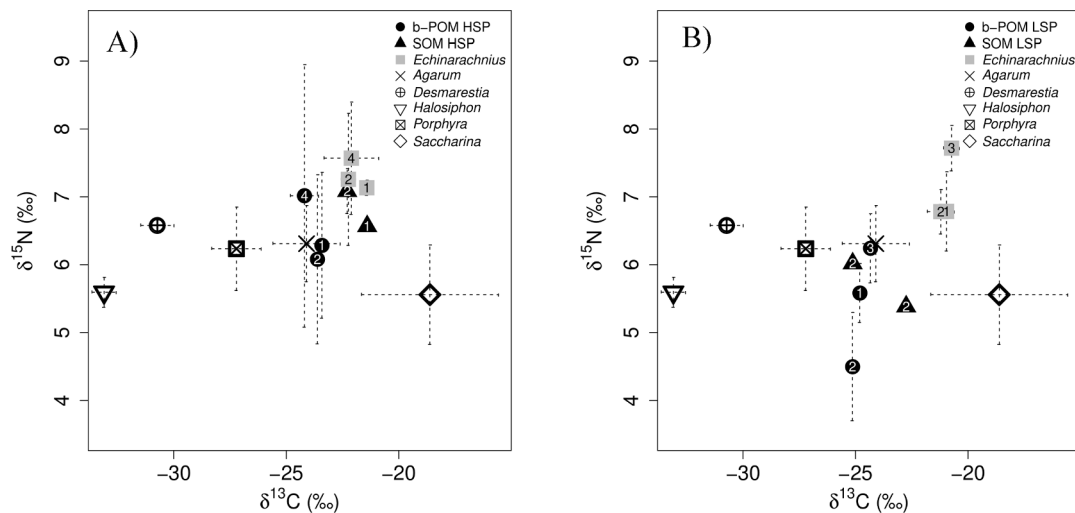


Fig. 5. Mean ($\pm$ SD) stable isotope signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) measured from *Echinarachnium parma* stomachs and the organism's potential food sources during High Stratification (August 2017, A) and Low Stratification (July 2018, B) periods (HSP and LSP, respectively). b-POM: bottom Particulate Organic Matter; SOM: Sedimentary Organic Matter. Numbers within symbols indicate stations.

surface waters during the High Stratification Period. Bottom water samples showed however higher organic matter quality in shallow areas (depth < 30 m) due to higher contributions of microalgal material to POM (fatty acid markers 16:1 ω 7, 18:4 ω 3, 20:5 ω 3, 22:6 ω 3).

4.2. Influence of stratification on POM quality and pelagic-benthic coupling

Differences in pelagic trophic conditions may arise from seasonal drivers of water column stratification and vertical mixing. Seawater surface temperatures at SPM rise in March and increase steadily until mid-September when water column stratification reaches its maximum (Lazure et al. 2018, Poitevin et al. 2018). Nutrient profiles from SPM waters show a typical vertical distribution with depleted nutrient concentrations at the surface (especially for nitrates and silicates) and nutrient-rich bottom waters (C. Jauzein pers. com.) during the stratified period. Extremely high-water column stratification during the High Stratification Period may then act as a barrier to nutrient exchange between surface and sub-surface waters. Limitation in nutrient vertical fluxes during the High Stratification Period and the absence of significant horizontal nutrient input to this oligotrophic environment by rivers (Doré et al. 2020) likely limit primary production compared to the Low Stratification Period. The much lower TSS concentrations recorded during the High Stratification Period ([TSS] = 1.5 ± 1.1 vs 4.0 ± 1.0 mg l⁻¹ for the High and Low Stratification periods, respectively) support this interpretation.

Spatial variation in POM fatty acid profiles during the High Stratification Period also seems to reflect the influence of stratification on pelagic-benthic coupling and b-POM freshness. Numerous studies have shown that nutrient limitations under increased stratification lead to shifts in the size distributions of phytoplankton communities from a predominance of larger to smaller cells (Kjørboe 1993, Falkowski & Oliver 2007, Finkel et al. 2010). Tighter coupling between smaller phytoplankton cells and heterotrophic bacteria promotes more efficient recycling of organic matter in surface waters (through regenerated primary production) and limits vertical export to sediment (Legendre & Le Fèvre 1995, Bopp, 2005, Turner, 2015). Warmer surface temperatures during the High Stratification Period may also enhance POM degradation by stimulating heterotrophic microbial activity (Piontek et al. 2009, Wohlers et al. 2009, Turner, 2015). Moreover, slower sedimentation rates of smaller cells usually increase the residence time of phytoplankton within the water column extending thus exposure to oxidation and microbial degradation (Turner, 2002, Guidi et al. 2009, Marañón

2015). Together, these processes reduce the quantity and freshness of the organic matter reaching the seabed (Budge and Parrish 1998, Parrish et al. 2005, Guidi et al. 2009, Turner, 2015). On both deep stations, extremely low PUFA levels were observed in bottom compared to surface waters that could reflect effects of stratification on phytoplankton size structure, microbial degradation and pelagic-benthic coupling strength. The higher relative levels of PUFAs measured in near shore bottom water samples (<30 m depth) may derive from autotrophic production of organic matter around the pycnocline supported by (small) local nutrient pulses from subsurface waters. Such subsurface autotrophic production has been widely reported in sub-Arctic/Arctic oligotrophic and highly-stratified surface waters. It is usually the result of a compromise between the low nutrient concentrations at the surface and low light availability in deep waters (Martin et al. 2010, Tremblay et al. 2015). Part of the subsurface fluorescence peak observed in this study may also reflect higher photosynthetic pigment concentrations in shade-adapted phytoplankton species growing in subsurface waters (Fennel and Boss 2003, Tremblay et al. 2015). Spatial variation in POM during the Low Stratification Period indicates a more efficient pelagic-benthic coupling under condition of continuous water column stratification. Smaller shifts in PUFA levels between surface and bottom waters during this period support this interpretation (Table S1).

Lower food availability and lower organic matter quality during the High Stratification Period conditions may also reflect the influence of sharp stratification on internal waves. Pronounced water column stratification caused by higher sea surface temperatures can result in more stable internal waves (Nielsen et al. 2004, Woodson 2018) and prevent their breakage (and their action on turbulence and nutrient mixing). This may have especially affected near shore stations (i.e. L1 and L2) during the High Stratification Period. Amplitudes of internal waves are usually dampened by water column stratification (Walter et al. 2014, Woodson 2018). Weaker vertical oscillation of the thermocline during the High Stratification Period may thus limit deep water nutrient inputs to surface waters.

Longer sedimentation rates during the High Stratification Period imply that POM is probably more subjected to horizontal advection during settling. This means that b-POM deposited at a given location may not originate from the same location at the surface. This effect introduces the possibility that seasonal variation in organic matter composition and quantity reflects POM advection rather than differences in stratification. Pronounced differences between surface and bottom currents (i.e. ~ 10 cm s⁻¹) and a low sedimentation rate (e.g. 5 m d⁻¹, i.e. 16 days of sedimentation between the surface and 80 m depth,

Turner, 2015) would place POM sampled at 80 m depth during the High Stratification Period ~130 km from surface waters where it originated. However, primary production and stratification are generally homogeneous around the Newfoundland Shelf (Craig and Colbourne, 2005, Cyr and Larouche 2015, Pepin et al. 2017). Therefore, although b-POM may have undergone some advection during the High Stratification Period, this would not influence POM quality and quantity since the impact of stratification on primary production and vertical sedimentation rates are likely homogeneous across the Newfoundland Shelf.

4.3. Additional contribution of macroalgae to POM

The high levels of 18:2 ω 6 and 18:3 ω 3 (Fig. 4, Table S1) reported here suggest that macroalgae represent a major source of POM around SPM, especially during the Low Stratification Period. An additional fatty acid, the 20:4 ω 6 marker, displays high levels in macroalgae samples but low relative abundance in POM samples (Table S4). This may arise from the lower relative chemical stability of certain macroalgal fatty acids. Also, microalgal fatty acids detected in POM derive primarily from living cells whereas macroalgal fatty acids mostly derive from thalli detritus subjected to more intensive degradational processes. The 18:2 ω 6 and 18:3 ω 3 may also derive from seagrass or terrestrial organic matter (Kelly and Scheibling 2012, Mathieu-Resuge et al. 2019). The distinctive $\delta^{13}\text{C}$ values measured from POM relative to known ranges for seagrass ($\delta^{13}\text{C} > -12\text{‰}$) and terrestrial organic matter ($\delta^{13}\text{C} < -28\text{‰}$) however argue against a contribution from these sources (see Peterson 1999).

Field observation also support the interpretation of a significant autochthonous macroalgal contribution to POM. Scuba diving surveys conducted near the sampling area have found that shallow areas are populated by the two macroalgal species *A. clathratum* and *S. latissima* (P. Poitevin pers. obs.). Kelp forests can constitute major sources of dissolved and particulate organic matter in marine coastal ecosystems via exudation and fragmentation processes (e.g. blade erosion, thalli dislodgment, blade shedding, Krumhansl & Scheibling 2011, Krumhansl & Scheibling 2012, Leclerc et al. 2013, Pessarrodona et al. 2018). Fragmentation processes depend on several factors (i.e. grazing, variations of temperature, hydrodynamics) that vary with time and season (Krumhansl & Scheibling 2011, Krumhansl & Scheibling 2012, Simonson et al. 2015). Although variation in macroalgal input between Low and High Stratification Periods should depend on such factors, their specific roles are difficult to assess. Larger proportions of macroalgal detritus in the shallowest area likely reflect autochthonous inputs (Krumhansl & Scheibling 2011, Krumhansl & Scheibling 2012), whereas lower macroalgae contributions in deeper areas should either reflect different degrees of thalli fragmentation or transport from shallow areas (Krumhansl & Scheibling 2012, Renaud et al. 2015, Filbee-Dexter et al. 2018).

Differentiating macroalgal input from the effects of stratification on the quality and composition of POM is complex. The higher proportions of Σ PUFA found in L2, L3 and L4 POM samples during the Low Stratification Period (e.g. s-POM = 13.7–25.8%) relative to those measured from the High Stratification Period (s-POM = 9.5–14.4%) along with similar concentrations of macroalgal markers (e.g. 18:2 ω 6, 18:3 ω 3) suggest that organic matter quality reflects the absence of sharp vertical stratification rather than macroalgal input. By contrast, strong seasonal variation in the macroalgal markers from the L1 POM samples coincided with relatively little variation in microalgal markers (e.g. 16:1 ω 7, 22:6 ω 3). This suggests that POM seasonality for most near shore stations reflected macroalgal pulses. Assessing the effects of stratification on the export and sedimentation of macroalgal detritus into deep water areas was not feasible in this study. Other studies have described the salient roles of temperature (Simonson et al. 2015), grazing (Wernberg & Filbee-Dexter 2018) or wave exposure (Krumhansl & Scheibling 2011) on these transfers, but none have yet investigated how stratification may limit such transport and deposition. Detection of fatty acid macroalgal markers in s-POM samples from offshore stations along with their

absence from b-POM samples (e.g. 18:2 ω 6 and 18:3 ω 3, station L3 and L4, Fig. 4, Table S1) suggest that stratification may limit sedimentation of macroalgal detritus. Given the future increases of stratification expected from rising sea surface temperatures, future research should seek to constrain these processes.

4.4. Organic matter transfers and spatiotemporal variations in SOM sources

Significant seasonal differences observed in SOM fatty acid profiles reflect different organic matter quality and origins between High and Low Stratification Periods (Table 3). Large levels of SFAs observed during the High Stratification Period (14:0, 16:0 and 18:0, especially) reveal a high degradation state of the organic matter (Table 2). Sources contributing to SOM during the High Stratification Period were limited and consisted of minor inputs from microphytobenthos (Σ of 20:5 ω 3 and 16:1 ω 7 < 5%) and macroalgae (Σ of 18:2 ω 6 and 18:3 ω 3 < 1%). SOM samples from the Low Stratification Period contained higher concentrations of PUFAs and EFAs (Σ PUFA = 12.9 and Σ EFA = 5.2 for Low Stratification vs Σ PUFA = 5.7% and Σ EFA = 2.2% for High Stratification) including diatom markers (16:1 ω 7, 20:5 ω 3 and 16:4 ω 1). These high temporal variations of SOM sources and quality result likely from the microphytobenthos dynamics, with a major bloom during the Low Stratification Period (illustrated by much higher contributions of 16:1 ω 7, 20:5 ω 3 and 16:4 ω 1) turning toward degraded OM during the High Stratification Period (reflected by high levels of Σ SFA). Such a pattern is consistent with the typical dynamics of microphytobenthos which usually includes one single massive bloom per year (e.g. occurring in April in the Gulf of Mexico and in the Bay of Brest, Pinckney & Lee 2008, Chatterjee et al. 2013; in July in the Seto Inland Sea, Yamaguchi et al. 2007). Although POM samples collected during the Low Stratification Period contained higher relative contributions of macroalgal fatty acids, these markers appeared in low concentrations in SOM profiles (Σ 18:2 ω 6, 18:3 ω 3, 18:4 ω 3 and 22:6 ω 3 < 1.6%) demonstrating that they represent only a minor source for the SOM pool. Low macroalgal and high microphytobenthic contributions in SOM samples may reflect a strong microbial degradation of macroalgal detritus by benthic heterotrophic bacteria and an effective recycling of nutrients released through this microbial loop by benthic microalgae (e.g. Hardison et al. 2010).

Several authors questioned about the trophic ecology of *E. parma*, especially if this species feed either on the sediment or on suspended particles from the water column (e.g. Seilacher 1979, Ellers & Telford 1984, Miller et al. 1992). Some studies have suggested that vertical orientations observed among several sand dollar species (e.g. *Dendraster excentricus*, *Encope michelini*, *Heliophora orbiculus*, *Rotula augusti*, Merrill & Hobson 1970, Lawrence et al. 2004 and references therein) may indicate filter-feeding (Timko 1976, O'Neill 1978) while others (Seilacher 1979, Ellers & Telford 1984, Miller et al. 1992) suggest that deposit-feeding occurs by using podia from both oral and aboral sides to select and transport food particles toward the mouth. Our study supports this latter hypothesis. Since carbon isotopic fractionation between primary and secondary producers is usually relatively low or nonexistent in high-turnover tissue (e.g. digestive glands, Gaillard et al. 2017, De Cesare et al. 2017, Bridier et al. 2019), similar $\delta^{13}\text{C}$ values for both SOM and sand dollar samples indicates a diet dominated by SOM. Such hypothesis is also confirmed by fatty acids profiles results: a dominant suspension feeding activity should have implied a high spatial variability of sand dollars' fatty acids profiles reflecting the high spatial variability of b-POM. Our almost identical sand dollars' fatty acids profiles from 10 to 80 m suggest thus a homogenous SOM pool along stations (although we were not able to collect SOM samples in the deepest areas). Previous studies have reported similar findings of homogenous SOM composition between near shore and offshore environments noting that SOM represents long-term accumulation from the water column (Chouvelon et al. 2015, Schaal et al. 2016).

Spatial homogeneity in fatty acid profiles from SOM and sand dollar samples contrasts the above interpretations that stratification diminishes both POM quality and pelagic-benthic coupling. However, the predominance of the 16:1 ω 7, 16:4 ω 1 and 20:5 ω 3 diatom markers indicates that microphytobenthos dominate the SOM pools. This dominance may explain the decoupling of POM and SOM pools. Homogenous benthic production along the bathymetric gradient could reflect the adaptation of microphytobenthos to both low light availabilities and nutrient depletion (by using nutrients released from the sediment, MacIntyre et al. 1996, Leynaert et al. 2009). A major and homogenous contribution of this food source to the diet of *Echinarachnius parma* with depth could thus counterbalance the impact of stratification on POM quality and pelagic-benthic coupling strength.

4.5. Conclusion

Characterization of organic matter sources and quality revealed multiple negative effects of highly stratified water column on the organic matter sources and quality from a sub-Arctic Archipelago. This study detected weaker pelagic-benthic coupling, lower food availability and more degraded organic matter delivered to benthic compartment during the High Stratification Period. Such observations may be explained by the strong water column stratification that would abate vertical organic matter transfer and limit nutrient replenishment of surface waters by reducing surface/sub-surface nutrient exchanges. By contrast, pronounced water column stratification would allow more efficient pelagic-benthic coupling and nutrient exchanges around the pycnocline and may facilitate nutrient upwelling through internal waves. Macroalgal material represents a major source of high organic matter quality in shallower areas. Considering complex processes of thalli fragmentation that includes numerous, interrelated environmental and biological factors, the intensity and seasonality of the pulses of macroalgal detritus could however vary significantly in time. In the context of ongoing climate change, our results suggest that intensified water column stratification associated with rising sea surface temperatures may strongly modify pelagic-benthic coupling as well as future quality and composition of POM pools from North-West Atlantic shelf ecosystems. Conversely, shallow areas may be more resilient to changes in water conditions due to local contribution of high-quality organic matter from benthic primary producers.

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.

Acknowledgements

We are grateful to Erwan Amice for his invaluable help in the field and Najet Thiney for her advice and assistance in the lab. A big thanks to Gilles Barnathan, Gaëtane Wielgosz-Collin and Aurélie Couzinet-Mossion for their help in identifying non-methylene-interrupted fatty acids in sand dollar samples. We are also very grateful to Herlé Gorager for his kindness and logistical support at the Ifremer/DTAM laboratory (Saint-Pierre-et-Miquelon). Warm thanks to Thomas Burel for help with macroalgae species identification as well as graphical edits to Fig. 4. We sincerely thank Pierre Poitevin for his advice on seafloor habitats around Saint-Pierre-et-Miquelon. We are greatly indebted to the crew from the N/O Antéa as well as the Club Nautique Saint-Pierrais for their help in the field. Funding was provided by the French National Centre for Scientific Research (CNRS-EC2CO-Matisse), Ifremer and the Observatoire Marin de l'IUEM (USM3113). Logistics were supported by DT-INSU and GENAVIR. This study is an international collaboration between the BeBEST International Laboratory (co-funded by UQAR/ISMER and CNRS-INEE), the Muséum National d'Histoire Naturelle (MNHN),

Ifremer and the Northwest Atlantic Fisheries Centre (NAFC). This work was conducted as a part of Ph.D. dissertation by Guillaume Bridier and supported through the Université de Bretagne Occidentale/LIA BeBEST and the "Allocation de Recherche Doctorale" from the Brittany Region Council. F3B14 mooring deployment, maintenance and recovery was funded by the Fisheries and Oceans Northwest Atlantic Fisheries Center (DFO-NAFC) and executed from the Canadian Coast Guard Ship Vladkov. This article greatly benefited from comments made by three anonymous referees.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.poccean.2020.102483>.

References

- Anderson, M.J., Walsh, D.C., 2013. PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: What null hypothesis are you testing? *Ecol. Monogr.* 83, 557–574. <https://doi.org/10.1890/12-2010.1>.
- Barbier, E., Hacker, S., Kennedy, C., Koch, E., Stier, A., Silliman, B., 2011. The value of estuarine and coastal ecosystem services. *Ecol. Monogr.* 81, 1521–1531. <https://doi.org/10.1890/10-1510.1>.
- Belkin, I.M., 2009. Rapid warming of large marine ecosystems. *Prog. Oceanogr.* 81, 207–213. <https://doi.org/10.1016/j.poccean.2009.04.011>.
- Bligh, E.G., Dyer, W.J., 1959. A rapid method of total lipid extraction and purification. *Can. J. Biochem. Physiol.* 37, 911–917. <https://doi.org/10.1139/y59-099>.
- Bopp, L., 2005. Response of diatoms distribution to global warming and potential implications: a global model study. *Geophys. Res. Lett.* 32, L19606. <https://doi.org/10.1029/2005GL023653>.
- Bridier, G., Meziane, T., Grall, J., Chauvaud, L., Sejr, M.K., Menneteau, S., Olivier, F., 2019. Coastal waters freshening and extreme seasonality affect organic matter sources, quality, and transfers in a High Arctic fjord (Young Sound, Greenland). *Mar. Ecol. Prog. Ser.* 610, 15–31. <https://doi.org/10.3354/meps12857>.
- Budge, S.M., Parrish, C.C., 1998. Lipid biogeochemistry of plankton, settling matter and sediments in Trinity Bay, Newfoundland. II. Fatty acids. *Org. Geochem.* 29, 1547–1559. [https://doi.org/10.1016/S0146-6380\(98\)00177-6](https://doi.org/10.1016/S0146-6380(98)00177-6).
- Campañá-Llovet, N., Snelgrove, P.V.R., Parrish, C.C., 2017. Rethinking the importance of food quality in marine benthic food webs. *Prog. Oceanogr.* 156, 240–251. <https://doi.org/10.1016/j.poccean.2017.07.006>.
- Chatterjee, A., Klein, C., Naegelen, A., Claguen, P., Masson, A., Legoff, M., Amice, E., L'Helguen, S., Chauvaud, L., Leynaert, A., 2013. Comparative dynamics of pelagic and benthic micro-algae in a coastal ecosystem. *Estuar. Coast. Shelf Sci.* 133, 67–77. <https://doi.org/10.1016/j.ecss.2013.08.015>.
- Chouvelon, T., Schaal, G., Grall, J., Pernet, F., Perdriau, M., A-Pernet, E.J., Le Bris, H., 2015. Isotope and fatty acid trends along continental shelf depth gradients: Inshore versus offshore hydrological influences on benthic trophic functioning. *Prog. Oceanogr.* 138, 158–175. <https://doi.org/10.1016/j.poccean.2015.07.013>.
- Clavier, J., Chauvaud, L., Amice, E., Lazure, P., van der Geest, M., Labrosse, P., Digne, A., Carlier, A., Chauvaud, S., 2014. Benthic metabolism in shallow coastal ecosystems of the Banc d'Arguin, Mauritania. *Mar. Ecol. Prog. Ser.* 501, 11–23. <https://doi.org/10.3354/meps10683>.
- Connolly, T.L., McClelland, J.W., Crump, B.C., Kellogg, C.T., Dunton, K.H., 2015. Seasonal changes in quantity and composition of suspended particulate organic matter in lagoons of the Alaskan Beaufort Sea. *Mar. Ecol. Prog. Ser.* 527, 31–45. <https://doi.org/10.3354/meps11207>.
- Connolly, T.L., Businski, T.N., Deibel, D., Parrish, C.C., Trela, P., 2016. Annual cycle and spatial trends in fatty acid composition of suspended particulate organic matter across the Beaufort Sea shelf. *Estuar. Coast. Shelf Sci.* 181, 170–181. <https://doi.org/10.1016/j.ecss.2016.08.016>.
- Craig, J.D.C., Colbourne, E.B., 2005. Trends in Stratification on the inner Newfoundland Shelf. Fisheries and Oceans Canada, Canadian Science Advisory Secretariat, Ottawa.
- Cyr, F., Larouche, P., 2015. Thermal fronts atlas of Canadian coastal waters. *Atmos.-Ocean* 53, 212–236. <https://doi.org/10.1080/07055900.2014.986710>.
- D'Alélio, D., Rampone, S., Cusano, L.M., Morfino, V., Russoc, L., Sanseverino, N., Cloern, J.E., Lomas, M.W., 2020. Machine learning identifies a strong association between warming and reduced primary productivity in an oligotrophic ocean gyre. *Sci. Rep.* 10, 3287. <https://doi.org/10.1038/s41598-020-59989-y>.
- Dalsgaard, J., John, M.S., Kattner, G., Müller-Navarra, D., Hagen, W., 2003. Fatty acid trophic markers in the pelagic marine environment. *Adv. Mar. Biol.* 46, 225–340. [https://doi.org/10.1016/S0065-2881\(03\)46005-7](https://doi.org/10.1016/S0065-2881(03)46005-7).
- Danovaro, R., Marrale, D., Della Croce, N., Parodi, P., Fabiano, M., 1999. Biochemical composition of sedimentary organic matter and bacterial distribution in the Aegean Sea: trophic state and pelagic-benthic coupling. *J. Sea Res.* 42, 117–129. [https://doi.org/10.1016/S1385-1101\(99\)00024-6](https://doi.org/10.1016/S1385-1101(99)00024-6).
- De Cesare, S., Meziane, T., Chauvaud, L., Richard, J., Sejr, M.K., Thébault, J., Winkler, G., Olivier, F., 2017. Dietary plasticity in the bivalve *Astarte moerchi* revealed by a multimarker study in two Arctic fjords. *Mar. Ecol. Prog. Ser.* 567, 157–172. <https://doi.org/10.3354/meps12035>.

- De Young, B., Hay, A., 1987. Density-current flow into the Fortune Bay, Newfoundland. *J. Phys. Oceanogr.* 17, 1066–1070. [https://doi.org/10.1175/1520-0485\(1987\)017<1066:DCFIIB>2.0.CO;2](https://doi.org/10.1175/1520-0485(1987)017<1066:DCFIIB>2.0.CO;2).
- Doré, J., Chailou, G., Poitevin, P., Lazure, P., Poirier, A., Chauvaud, L., Archambault, P., Thébaud, J., 2020. Assessment of Ba/Ca in *Arctica islandica* shells as a proxy for phytoplankton dynamics in the Northwestern Atlantic Ocean. *Estuar. Coast. Shelf Sci.* 237, 106628. <https://doi.org/10.1016/j.ecss.2020.106628>.
- Ellers, O., Telford, M., 1984. Collection of food by oral surface podia in the sand dollar, *Echinarchinus parma* (Lamarck). *Biol. Bull.* 166, 574–582. <https://doi.org/10.2307/1541163>.
- Falkowski, P.G., Oliver, M.J., 2007. Mix and match: how climate selects phytoplankton. *Nat. Rev. Microbiol.* 5, 813–819. <https://doi.org/10.1038/nrmicro1751>.
- Fennel, K., Boss, E., 2003. Subsurface maxima of phytoplankton and chlorophyll: Steady-state solutions from a simple model. *Limnol. Oceanogr.* 48, 1521–1534. <https://doi.org/10.4319/lo.2003.48.4.1521>.
- Filbee-Dexter, K., Wernberg, T., Norderhaug, K.M., Ramirez-Llodra, E., Pedersen, M.F., 2018. Movement of pulsed resource subsidies from kelp forests to deep fjords. *Oecologia* 187, 291–304. <https://doi.org/10.1007/s00442-018-4121-7>.
- Finkel, Z.V., Beardall, J., Flynn, K.J., Quigg, A., Rees, T.A.V., Raven, J.A., 2010. Phytoplankton in a changing world: cell size and elemental stoichiometry. *J. Plankton Res.* 32, 119–137. <https://doi.org/10.1093/plankt/fbp098>.
- Fry, B., 2006. Stable Isotope Ecology. Springer, New York. <https://doi.org/10.1007/0-387-33745-8>.
- Gaillard, B., Meziane, T., Tremblay, R., Archambault, P., Blicher, M.E., Chauvaud, L., Rysgaard, S., Olivier, F., 2017. Food resources of the bivalve *Astarte elliptica* in a sub-Arctic fjord: a multi-biomarker approach. *Mar. Ecol. Prog. Ser.* 567, 139–156. <https://doi.org/10.3354/meps12036>.
- Griffiths, J.R., Kadin, M., Nascimento, F.J.A., Tamelander, T., Törnroos, A., Bonaglia, S., Bonsdorff, E., Brüchert, V., Gårdmark, A., Järnström, M., Kotta, J., Lindegren, M., Nordström, M.C., Norkko, A., Olsson, J., Weigel, B., Zydels, R., Blenckner, T., Niiranen, S., Winder, M., 2017. The importance of benthic-pelagic coupling for marine ecosystem functioning in a changing world. *Glob. Change Biol.* 23, 2179–2196. <https://doi.org/10.1111/gcb.13642>.
- Guidi, L., Stemann, L., Jackson, G.A., Ibanez, F., Claustre, H., Legendre, L., Picheral, M., Gorsky, G., 2009. Effects of phytoplankton community on production, size, and export of large aggregates: A world-ocean analysis. *Limnol. Oceanogr.* 54, 1951–1963. <https://doi.org/10.4319/lo.2009.54.6.1951>.
- Hardison, A.K., Canuel, E.A., Anderson, I.C., Veuger, B., 2010. Fate of macroalgae in benthic systems: carbon and nitrogen cycling within the microbial community. *Mar. Ecol. Prog. Ser.* 414, 41–55. <https://doi.org/10.3354/meps08720>.
- Harrison, W.G., Børsheim, K.Y., Li, W.K.W., Maillet, G.L., Pepin, P., Sakshaug, E., Skogen, M.D., Yeats, P.A., 2013. Phytoplankton production and growth regulation in the Subarctic North Atlantic: a comparative study of the Labrador Sea-Labrador/Newfoundland shelves and Barents/Norwegian/Greenland seas and shelves. *Prog. Oceanogr.* 114, 26–45. <https://doi.org/10.1016/j.pcean.2013.05.003>.
- Hay, A., De Young, B., 1989. An oceanographic flip-flop: deep-water exchange in Fortune Bay, Newfoundland. *J. Geophys. Res. - Oceans* 94, 843–853. <https://doi.org/10.1029/JC094iC01p00843>.
- Iken, K., Bluhm, B., Dunton, K., 2010. Benthic food-web structure under differing water mass properties in the southern Chukchi Sea. *Deep Sea Res. II* 57, 71–85. <https://doi.org/10.1016/j.dsr2.2009.08.007>.
- Jantzen, C., Schmidt, G.M., Wild, C., Roder, C., Khokiatwong, S., Richter, C., 2013. Benthic Reef Primary Production in Response to Large Amplitude Internal Waves at the Similan Islands (Andaman Sea, Thailand). *PLoS ONE* 8, e81834. <https://doi.org/10.1371/journal.pone.0081834>.
- Kelly, J.R., Scheibling, R.E., 2012. Fatty acids as dietary tracers in benthic food webs. *Mar. Ecol. Prog. Ser.* 446, 1–22. <https://doi.org/10.3354/meps09559>.
- Kharlamenko, V.I., Kiyashko, S.I., Imbs, A.B., Vyshkvartzev, D.I., 2001. Identification of food sources of invertebrates from the seagrass *Zostera marina* community using carbon and sulfur stable isotope ratio and fatty acid analyses. *Mar. Ecol. Prog. Ser.* 220, 103–117. <https://doi.org/10.3354/meps220103>.
- Kjørboe, T., 1993. Turbulence, phytoplankton cell size, and the structure of pelagic food webs. *Adv. Mar. Biol.* 29, 1–72. [https://doi.org/10.1016/S0065-2881\(08\)60129-7](https://doi.org/10.1016/S0065-2881(08)60129-7).
- Krumhansl, K.A., Scheibling, R.E., 2011. Detrital production in Nova Scotian kelp beds: patterns and processes. *Mar. Ecol. Prog. Ser.* 421, 67–82. <https://doi.org/10.3354/meps08905>.
- Krumhansl, K.A., Scheibling, R.E., 2012. Production and fate of kelp detritus. *Mar. Ecol. Prog. Ser.* 467, 281–302. <https://doi.org/10.3354/meps09940>.
- Lawrence, J.M., Herrera, J., Cobb, J., 2004. Vertical posture of the clypeasteroid sand dollar *Encope michelini*. *J. Mar. Biol. Assoc. UK* 84, 407–408. <https://doi.org/10.1017/S002531540400935Xh>.
- Lazure, P., Le Cann, B., Bezaud, M., 2018. Large diurnal bottom temperature oscillations around the Saint Pierre and Miquelon archipelago. *Sci. Rep.* 8, 13882. <https://doi.org/10.1038/s41598-018-31857-w>.
- Leclerc, J.C., Riera, P., Leroux, C., Lévêque, L., Davout, D., 2013. Temporal variation in organic matter supply in kelp forests: linking structure to trophic functioning. *Mar. Ecol. Prog. Ser.* 494, 87–105. <https://doi.org/10.3354/meps10564>.
- Legendre, L., Le Fèvre, J., 1995. Microbial food webs and the export of biogenic carbon in oceans. *Aquat. Microb. Ecol.* 9, 69–77. <https://doi.org/10.3354/ame009069>.
- Legendre, P., Gallagher, E.D., 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia* 129, 271–280. <https://doi.org/10.1007/s004420100716>.
- Leu, E., Falk-Petersen, S., Kwaśniewski, S., Wulff, A., Edvardsen, K., Hessen, D.O., 2006. Fatty acid dynamics during the spring bloom in a High Arctic fjord: importance of abiotic factors versus community changes. *Can. J. Fish. Aquat. Sci.* 63, 2760–2779. <https://doi.org/10.1139/f06-159>.
- Leynaert, A., Longphuir, S.N., Claquin, P., Chauvaud, L., Ragueneau, O., 2009. No limit? The multiphasic uptake of silicic acid by benthic diatoms. *Limnol. Oceanogr.* 54, 571–576. <https://doi.org/10.4319/lo.2009.54.2.0571>.
- Lorrain, A., Paulet, Y.M., Chauvaud, L., Savoye, N., Donval, A., Saout, C., 2002. Differential $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures among scallop tissues: implications for ecology and physiology. *J. Exp. Mar. Biol. Ecol.* 275, 47–61. [https://doi.org/10.1016/S0022-0981\(02\)00220-4](https://doi.org/10.1016/S0022-0981(02)00220-4).
- Lorrain, A., Savoye, N., Chauvaud, L., Paulet, Y.M., Naulet, N., 2003. Decarbonation and preservation method for the analysis of organic C and N contents and stable isotope ratios of low-carbonated suspended particulate material. *Anal. Chim. Acta* 491, 125–133. [https://doi.org/10.1016/S0003-2670\(03\)00815-8](https://doi.org/10.1016/S0003-2670(03)00815-8).
- MacIntyre, H.L., Geider, R.J., Miller, D.C., 1996. Microphytobenthos: The Ecological Role of the “Secret Garden” of Unvegetated, Shallow-Water Marine Habitats. I. Distribution Abundance and Primary Production. *Estuaries* 19, 186–201. <https://doi.org/10.2307/1352224>.
- Maillet, G., Bélanger, D., Doyle, G., Robar, A., Fraser, S., Higdon, J., Ramsay, D., Pepin, P., 2019. Optical, Chemical, and Biological Oceanographic Conditions on the Newfoundland and Labrador Shelf during 2016–2017. Fisheries and Oceans Canada, Canadian Science Advisory Secretariat, Ottawa.
- Marañón, E., 2015. Cell size as a key determinant of phytoplankton metabolism and community structure. *Annu. Rev. Mar. Sci.* 7, 241–264. <https://doi.org/10.1146/annurev-marine-010814-015955>.
- Martin, J., Tremblay, É., Gagnon, J., Tremblay, G., Lapoussière, A., Jose, C., Poulin, M., Gosselin, M., Gratton, Y., Michel, C., 2010. Prevalence, structure and properties of subsurface chlorophyll maxima in Canadian Arctic waters. *Mar. Ecol. Prog. Ser.* 412, 69–84. <https://doi.org/10.3354/meps08666>.
- Mathieu-Resuge, M., Kraffe, E., Le Grand, F., Boens, A., Bideau, A., Lluch-Cota, S.E., Racotta, I.S., Schaal, G., 2019. Trophic ecology of suspension-feeding bivalves inhabiting a north-eastern Pacific coastal lagoon: Comparison of different biomarkers. *Mar. Environ. Res.* 145, 155–163. <https://doi.org/10.1016/j.marenvres.2019.02.016>.
- Mayzaud, P., Boutoute, M., Noyon, M., Narcy, F., Gasparini, S., 2013. Lipid and fatty acids in naturally occurring particulate matter during spring and summer in a High Arctic fjord (Kongsfjorden, Svalbard). *Mar. Biol.* 160, 383–398. <https://doi.org/10.1007/s00227-012-2095-2>.
- McTigue, N.D., Bucolo, P., Liu, Z., Dunton, K.H., 2015. Pelagic-benthic coupling, food webs, and organic matter degradation in the Chukchi Sea: Insights from sedimentary pigments and stable carbon isotopes. *Limnol. Oceanogr.* 60, 429–445. <https://doi.org/10.1002/lno.10038>.
- Merrill, R.J., Hobson, E.S., 1970. Field observations of *Dendroaster excentricus*, a sand dollar of western North America. *Am. Midl. Nat.* 83, 585–662. <https://doi.org/10.2307/2423965>.
- Meziane, T., Tsuchiya, M., 2000. Fatty acids as tracers of organic matter in the sediment and food web of a mangrove/intertidal flat ecosystem, Okinawa, Japan. *Mar. Ecol. Prog. Ser.* 200, 49–57. <https://doi.org/10.3354/meps200049>.
- Meziane, T., Tsuchiya, M., 2002. Organic matter in a subtropical mangrove-estuary subjected to wastewater discharge: origin and utilisation by two macrozoobenthic species. *J. Sea Res.* 47, 1–11. [https://doi.org/10.1016/S1385-1101\(01\)00092-2](https://doi.org/10.1016/S1385-1101(01)00092-2).
- Miller, D.C., Bock, M.J., Turner, E.J., 1992. Deposit and suspension feeding in oscillatory flows and sediment fluxes. *J. Mar. Res.* 50, 459–520. <https://doi.org/10.1357/002224092784797601>.
- Müller-Navarra, D.C., Brett, M.T., Park, S., Chandra, S., Ballantyne, A.P., Zorita, E., Goldman, C.R., 2004. Unsaturated fatty acid content in seston and tropho-dynamic coupling in lakes. *Nature* 427, 69–72. <https://doi.org/10.1038/nature02210>.
- Napolitano, G.E., Pollero, R.J., Gayoso, A.M., Macdonald, B.A., Thompson, R.J., 1997. Fatty acids as trophic markers of phytoplankton blooms in the Bahía Blanca estuary (Buenos Aires, Argentina) and in Trinity Bay (Newfoundland, Canada). *Biochem. Syst. Ecol.* 25, 739–755. [https://doi.org/10.1016/S0305-1978\(97\)00053-7](https://doi.org/10.1016/S0305-1978(97)00053-7).
- Nielsen, T.G., Bjørnsen, P.K., Boonruang, P., Fryd, M., Hansen, P.J., Janekarn, V., Limtrakulvong, V., Munk, P., Hansen, O.S., Satapoomin, S., Sawangarunruks, S., Thomsen, H.A., Østergaard, J.B., 2004. Hydrography, bacteria and protist communities across the continental shelf and shelf slope of the Andaman Sea (NE Indian Ocean). *Mar. Ecol. Prog. Ser.* 274, 69–86. <https://doi.org/10.3354/meps274069>.
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szeecs, E., Wagner, H., 2019. Vegan: community ecology package. R package version 2.5-6. Available at <<https://CRAN.R-project.org/package=vegan>>.
- O'Neill, P.L., 1978. Hydrodynamic Analysis of Feeding in Sand Dollars. *Oecologia* 345, 157–174. <https://doi.org/10.1007/BF00345164>.
- Paulet, Y.-M., Lorrain, A., Richard, J., Pouvreau, S., 2006. Experimental shift in diet d13C: A potential tool for ecophysiological studies in marine bivalves. *Org. Geochem.* 37, 1359–1370. <https://doi.org/10.1016/j.orggeochem.2006.01.008>.
- Parrish, C.C., Thompson, R.J., Deibel, D., 2005. Lipid classes and fatty acids in plankton and settling matter during the spring bloom in a cold ocean coastal environment. *Mar. Ecol. Prog. Ser.* 286, 57–68. <https://doi.org/10.3354/meps286057>.
- Parrish, C.C., 2009. Essential fatty acids in aquatic food webs. In: Arts, M.T., Brett, M.T., Kainz, M.J. (Eds.), *Lipids in aquatic ecosystems*. Springer, Dordrecht, pp. 309–326. https://doi.org/10.1007/978-0-387-89366-2_13.
- Pazos, A.J., Sánchez, J.L., Román, G., Luz Pérez-Parallé, M., Abad, M., 2003. Seasonal changes in lipid classes and fatty acid composition in the digestive gland of *Pecten maximus*. *Comp. Biochem. Physiol. B* 134, 367–380. [https://doi.org/10.1016/S1096-4959\(02\)00286-5](https://doi.org/10.1016/S1096-4959(02)00286-5).
- Pendleton, L., Donato, D.C., Murray, B.C., Crooks, S., Jenkins, A., Sifleet, S., Craft, C., Fourqurean, J.W., Kauffman, J.B., Marbà, N., Megonigal, P., Pidgeon, E., Herr, D., Gordon, D., Baldera, A., 2012. Estimating global 'blue carbon' emissions from

- conversion and degradation of vegetated coastal ecosystems. *PLoS ONE* 7, e43542. <https://doi.org/10.1371/journal.pone.0043542>.
- Pepin, P., Maillet, G., Fraser, S., Doyle, G., Robar, A., Shears, T., Redmond, G., 2017. Optical, chemical, and biological oceanographic conditions on the Newfoundland and Labrador Shelf during 2014–2015. Fisheries and Oceans Canada, Canadian Science Advisory Secretariat, Ottawa.
- Perez, V., Olivier, F., Tremblay, R., Neumeier, U., Thébault, J., Chauvaud, L., Meziane, T., 2013. Trophic resources of the bivalve, *Venus verrucosa*, in the Chaufey archipelago (Normandy, France) determined by stable isotopes and fatty acids. *Aquat. Living Resour.* 26, 229–239. <https://doi.org/10.1051/alr/2013058>.
- Pessarrodona, A., Moore, P.J., Sayer, M.D.J., Smale, D.A., 2018. Carbon assimilation and transfer through kelp forests in the NE Atlantic is diminished under a warmer ocean climate. *Glob. Change Biol.* 24, 4386–4398. <https://doi.org/10.1111/gcb.14303>.
- Peterson, B.J., 1999. Stable isotopes as tracers of organic matter input and transfer in benthic food webs: a review. *Acta Oecol.* 20, 479–487. [https://doi.org/10.1016/S1146-609X\(99\)00120-4](https://doi.org/10.1016/S1146-609X(99)00120-4).
- Peterson, B.J., Fry, B., 1987. Stable isotopes in ecosystem studies. *Ann. Rev. Ecol. Syst.* 18, 293–320. <https://doi.org/10.1146/annurev.es.18.110187.001453>.
- Pinckney, J.L., Lee, A.R., 2008. Spatiotemporal patterns of subtidal benthic microalgal biomass and community composition in Galveston Bay, Texas, USA. *Estuar Coasts* 31, 444–454. <https://doi.org/10.1007/s12237-007-9020-9>.
- Piontek, J., Händel, N., Langer, G., Wohlers, J., Riebesell, U., Engel, A., 2009. Effects of rising temperature on the formation and microbial degradation of marine diatom aggregates. *Aquat. Microb. Ecol.* 54, 305–318. <https://doi.org/10.3354/ame01273>.
- Poitevin, P., Thébault, J., Schöne, B.R., Jolivet, A., Lazure, P., Chauvaud, L., 2018. Ligament, hinge, and shell cross-sections of the Atlantic surfclam (*Spisula solidissima*): Promising marine environmental archives in NE North America. *PLoS ONE* 13, e0199212. <https://doi.org/10.1371/journal.pone.0199212>.
- Poitevin, P., Thébault, J., Siebert, V., Donnet, S., Archambault, P., Doré, J., Chauvaud, L., Lazure, P., 2019. Growth response of *Arctica islandica* to North Atlantic oceanographic conditions since 1850. *Front. Mar. Sci.* 6, 483. <https://doi.org/10.3389/fmars.2019.00483>.
- R Core Team, 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Randelhoff, A., Holding, J., Janout, M., Sejr, M.K., Babin, M., Tremblay, J.-É., Alkire, M. B., 2020. Pan-Arctic Ocean Primary Production Constrained by Turbulent Nitrate Fluxes. *Front. Mar. Sci.* 7, 150. <https://doi.org/10.3389/fmars.2020.00150>.
- Renaud, P.E., Løkken, T.S., Jørgensen, L.L., Berge, J., Johnson, B.J., 2015. Macroalgal detritus and food-web subsidies along an Arctic fjord depth-gradient. *Front. Mar. Sci.* 2, 31. <https://doi.org/10.3389/fmars.2015.00031>.
- Reuss, N., Poulsen, L.K., 2002. Evaluation of fatty acids as biomarkers for a natural plankton community. A field study of a spring bloom and a post-bloom period off West Greenland. *Mar. Biol.* 141, 423–434. <https://doi.org/10.1007/s00227-002-0841-6>.
- Rhead, M.M., Eglinton, G., Draffan, G.H., England, P.J., 1971. Conversion of oleic acid to saturated fatty acids in Severn Estuary sediments. *Nature* 232, 327–330. <https://doi.org/10.1038/232327a0>.
- Riebesell, U., Kortzinger, A., Oschlies, A., 2009. Sensitivities of marine carbon fluxes to ocean change. *PNAS* 106, 20602–20609. <https://doi.org/10.1073/pnas.0813291106>.
- Riera, P., Richard, P., 1997. Temporal variation of $\delta^{13}\text{C}$ in particulate organic matter and oyster *Crassostrea gigas* in Marennes-Oleron Bay (France): effect of freshwater inflow. *Mar. Ecol. Prog. Ser.* 147, 105–115. <https://doi.org/10.3354/meps147105>.
- Schaal, G., Nerot, C., Grall, J., Chouvelon, T., Lorrain, A., Mortillaro, J.M., Savoye, N., Brind'Amour, A., Paulet, Y.M., Le Bris, H., 2016. Stable isotope ratios in benthic demersal biota along a depth gradient in the Bay of Biscay: A multitrophic study. *Estuar. Coast. Shelf Sci.* 179, 201–206. <https://doi.org/10.1016/j.ecss.2015.10.023>.
- Schomburg, G., 1987. *Gaschromatographie Grundlagen, Praxis und Kapillartechnik*, 2nd edn. Wiley, VCH, Weinheim, pp. 62–72.
- Seilacher, A., 1979. Constructional morphology of sand dollars. *Paleobiology* 5, 191–221. <https://doi.org/10.1017/S0094837300006527>.
- Snelgrove, P.V.R., Thrush, S.F., Wall, D.H., Norkko, A., 2014. Real world biodiversity–ecosystem functioning: a seafloor perspective. *Trends Ecol. Evol.* 29, 398–405. <https://doi.org/10.1016/j.tree.2014.05.002>.
- Søreide, J.E., Tamelander, T., Hop, H., Hobson, K.A., Johansen, I., 2006. Sample preparation effects on stable C and N isotope values: a comparison of methods in Arctic marine food web studies. *Mar. Ecol. Prog. Ser.* 328, 17–28. <https://doi.org/10.3354/meps328017>.
- Søreide, J.E., Carroll, M.L., Hop, H., Ambrose, W.G., Hegseth, E.N., Falk-Petersen, S., 2013. Sympagic-pelagic-benthic coupling in Arctic and Atlantic waters around Svalbard revealed by stable isotopic and fatty acid tracers. *Mar. Biol. Res.* 9, 831–850. <https://doi.org/10.1080/17451000.2013.775457>.
- Simonson, E.J., Scheibling, R.E., Metaxas, A., 2015. Kelp in hot water: I. Warming seawater temperature induces weakening and loss of kelp tissue. *Mar. Ecol. Prog. Ser.* 537, 89–104. <https://doi.org/10.3354/meps11438>.
- Soudant, P., Marty, Y., Moal, J., Robert, R., Quéré, C., Le Coz, J.R., Samain, J.F., 1996. Effect of food fatty acid and sterol quality on *Pecten maximus* gonad composition and reproduction process. *Aquaculture* 143, 361–378. [https://doi.org/10.1016/0044-8486\(96\)01276-8](https://doi.org/10.1016/0044-8486(96)01276-8).
- Thyrring, J., Tremblay, R., Sejr, M.K., 2017. Importance of ice algae and pelagic phytoplankton as food sources revealed by fatty acid trophic markers in a keystone species (*Mytilus trossulus*) from the High Arctic. *Mar. Ecol. Prog. Ser.* 572, 155–164. <https://doi.org/10.3354/meps12143>.
- Timko, P.L., 1976. Sand dollars as suspension feeders: a new description of feeding in *Dendraster excentricus*. *Biol. Bull.* 151, 247–259. <https://doi.org/10.2307/1540718>.
- Tremblay, J.-É., Anderson, L.G., Matrai, P., Coupel, P., Bélanger, S., Michel, C., Reigstad, M., 2015. Global and regional drivers of nutrient supply, primary production and CO₂ drawdown in the changing Arctic Ocean. *Prog. Oceanogr.* 139, 171–196. <https://doi.org/10.1016/j.pocean.2015.08.009>.
- Turner, J.T., 2002. Zooplankton fecal pellets, marine snow and sinking phytoplankton blooms. *Aquat. Microb. Ecol.* 27, 57–102. <https://doi.org/10.3354/ame027057>.
- Turner, J.T., 2015. Zooplankton fecal pellets, marine snow, phytodetritus and the ocean's biological pump. *Prog. Oceanogr.* 130, 205–248. <https://doi.org/10.1016/j.pocean.2014.08.005>.
- Walter, R.K., Woodson, C.B., Leary, P.R., Monismith, S.G., 2014. Connecting wind-driven upwelling and offshore stratification to nearshore internal bores and oxygen variability. *J. Geophys. Res. C: Oceans* 119, 3517–3534. <https://doi.org/10.1002/2014JC009998>.
- Wang, Y.H., Dai, C.F., Chen, Y.Y., 2007. Physical and ecological processes of internal waves on an isolated reef ecosystem in the South China Sea. *Geophys. Res. Lett.* 34, L18609. <https://doi.org/10.1029/2007GL030658>.
- Wassmann, P., Reigstad, M., 2011. Future Arctic Ocean seasonal ice zones and implications for pelagic-benthic coupling. *Oceanography* 24, 220–231. <https://doi.org/10.5670/oceanog.2011.74>.
- Wernberg, T., Filbee-Dexter, K., 2018. Grazers extend blue carbon transfer by slowing sinking speeds of kelp detritus. *Sci. Rep.* 8, 17180. <https://doi.org/10.1038/s41598-018-34721-z>.
- White, M., Hay, A., 1994. Dense overflow into a large silled embayment: Tidal modulation, fronts and basin modes. *J. Mar. Res.* 52, 459–487. <https://doi.org/10.1357/0022240943077055>.
- Wiekling, G., Kröncke, I., 2005. Is benthic trophic structure affected by food quality? The Dogger Bank example. *Mar. Biol.* 146, 387–400. <https://doi.org/10.1007/s00227-004-1443-2>.
- Wohlers, J., Engel, A., Zöllner, E., Breithaupt, P., Jürgens, K., Hoppe, H.-G., Sommer, U., Riebesell, U., 2009. Changes in biogenic carbon flow in response to sea surface warming. *PNAS* 106, 7067–7072. <https://doi.org/10.1073/pnas.0812743106>.
- Woodson, C.B., 2018. The fate and impact of internal waves in nearshore ecosystems. *Annu Rev Mar Sci* 10, 2.1–2.21. <https://doi.org/10.1146/annurev-marine-121916-063619>.
- Wu, Y., Tang, C., Hannah, C., 2012. The circulation of eastern Canadian seas. *Prog. Oceanogr.* 106, 28–48. <https://doi.org/10.1016/j.pocean.2012.06.005>.
- Yamaguchi, H., Montani, S., Tsutsumi, H., Hamada, K., Ueda, N., Tada, K., 2007. Dynamics of microphytobenthic biomass in a coastal area of western Seto Inland Sea, Japan. *Estuar Coast Shelf Sci* 75, 423432. <https://doi.org/10.1016/j.ecss.2007.05.025>.