Journal of Sea Research 121 (2017) 11–23

Contents lists available at ScienceDirect

Journal of Sea Research

journal homepage: www.elsevier.com/locate/seares

Nursery function of coastal temperate benthic habitats: New insight from the bivalve recruitment perspective

Pierrick Barbier [a,*], Tarik Meziane [a], Martin Forêt [a,b], Réjean Tremblay [b], René Robert [c], Frédéric Olivier [a]

[a] *Unité Mixte de Recherche Biologie des organismes et écosystèmes aquatiques (BOREA UMR 7208), Sorbonne Université, Muséum national d'Histoire naturelle, Université Pierre et Marie Curie, Université de Caen, C.P. 53, 61 rue Buffon, Bât. des Arthropodes, 75005 Paris, France*
[b] *Institut des Sciences de la Mer (ISMER) - Université du Québec à Rimouski (UQAR), 310, Allée des Ursulines, Rimouski, Québec G5L3A1, Canada*
[c] *Ifremer, Unité littoral, Centre Bretagne, ZI de la Pointe du Diable, 29280 Plouzané, France*

ARTICLE INFO

Article history:
Received 21 January 2016
Received in revised form 28 October 2016
Accepted 18 December 2016
Available online 13 January 2017

Keywords:
Benthic habitats
Bivalve recruitment
Nursery function
Ostrea edulis
Fatty acids

ABSTRACT

Marine habitat function has been typically investigated in terms of biogeochemical regulation but rarely in terms of population renewal, which is mainly controlled by recruitment dynamics. The recruitment phase is crucial for organisms with a bentho-pelagic life cycle, such as bivalves, and it regulates the population renewal success. This study provides new insight on the role of temperate benthic habitats on bivalve recruitment, as a function of nursery areas. Six dominant benthic habitats of the Chausey archipelago (Normandy, France) were studied. In each habitat, bivalve recruit assemblages were described at the end of two reproductive seasons. Furthermore, *Ostrea edulis* juveniles were immerged on each habitat during two months to compare growth performances and feeding status, estimated by fatty acid composition. Recruit assemblages differ from each habitat according to sediment grain-size composition and bathymetrical levels. Subtidal habitats, and especially *Crepidula fornicata* banks and *Glycymeris glycymeris* coarse sands, supported the highest species abundance and richness of recruits. All *O. edulis* juveniles fed on the same trophic resources but digestive glands of juveniles from *C. fornicata* banks were more concentrated in total fatty acids than those from subtidal *G. glycymeris* coarse sands and maerl banks. Our results depict the key role of subtidal and structured habitats, composed of ecosystem engineers, in enhancing bivalve recruitment and extending the bivalve population renewal. This study suggests that the crucial role of these habitats as bivalve nurseries must be integrated in management perspectives.

1. Introduction

The marine seafloor is comprised of 70% soft sediment areas, including a large diversity of benthic habitats (Snelgrove, 1999), which ensure multiple functions at the base of the ecosystem goods and services (De Groot et al., 2010; Bardgett and van der Putten, 2014). A habitat, as strictly defined by Begon et al. (1996), is a place where an organism (microorganisms, plants, animals) lives. However, the most widely used definition is a spatially defined area, where the physical, chemical, or biological environment is distinctly different from those surrounding it (Kostylev et al., 2001). This implies that spatial boundaries coincide with environmental preferences or survival of an organism or a group of organisms that share the same habitat. In Europe, major habitats are defined and surveyed according to the EUNIS (European Union Nature Information System) habitat classification (Davies et al., 2004), providing a comprehensive typology based on hierarchical levels, for which the first concerns "Marine habitats" (EUNIS habitat type hierarchical view http://eunis.eea.europa.eu/habitats-code-browser.jsp). With the exception of the pelagic water column and ice-associated marine habitats, all habitat classifications are benthic. Among these habitat types, several are defined by ecosystem engineer species. These species, as defined by Jones et al. (1994) are "organisms that modulate resource availability for other species through their abiotic or biotic material, leading to the maintenance or creation of new habitats". The engineering effects of structuring species, in addition to their direct impact on resources, positively and negatively affect abundance and species richness at small scales, leading to the emergence of particular habitat functions (Jones et al., 1994; Jones et al., 1997).

According to De Groot et al. (2002) the ecosystem or habitat "function" is "the capacity of natural processes and components to provide goods and services that satisfy human needs, directly or indirectly". To propose effective biodiversity conservation policies, Liquete et al. (2013) reviewed ecosystem services associated with marine and coastal environments. Due to the initial influence of comparable terrestrial studies (*i.e.* Bardgett and van der Putten, 2014), benthic habitat functions were often investigated solely in terms of energy and matter fluxes. In addition to such physicochemical properties/roles/functions, benthic habitats have ecological functions, such as providing shelter

---

* Corresponding author at: UMR CNRS 7208 - BOREA, 61 rue Buffon, CP53 Bâtiment des Arthropodes, 75005 Paris, France.
E-mail address: pierrickbarbier@hotmail.com (P. Barbier).

http://dx.doi.org/10.1016/j.seares.2016.12.007

from prey, nursery habitat, and feeding areas, depending on species composition and abundances (Eyre et al., 2011; Snelgrove, 1999; Thrush and Dayton, 2002). Moreover, these ecological functions can be enhanced when habitats interact (Srivastava, 2006). The "reproduction and nursery area" habitat function was almost exclusively assessed for fisheries (Seitz et al., 2014). This function, defined as "the provision of the appropriate environmental conditions for reproduction and growing during the early stages of marine species" (Salomidi et al., 2012), is essential for the renewal of dominant populations.

In temperate marine systems, a large majority of marine invertebrates, such as bivalves, have a bentho-pelagic life cycle with a long pelagic phase represented by a large number of planktonotrophic larvae (Thorson, 1950). Renewal of bivalve populations is thus mainly due to the recruitment success, *i.e.* the settlement-metamorphosis, and the subsequent juvenile survival in the benthic compartment. During this critical life stage, the loss ratio between invertebrate larvae and adult stage is generally over 97% (Pedersen et al., 2008). Recruit assemblages observed in a benthic habitat result from pre- and post-settlement processes that condition the presence or absence of organisms. Pre-settlement processes act on the larval pool from fecundation to metamorphosis, and post-settlement processes control post-larval and juvenile stages. Such processes are under the influence of many abiotic factors, including water physicochemical parameters and hydrodynamic disturbances, as well as biotic factors, such as food availability, biological interactions, and species behavior (Hunt and Scheibling, 1997; Pechenik, 1999; Pineda et al., 2009). It is well known that specific benthic boundary flows can cause sediment resuspension and subsequent drifting of benthic organisms in the water column, which may have important consequences on population dynamics (Olivier et al., 1996; Olivier and Retière, 1998). Recent studies have emphasized the crucial role of trophic resources (quality and quantity) in the recruitment success. For example, the bivalve diets at each development stage may affect the genitor gonadic development, the larval survival and growth, and even the trigger of their settlement (González-Araya et al., 2011; González-Araya et al., 2012; Jolivet et al., 2016; Toupoint et al., 2012). Stresses that affect early life cycle stages are sources of latent-effects, inducing within-species variations of juveniles and adults' survival and reproduction (Pechenik, 2006). Recently, St-Onge et al. (2015) showed that, at a reproductive season scale, bivalve larvae in a kin aggregated larval pool issued from multi-spawning events do not have the same recruitment survival success and the first produced larvae will mainly regulate the final recruitment composition. It seems thus crucial to understand accurately all factors insuring minimum recruitment to keep bivalve population sustainable.

Bivalves constitute a major component of benthic habitat as they often dominate the biomass of soft-bottom sediments (Peterson, 1977) and have key functions (Gosling, 2003), including bioturbation and primary consumers, affecting their surrounding environment. The persistence of bivalve populations can provide numerous ecosystem services that include provision, regulating and maintenance services (Katsanevakis et al., 2014; Liquete et al., 2013). Moreover, bivalves are an important economic resource, as shellfish farming areas, like the Mont Saint Michel Bay (MSMB), produce tens of millions of shellfish and generate more than 30 million Euros per year (Cugier et al., 2010). The present study was carried out in Chausey Archipelago (MSMB, Normandy, France), which is characterized by semidiurnal tidal pattern and a maximal tidal range of 14 m during spring tides. This archipelago covers a surface of 5100 ha, including emerged islands, subtidal and intertidal seabeds, where almost a third is represented by sandflats (1388 ha; Godet et al., 2009). About nine intertidal and seven subtidal benthic habitats are found across the archipelago supporting 769 marine invertebrate species, with about 100 known bivalve species (Fournier et al., 2014; Godet et al., 2010).

The aim of this study is to provide new insights on the renewal of wild bivalve populations within a temperate coastal megatidal system, and in particular, with regards to the "reproductive and nursery area" habitat function across several benthic habitats (Table 1). We analyzed this function during two main phases of the bivalve recruitment: 1) at the end of a reproductive season by determining the natural bivalve recruit assemblages and 2) during the development of *Ostrea edulis* juveniles, by estimating their growth performances and feeding status.

2. Materials and methods

2.1. Study site

The present study focuses on six main benthic habitats of the archipelago (Table 1) as defined by their surface area and ecological significance. The *Glycymeris glycymeris* coarse sands (Godet, 2008; Coarse sands and gravels from coastal circumlittoral with *Mediomastus fragilis*, *Lumbrineris* spp. and *Veneridae* bivalves, A5.142 EUNIS Classification 2008), the most widespread habitat of the English channel (Larsonneur et al. 1982), were investigated at intertidal (SHI) and subtidal (SHS) levels where they are found on 1/4 (350 ha) of the Chausey soft-sediment tidal flats (Godet, 2008). Intertidal beds of *Lanice conchilega* (*Polychaeta*, *Terebellidae*) (L) (Godet, 2008; *L. conchilega* in littoral sand, A2.245 EUNIS Classification 2008), a commonly European found tube-building polychaete and engineer species forming large bioherms when reaching a specific threshold density (Godet et al., 2011). Intertidal *Zostera marina* beds (Z) (Godet, 2008; *Z. marina*/*Z. angustifolia* beds on lower shore or infralittoral clean or muddy sand, A5.5331 EUNIS Classification 2008) are the most represented seagrass over the archipelago acting like a nursery to numerous marine species (Godet et al., 2008a; Boström et al., 2014). This marine plant beds can also be considered as key ecosystem engineer (Jones et al., 1994, but see also Passarelli et al., 2014). Subtidal maerl (Corallinophycidae, Rhodophyta) beds (M) (maerl beds on infralittoral muddy gravel, A5.513 EUNIS Classification 2004) are characterized by a high macrofaunal specific richness, especially of molluscan species (Grall and Glemarec, 1997). Subtidal slipper limpet's (*Crepidula fornicata*) banks (C) (*C. fornicata* with ascidians and anemones on infralittoral coarse mixed sediments, A5.431 EUNIS Classification 2004) are constituted by the introduced species from North America, *C. fornicata*, which became invasive on the European coasts at the end of the 19th century (Blanchard, 1997). Sampling and experiment sites of this study were carefully chosen according to previous studies conducted in the Chausey archipelago, allowing us to select the most adequate sites for each benthic habitat (Fournier et al., 2014; Godet, 2008; Godet et al., 2008a; Godet et al., 2008b; Godet et al., 2009; Godet et al., 2011; Perez et al., 2013; Toupoint et al., 2008).

Sampling sites selection mainly depends on the habitat recovering at the sea bottom. For example, maerl beds are mostly present in the Northern part of the archipelago, while *Lanice conchilega* beds dominated soft bottoms from the West-center area. We consider the effects of a heterogeneous distribution of larval pool along the water column should not be considered due to high hydrodynamic constraints located in this kind of megatidal environment and post-settlement processes (*i.e.* secondary migration) that structure bivalve recruits assemblages at the end of each reproductive season (Toupoint et al., 2016).

2.2. Assemblages of bivalve recruits at the end of the reproductive season

In order to compare bivalve recruitment assemblages on dominant benthic habitats of the archipelago, two sampling campaigns (September the 10th 2013 and October the 3rd 2014) were conducted at the end of the reproductive season of most wild bivalves species of European coasts (reviewed by Gosling, 2003). Distributed from the center towards the West of the archipelago (Fig. 1a), three sites per habitat were sampled using a Smith-McIntyre Grab (one replicate of 0.2 m^{-2} per site; Smith and McIntyre, 1954). Collected material was sorted through a 5 and 2 mm circular mesh sieves to keep only bivalve recruits of the sampled year. Even if few studies have examined bivalve post-