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Prey-Predation Relationships between Bivalves and Predatory Gastropods: Experiments on English Channel Populations

Jean-Philippe Pezy[1]*, Aurore Raoux[1], Jean Claude Dauvin[1], Thomas Schwanka[2], Claire Michelet[2], Olivier Basuyaux[2]

Abstract

Predatory gastropods represent a potential menace for intertidal shellfish aquaculture along the French coast of the English Channel. Experimental studies have been established to analyse the predation of two drilling gastropods *Ocenebra erinaceus* and *Ocinebrellus inornatus* on the Manila clam (*Ruditapes philippinarum*) and the Japanese oyster (*Crassostrea gigas*) and to test if the feeding behaviour of these two predatory gastropods is influenced by the burying of the Manila clam in sediment. Both gastropods show significant predation on both bivalves, with feeding preference changing according to prey species and their availability. Moreover, the burying of clams does not significantly influence the feeding behaviour of their predators. Monitoring of this danger for oyster and clam farming should be encouraged on some sites of the western coast of Cotentin.

Keywords

Ocinebrellus inornatus; Ocenebra erinaceus; Non-indigenous species; Ruditapes philippinarum; Crassostrea gigas

Introduction

Ecosystem invasions by Non-Indigenous Species (NIS) are considered nowadays as one of the greatest threats to biodiversity world-wide[1-3]. NIS introductions into coastal zones have accelerated thorough the worldwide ocean in recent decades, mainly due to increased human activities such as aquaculture, maritime traffic and tourism[4-7]. In fact,NIS present a wide range of threats to native ecosystems, could be responsible for the decline of native species by competition and predation, and thus could lead to a loss of biodiversity[8-10]. Moreover, NIS could cause direct economic impacts on the structure of human activities and aquaculture [11-14].

In Normandy waters, a total of 152 NIS are recorded; among these species, 86 have been introduced through shipping (ballast waters and fouling) and 66 through aquaculture activities [15]. For instance, the voluntary introduction of the Japanese oyster *Crassostrea gigas* and its transfer between centres of production on the Atlantic and English Channel coasts has led to the accidental introduction of many NIS (vagile and sessile species) into the English Channel [16].

The oyster *Crassostrea gigas* was voluntary introduced in France in the late 1960s, after the disappearance of the Portuguese oyster *C. angulata*- due to two viral diseases in the oyster farms of Arcachon and Marennes-Oleron on the Atlantic seaboard [16]. Recruitment of *Crassostrea gigas* on the intertidal zone was first observed in 1975 at Marennes-Oleron; from the mid-1990s, natural settlement was observed in North Brittany and extended from the Normano-Breton Gulf to the Spanish frontier [16]. Since the end of the 1970s, oyster farms have been established in Normandy, and then along the Opal coast (Dover Strait); as in other centres of production, transfer of oysters from the Atlantic to Normandy was permanent and favoured the transfer of other species including the NIS [15].

The Manila clam *Ruditapes philippinarum* was voluntary introduced in France in the 1970s and now dominates the native European grooved carpet shell *Ruditapes decusattus* in the intertidal zone of the western Cotentin (English Channel) and more than 95% of the clams are *R. philippinarum* [17-18. In Normandy, this latter species was introduced in the Chausey Islands off the western coast of Cotentin (15 km), where clam farms have continued to cultivate this target introduced species. Nowadays, the introduced Manila clam and the native grooved carpet shell are among the target species for recreational and professional fishing on the west coast of Cotentin [18].

The Muricidae are a family of predatory gastropod. This family is known to have a carnivorous diet based on the ability to drill holes in hard-shelled organisms. It preys upon barnacles and bivalve species. Due to their eating behaviour, these gastropods cause problems in shellfish aquaculture, in particular for mussel [19] and oyster farming [20]. Indeed, these predatory gastropods could be responsible for significant mortality in shellfish concessions (essentially for young individuals). In the English Channel, two indigenous species of piercing or drilling gastropod are recorded: *Nucella lapillus* and *Ocenebra erinaceus*, *N. lapillus* has a diet preference for barnacles and the blue mussel *Mytilus edulis* [21], whereas *O. erinaceus* preferentially predates on bivalves, in particular the NIS *Crassostrea gigas* [22]. Apart from these two indigenous species, two NIS of drilling gastropods have been introduced into the English channel: *Ocinebrellus inornatus* and *Stramonita haemastoma*. The first species, *O. inornatus*, was accidently introduced in France in 1995 in the Marennes-Oleron bay through transfer of the oyster *C. gigas*. The second species *S. haemastoma*, was recorded for the first time in the English Channel on the king scallop *Pecten maximus* [23] along the western coast of Cotentin in 2018 in an area with extensive mussel and oyster farming.

As predatory gastropods exhibit a potential threat to intertidal shellfish cultivation in the English Channel, the main goals of the present study are:

- To analyse experimentally the feeding behaviour of two drilling gastropods *Ocenebra erinaceus* and *Ocinebrellus inornatus* on the Manila clam (*Ruditapes philippinarum*) and the Japanese oyster (*Crassostrea gigas*)

***Corresponding author:** Jean-Philippe Pezy, Continental and Coastal Morphodynamics Laboratory, Normandie University, France, E-mail: jean-philippe.pezy@unicaen.fr

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- To test if the feeding behaviour of these two predatory gastropods is influenced by the burying of Manila clams in sediment

Material and Methods

Sites and species

Fifty adults of *Ocenebra erinaceus* (35 mm-46 mm height) and twenty *Ocinebrellus inornatus* (38 mm-50 mm height) were collected in April 2017 at Blainville-sur-mer and St-Martin-de-Bréhal (Figure 1). In addition, 50 individuals of *Ruditapes philippinarum* (with a length size >40 mm) were collected at Blainville-sur-mer. A total of 50 oysters (*Crassostrea gigas*) for a range size of 99.20 mm-112.67 mm were collected at Blainville-sur-mer directly at the oyster production site. Then, all the individuals of the four species were stored in aquaria with a regulated seawater temperature of 14°C and a salinity of 35, corresponding to the spring environmental conditions of seawater in the Normano-Breton Gulf; all the individuals were stored quietly during 24 h before the beginning of the experiments. All the aquaria were fitted with a bubbling aeration system and underwent daily renewal of seawater before the experiments. Sediment was collected and sieved, on a 5 mm mesh size to homogenize the sediment used in the experiments and eliminate the gravel and other bivalve species. For both experiments, each individual was used only once.

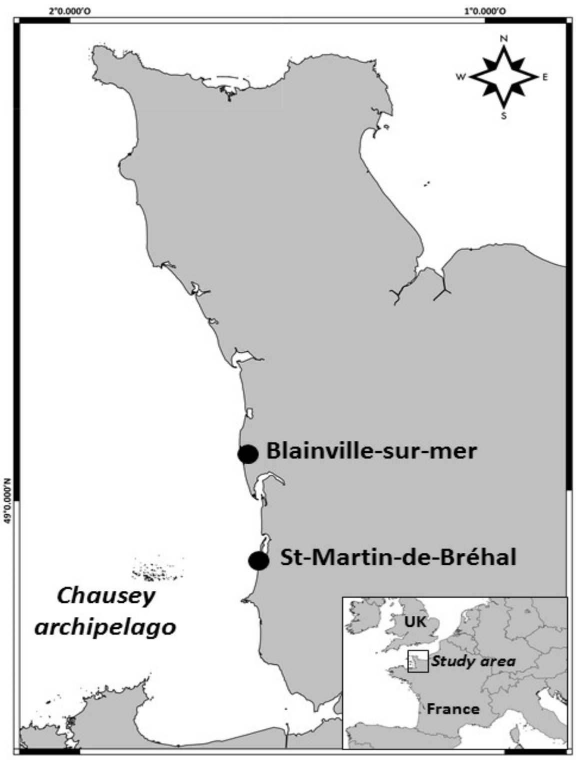

Figure 1: Localization of the sampling sites where the gastropods and bivalves were collected.

Experiments were conducted in a total of 18 aquaria with a 10 L capacity (32.5 × 17.5 × 18.5) cm with a bubbling system for oxygenation (Figure 2), equipped with a camera to record the behaviour of the predatory gastropods.

Diet preference

The first experiment consisted of assessing the diet preference of both predatory gastropods, the indigenous *O. erinaceus* and the non-indigenous *O. inornatus*, on two preys (clam and oyster). One individual clam and one individual oyster were placed at either end of the tank, while the predator (one individual) was placed at the centre of the aquarium. A total of 18 experiments were carried out to observe the behaviour of *O. erinaceus* and 18 experiments for *O. inornatus*. The experiments were continued until the death of the bivalves to estimate the time necessary for the piercer to fully perforate the shell and to kill their prey. In this experiment, all the individuals were free of substrate.

The second experiment investigated the role of the cue in the choice of prey for the predatory gastropods. As for experiment 1, both species of gastropods (one individual per species) were placed in the presence of an oyster (one individual) and a clam (one individual).

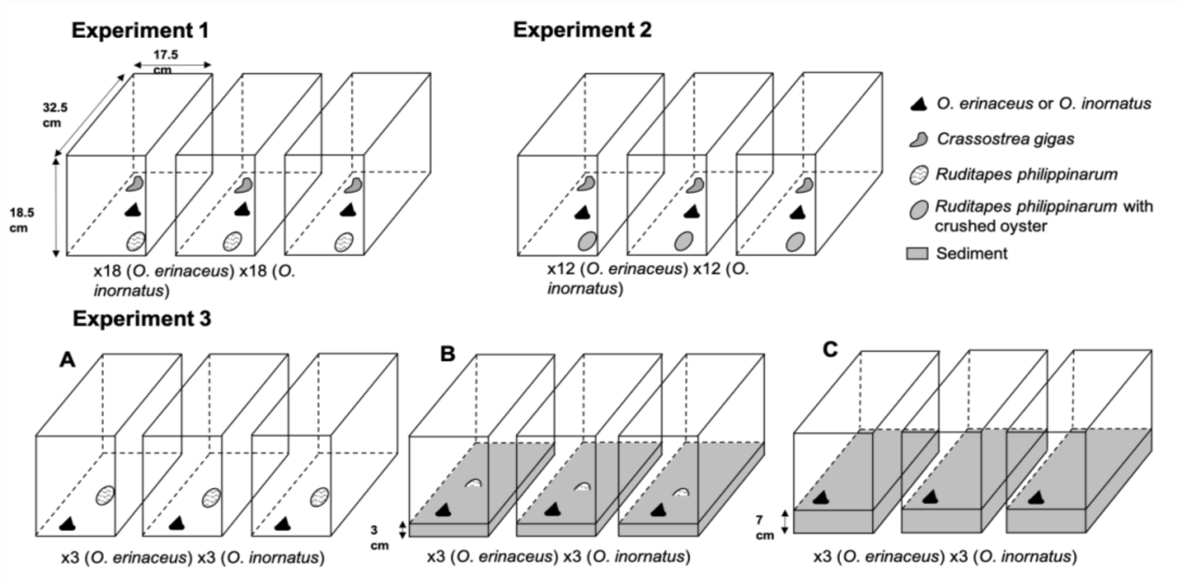

Figure 2: Distribution of tanks in the three experiments.

However, clams were placed previously in crushed oysters: i.e. muscles of oysters were crushed and then the clams were covered with this mixture during ten minutes outside water. The aim of this experiment was to test the ability of the predator gastropod to recognize their prey by their odour and if they were able to detect their prey in the event that they preferred clams to oysters. A total of 12 experiments were performed for each species of predatory gastropod.

Burial of clams

The third experiment aimed to observe the capacity of the predator (one individual) to consume clam (one individual) buried in the sediment. For this purpose, several thicknesses of sediment were tested: no sediment, 3 cm of sediment and 7 cm of sediment. Before the experiments, the sediment was sieved on a 5 mm mesh to extract shell fragments and living organisms. Clams were placed in tank before experiment during 24 h to burrow into the sediment themselves. A total of 9 (3 × 3) experiments were carried out in the presence of *O. inornatus* or *O. erinaceus* taking into account the different sedimentary thicknesses.

Statistical analysis

The R software package was used to perform Chi^2 tests.

Results

Diet preference

The first experiment showed that *O. erinaceus* selected 83.3% oyster prey as against 11.1% clams (Figure 3, Table 1), whereas *O. inornatus* selected 50.0% clams as against 33.3% oysters (Table 1). With *O. inornatus*, three individuals did not choose any prey (Figure 3, Table 1). Moreover, we found that *O. erinaceus* had a significant preference for oysters (chi^2, p<0.05). By contrast, the results showed that *O. inornatus* did not have a significant preference between either prey (chi^2, p>0.05). Out of the 15 oysters selected by *O. erinaceus*, 11 exhibited a drilling hole (Figure 4, Table 1), as well as two clams selected by this predator. However, out of the six oysters selected by *O. inornatus*, only two showed a drilling hole, and out of the nine clams selected, eight displayed a drilling hole (Figure 4, Table 1).

The second experiment highlighted that *O. erinaceus* had a prey preference for clams (66.7%) as against oysters (25.0%). *O. inornatus* had a prey preference for clams (41.7%) as against oysters (8.3%), but 50% did not select any prey (Figure 3, Table 1). However, results showed that *O. erinaceus* did not have a significant preference between preys (chi^2, p>0.05). On the other hand, results showed that *O. inornatus* had a significant preference for clams (chi^2, p<0.05). The three oysters selected by *O. erinaceus* showed a drilling hole (Figure 4, Table 1). In addition, out of the eight clams selected by *O. erinaceus*, five showed a drilling hole. Whereas for *O. inornatus*, the selected oyster did not show a drilling hole, the selected five clams by *O. inornatus* showed a drilling hole (Figure 4, Table 1).

Burying of clams

We found that the burying of clams did not significantly influence the feeding behaviour of their predators (*O. erinaceus and O. inormata)* (chi^2, p value >0,05) (Table 2). *O. erinaceus* showed a similar percentage of predation whether the clams were buried under 3 cm (14%) or whether they were not buried (11%) (Table 2). Nevertheless, clams buried under 7 cm were less consumed (6%). For *O. inornata*, results showed that only 11% of the clams were consumed under 3 cm of sediment.

Table 1: Results of experiments 1 and 2.

			O. erinaceus	***O. inornatus***
Experiment 1	Prey choice	Oyster	15 (83.3%)	6 (33.3%)
		Clam	2 (11.1%)	9 (50.0%)
		No choice	1 (5.6%)	3 (16.7%)
	Drilling hole	Oyster	11	2
		Clam	2	8
Experiment 2	Prey choice	Oyster	3 (25.0%)	1 (8.3%)
		Clam	8 (66.7%)	5 (41.7%)
		No choice	1 (8.3%)	6 (50.0%)
	Drilling hole	Oyster	3	-
		Clam	5	5

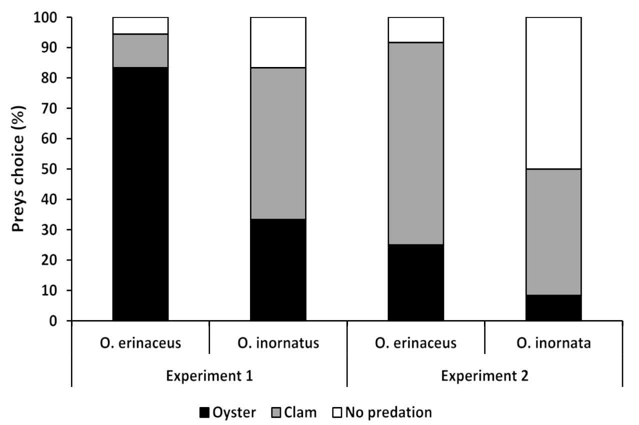

Figure 3: Percentage of prey choice for experiments 1 and 2.

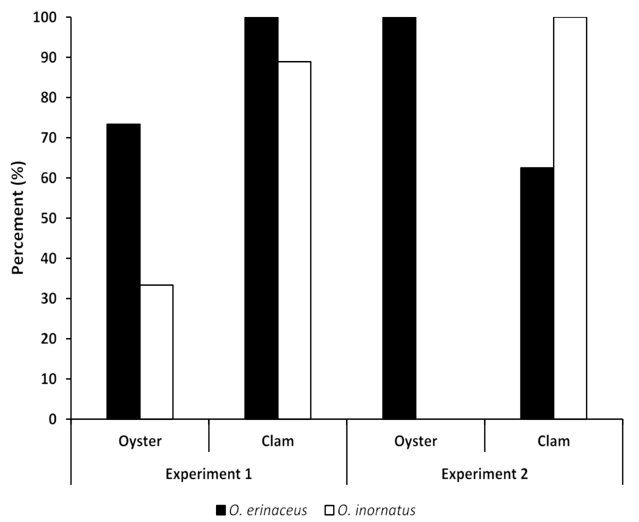

Figure 4: Percentage of preys with a drilling hole after prey choice in experiments 1 and 2.

Table 2: Results of experiment 3 in percentage of predation on clams according to sediment thickness.

Sedimentary conditions	*O. erinaceus*	*O. inornatus*
without sediment	11	0
3 cm	14	11
7 cm	6	0
No predation	69	89
Total	100	100

Behaviour

Using cameras and tank photos of the different experiments without sediment (taken at a rate of one photo per minute), we were able to follow the movement of predators and clams over a period of approximately four hours (oyster did not have the possibility of movement).

Exploration phases by the predators could be observed for several minutes with sometimes their fixation on clams or oysters for experiment based on choice. They could also move in the aquaria including displacement on its walls. The clams also showed activity phases during which they were able to move several cm in the aquarium.

During the burial experiment, we observed what appeared to be flight behaviour of a clam in front of the predator; in fact, at the approach of the predator, the clam retracted its siphons and then moved into the sediment over several cm. However, this behaviour was only observed once; in other cases, the piercers simply left the sediment to fix themselves on the wall of the aquarium out of the water. These observations highlight the ability of piercers to move on a loose substrate, but fail to show any ability to settle on clams buried completely in the sediment.

Discussion

Predatory gastropods have a preference for bivalve preys [24]. Previous studies have highlighted that indigenous species prey preferentially upon oysters whereas *O. inornatus* preys upon a large range of species [25-27]. It has been demonstrated that predator gastropods can prey upon clams even when they are buried in sediment [28]. Our experiments confirm the predation of clams by predators even when they are hidden in sediment, although the predation rate remains low. This weak predation rate can be explained by the environment, composed of sediment in the majority of tanks, which can tend to slow down the movement of the predators. The final set of laboratory experiments shows that odour plays a role in the efficiency of predation by both predators. Indeed, while *O. erinaceus* has a preference for oysters, its food choice is not influenced when clams are added to the oysters. Conversely, the lack of food preference for *O. inornatus* switches to a preference for clams. The predation is effectively influenced by the odours emitted by bivalves and detected by the predator's olfactory organ, the osphradium [24]. This could explain why the predation of *O. erinaceus* is no longer oriented towards a preferential prey if the predator is deceived by the odour given off by the bivalves. However, this same hypothesis does not explain why the Japanese species is preferentially oriented towards clams. A second hypothesis could be that there is a link between the amount of available resources, predation and energy cost. In fact, predation is positively correlated with the amount of food available [29]. When the oyster odour is added to the clam, this may deceive the species *O. inornatus* on the quantity of food present and thus favour its predation. In addition, it is known that this species of predator takes up to seven days to eat a clam, as against almost two weeks for an oyster (time of handling of the prey); the energy cost of the predation of the piercer could explain its choice in favour of the clam [26,29,30]. Another hypothesis is that, even if the odour deceives the piercer setting out in both cases to predate an oyster, *O. inornatus* will choose its prey at random.

The REMORA network (French monitoring network for oyster growth) shows that the mortality rate caused by predatory gastropods can be responsible of 60% of spat mortality and 30% of adult mortality along the French Atlantic coast [31]. With regard to flat farming, this rate is lower and represents 20% of mortality [31]. Along the Normandy coast, predation is highly variable between sectors and is the most important on the rocky shores of the Cotentin west coast where oyster densities are highest [32]. The number of dead oysters per batch is generally between 10 and 30 in six months of rearing, some professionals indicating up to 30% of mortality in some batches of spat. It is common to find a dozen of *O. erinacea* individuals per batch, while *O. inornatus* is becoming increasingly abundant [32]. In addition, predatory gastropods can be responsible for 67% of clam mortality (Basuyaux, personal communication).

Another non-indigenous gastropod was recently reported in this area, *Stramonita haemastoma*, occurring on the bivalve *Pecten maximus*. The presence of these different rock snails may have an impact on local economic resources due to their feeding on bivalve shellfish in aquaculture [23,33].

Our experiments show considerable predation by both gastropods. *In situ* observations on the cultivated Japanese oyster and the wild manila clam *Ruditapes philippinarum* show significant predation. In the future, the prey-predation relationships between bivalves and predatory gastropods should present a threat for oyster farmers and clam fishers. A monitoring of this danger should be encouraged with an annual survey of some sites on the western coast of Cotentin.

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Author Affiliation

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[1]*Continental and Coastal Morphodynamics Laboratory, Normandie University, France*

[2]*Synergie Mer et Littoral (SMEL), Blainville sur mer, France*