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Carbon and nitrogen elemental and isotopic ratios of filter-feeding bivalves along the French coasts: An assessment of specific, geographic, seasonal and multi-decadal variations

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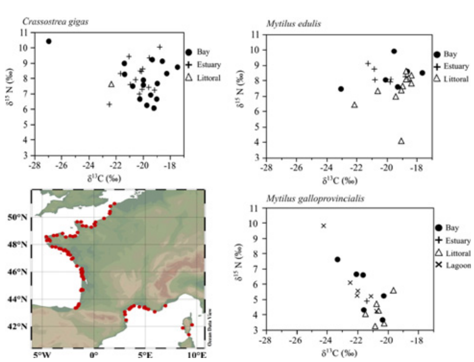
HIGHLIGHTS

- Trophic status of coastal ecosystems explains the geographical variation of bivalve $\delta^{13}C$ and $\delta^{15}N$.
- Seasonal variability in C/N is related to reproduction cycle for mussel species.
- $\delta^{13}C$ seasonal variability is related to trophic resource variability for *C. gigas* and *M. edulis*.
- Multi-decadal shifts and trends in C/N ratio, $\delta^{13}C$ and $\delta^{15}N$ were detected and likely related to climate change.

GRAPHICAL ABSTRACT



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ABSTRACT

Primary consumers play a key role in coastal ecosystems by transferring organic matter from primary producers to predators. Among them, suspension-feeders, like bivalve molluscs are widely used in trophic web studies. The main goal of this study was to investigate variations of C and N elemental and isotopic ratios in common bivalves (*M. edulis*, *M. galloprovincialis*, and *C. gigas*) at large spatial (i.e. among three coastal regions) and different temporal (i.e. from seasonal to multi-decadal) scales in France, in order to identify potential general or specific patterns and speculate on their drivers.

The observed spatial variability was related to the trophic status of the coastal regions (oligotrophic Mediterranean Sea versus meso- to eutrophic English Channel and Atlantic ocean), but not to ecosystem typology (estuaries, versus lagoons versus bays versus littoral systems). Furthermore, it highlighted local specificities in terms of the origin of the POM assimilated by bivalves (e.g., mainly continental POM vs. marine phytoplankton vs. microphytobenthic algae). Likewise, seasonal variability was related both to the reproduction cycle for C/N ratios of *Mytilus* spp. and to changes in trophic resources for $\delta^{13}C$ of species located close to river mouth. Multi-decadal evolution exhibited shifts and trends for part of the 30-year series with decreases in $\delta^{13}C$ and $\delta^{15}N$. Specifically, shifts appeared in the early 2000's, likely linking bivalve isotopic ratios to a cascade of processes affected by local drivers.

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1. Introduction

Representing significant aquaculture resources on a worldwide level, bivalve molluscs such as mussels or oysters are species of high economic interest (FAO – Fisheries and Aquaculture Department). As filter-feeding animals and primary consumers, they also constitute a major component of coastal trophic network and ecosystem functioning. However, being mainly located in coastal areas, they are subject to a highly variable environment (e.g. water temperature, salinity, river discharges, inputs of chemical contaminants etc.). These variable environmental conditions can notably impact the quality (origin, composition) of their food sources and their physiological state (Hawkins et al., 1985; Thompson and Harrison, 1992; Prins et al., 1997; Gasmi et al., 2017).

As filter-feeders, bivalves rely on biological material suspended in the water column including detritus, (micro)algae, and other microorganisms. Several studies showed that bivalves from estuarine and coastal environments are subject to a fluctuating and unpredictable food supply (e.g. Kreeger et al., 1988; Crosby et al., 1990), especially depend on the season. In addition to marine phytoplankton, suspended particulate organic matter (POM) originating from river discharge can thus represent a significant food source for estuarine and coastal bivalves (Hackney and Haines, 1980; Stephenson and Lyon, 1982; Riera and Richard, 1996a). River-derived POM includes a mix of freshwater phytoplankton, sloughed-off periphyton, terrestrial POM (i.e. vascular plant detritus, soil) and anthropogenic (i.e. waste-water) POM (Raikow and Hamilton, 2001; Savoye et al., 2012; Liénart et al., 2016). However, phytoplankton is generally considered as a high-quality food for bivalves, and variability in this resource can impact the ecological performance of these primary consumers in the field (e.g. size, weight…) (Kiorboe and Mohlenberg, 1981; Blanton et al., 1987; Grant, 1996; Cranford and Hill, 1999).

There are inherent difficulties to accurately assess the food sources ingested and/or assimilated by filter-feeding or planktivorous organisms using traditional methods, such as of stomach or gut contents analyses. In the last decades, the analysis of carbon (C) and nitrogen (N) stable isotope ratios (δ^{13}C and δ^{15}N values) in biological tissues has proven to be a useful approach for identifying the relative contribution of the different food sources in the diet of estuarine and coastal primary consumers (e.g., Simenstad and Wissmar, 1985; Peterson and Fry, 1987; Fry and Sherr, 1984; Currin et al., 1995; Lefebvre et al., 2009; Dubois et al., 2014). Indeed, the different primary producers and/or POM components (e.g. material from terrestrial vs. marine origin, fresh vs. detrital material, etc.) generally display different isotopic compositions (e.g., Dubois et al., 2014). Furthermore, C and N stable isotope compositions of consumers' tissues have been shown to closely resemble those of their food sources (De Niro and Epstein, 1978; De Niro and Epstein, 1981). Also, the enrichment between sources and consumers is relatively predictable (De Niro and Epstein, 1978; Minagawa and Wada, 1984; Peterson and Fry, 1987), although it may vary depending on the tissues considered, taxa, food sources, physiological state of consumers, etc. (e.g. Lorrain et al., 2002; Emmery and Lefebvre, 2011). Nonetheless, across such bivalve species as mussels and oysters, this enrichment (usually called "trophic enrichment factor", TEF) has been reported to be quite consistent (Dubois et al., 2007a,b). Moreover, the bulk C/N ratio measured in biological tissues (as well as δ^{13}C values to a lesser extent) may inform on the lipid content and/or the physiological state (i.e., repletion status) of organisms. Lipids are effectively enriched in carbon chains and depleted in ^{13}C relative to other tissue components (De Niro and Epstein, 1978; Bodin et al., 2007). Since bivalves are primary consumers and constitute a major component of littoral trophic networks and ecosystems, their stable isotope ratios are used as "baseline" isotopic values for local biological communities (e.g. Abrantes and Sheaves, 2009). Indeed bivalves may represent useful model organisms able to exhibit time-integrated isotopic values relative to local primary producers, or local POM composition and origin.

Carbon and nitrogen elemental and isotope compositions of various bivalve species in France have already been described and extensively studied for some specific and local spots (e.g. Riera and Richard, 1996a,b; Lefebvre et al., 2009; Dubois et al., 2014). It is the first study to examine C and N elemental and isotope compositions at large spatial and temporal scales, probably due to difficulties in adequate sample acquisition and curation. In this general context, the present study proposes to achieve for the first time an instantaneous global cartography of C/N ratios, δ^{13}C and δ^{15}N values measured in bivalves collected in 2014 along the coastline belonging to three regions and to a large diversity of ecosystems and environmental conditions, and for selected sites, over three decades. The specific objectives of this study were to investigate (i) spatial (ii) seasonal and (iii) multi-decadal variations in C and N elemental and isotopic ratios of bivalves in order to identify potential general trends and environmental drivers of bivalve food resources and physiological status. As companion paper of a two mercury papers (Briant et al., 2017), δ^{13}C and δ^{15}N were used as proxies of food sources and the C/N ratio as a proxy of body condition. The study was performed along the three regions of the French coastal ocean between 1987 and 2014.

2. Materials and methods

2.1. Study sites and sampling strategy

Since the end of 1970's, a French Mussel-Watch program, the National Monitoring Network "ROCCH" (for "Réseau d'Observation de la Contamination CHimique") uses wild local bivalves as biomonitors and semi-quantitative indicators of the chemical contamination of the national coastline (Claisse, 1989). Currently, the network includes nearly 80 stations distributed along the coastline of continental France and the French Antilles. At each station, similar-sized bivalves are collected twice a year (in autumn and in winter). In the first years and until the early 2000's, the stations were sampled all four seasons.

The analyses presented in this study concern 189 samples of bivalves from 74 sampling stations chosen along the three maritime façades of metropolitan France (the English Channel, the Atlantic Ocean, the Mediterranean Sea) (Fig. 1). Sites have been selected to sample the high diversity of environmental conditions encountered by the bivalves along the coastline: sites are located in estuaries, semi-enclosed systems, open bays, lagoons, rocky or sandy-bottom areas, in eutrophic, mesotrophic or oligotrophic systems, are subject to temperate oceanic or Mediterranean climate, etc. (Table 1). In this study, following criteria of the ROCCH program, four locations were distinguished. "Littoral" characterizes each open sea site that can be rock or sand ground; "estuary" is used when the site is at the vicinity of a coastal river mouth, whatever the size of the river; "bay" represents each site within a semi-enclosed area; and "lagoon" is typical to some Mediterranean sites (almost closed lagoons). The four cases allow to describe the general type of environment and associated hydrological dynamic for the different sites. Despite the contrasts between these environments, only three different species of bivalves were collected: the mussel *Mytilus edulis* in the English Channel and the Atlantic Ocean, the mussel *Mytilus galloprovincialis* in the English Channel and the Mediterranean Sea, and the oyster *Crassostrea gigas* in the English Channel and the Atlantic Ocean (Fig. 1).

The seasonal variability was investigated using results from *M. edulis*, *C. gigas*, and *M. galloprovincialis* sampled during winter, spring, summer and fall of 1998 and 1999 in the three sites: Pointe Chemoulin and Bourgneuf-Coupelasse in the Atlantic Ocean, and Cap Couronne in the Mediterranean Sea. The spatial variability was investigated using samples of the three species sampled at the 74 sites during winter (between late January and early March) 2014. Finally, the decadal variability was investigated using samples of the three species sampled each three years from winter 1987 to winter 2014 in ten sites of the three