Estuarine, Coastal and Shelf Science 317 (2025) 109206

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

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

Manila clam (*Ruditapes philippinarum*) in France: Fishing activity, governance and present knowledge challenges regarding its biology and ecology

Nathalie Caill-Milly [a,*], Florence Sanchez [a], Muriel Lissardy [a], Noëlle Bru [b], Claire Kermorvant [b], Xavier de Montaudouin [c], Sylvie Lapègue [d], Florentine Riquet [e], Ludovic Bouché [f], Céline D'Hardivillé [g], Franck Lagarde [d], Aurélie Chambouvet [h], Nicolas Mayot [i], Jean-Claude Dauvin [j], Jean-Philippe Pezy [j], Olivier Basuyaux [k], Anthony Guéguen [l], Yohan Weiller [m], Isabelle Arzul [e], Christine Paillard [n], Caitriona Carter [o]

[a] Ifremer, COAST, Anglet, F-64600, France
[b] Laboratory of Mathematics and its Applications of PAU - MIRA, University of Pau & Pays Adour/E2S UPPA, UMR 5142 CNRS, Anglet, F-64600, France
[c] University of Bordeaux, CNRS, Bordeaux INP, EPOC 5805, Marine Station, Arcachon, F-33120, France
[d] MARBEC, Univ Montpellier, CNRS, Ifremer, IRD, Montpellier, France
[e] Ifremer, ASIM Adaptation et Santé des Invertébrés Marins, La Tremblade, F-17390, France
[f] DECOD, L'Institut Agro, IFREMER, INRAE, Lorient, 56100, France
[g] Comité Départemental des Pêches Maritimes et des Élevages Marins du Morbihan, Auray, F-56400, France
[h] Sorbonne University, CNRS, Adaptation and Diversity in Marine Environments, AD2M, Roscoff, F-29680, France
[i] GIPREB, Berre l'étang, F-13130, France
[j] Normandie Université, UNICAEN, M2C (Morphodynamique Continentale et Côtière), CNRS UMR 6143, Caen, F-14000, France
[k] Mer Expertise Environnement Études et Conseils, Blainville-sur-Mer, F-50560, France
[l] Comité Régional des Pêches Maritimes et des Élevages Marins de Nouvelle-Aquitaine, Ciboure, F-64500, France
[m] Parc naturel marin de l'estuaire de la Gironde et de la mer des Pertuis, Office français de la biodiversité, Direction régionale de Nouvelle-Aquitaine, F-17300 Rochefort, France
[n] Laboratoire des Sciences de l'Environnement Marin, LEMAR, UMR CNRS 6539, Institut Universitaire Européen de la Mer, Plouzané, F-29280, France
[o] Inrae, UR ETTIS, Centre de Nouvelle Aquitaine, Cestas, F-33610, France

ARTICLE INFO

Keywords:
Manila clam
Life-history traits
Fishery management
Sustainability
France
Europe

ABSTRACT

Originally introduced to France in the 1970s for aquaculture purposes, the clam *Ruditapes philippinarum* (Adam and Reeve, 1850) has thrived in favourable conditions across numerous sites along the Bay of Biscay, English Channel and Mediterranean coasts forming neo-naturalized populations. It is harvested by both recreational and professional fishers, with an estimated production ratio of 2.4 for both activities combined. Total French commercial fishing production is roughly estimated at around 2000 to 3000 tons per year. This activity is managed by three types of regulation at different scales: European (Minimum Conservation Reference Size - MCRS), national (licenses), and regional. Regional instruments govern fishing practices by setting spatial and temporal access rules to fishing grounds (also referred to as deposits), prohibiting certain gear types at the local scale, determining the minimum size of clam fishing (above MCRS) and setting fishing quotas. Not all of them are implemented everywhere; most often, they are based on stock assessment results and specific research programs, which are not available in every location. This article first provides a review of available information on current Manila clam production in France, and its regulation. Second, it offers an overview of recent knowledge mobilized for management purposes. This overview covers biological and ecological processes (*i.e.* population dynamics, reproduction and spawning, habitats considerations, biotic interactions and infectious diseases), and enables us to identify future research prospects of interest.

This article is part of a special issue entitled: The Manila Clam published in Estuarine, Coastal and Shelf Science.

* Corresponding author
E-mail address: Nathalie.Caill.Milly@ifremer.fr (N. Caill-Milly).

https://doi.org/10.1016/j.ecss.2025.109206
Received 17 October 2024; Received in revised form 11 February 2025; Accepted 19 February 2025
Available online 21 February 2025

1. Introduction

The Manila clam [*Ruditapes philippinarum* (Adams and Reeve, 1850)] – also called the Asari clam - was initially introduced to France for aquaculture purposes in the early 1970s. This species has demonstrated better growth performance than the native species (*Ruditapes decussatus*, Linnaeus 1758) and shellfish farmers have developed and implemented various techniques to optimize its yields. But rapidly the Manila clam culture underwent difficulties (due to concession availability and use, zootechnical errors, predation, infectious diseases, economical competition, regulatory disparities …) which led to its decline at the end of the 1980s. Following this period, Manila clam has thrived in favourable conditions across numerous sites along the Bay of Biscay, English Channel and Mediterranean coasts forming various neo-naturalized populations (de Montaudouin et al., 2016a).

Since the 1990s, this species is fished both by professional and recreational fishers along the coast and in lagoons (de Montaudouin et al., 2015). For coastal areas, it is an important socio-economic activity. Clam landings in France account for 13% of total clam landings in the European Union (EU) (EUMOFA, 2019). Among the shellfish harvested by recreational fishers, clams (*Ruditapes* spp.) rank 2nd after the cockle [*Cerastoderma edule* (Linnaeus, 1758)] (FranceAgriMer, 2018). Regarding consumption in France, clams are among the most commonly consumed shellfish after mussels, king scallop, oysters, whelks and winkles (Lunghi et al., 2023).

For French waters, and more generally for North-East Atlantic waters, various political commitments guide fisheries' management decisions: the 1995 United Nations Fish Stocks Agreement, the European Plan for Maximum Sustainable Yield [COM (2006) 360 final], the Common Fisheries Policy (EEC no. 170/83, EEC no. 3760/92, EC no. 2371/2002 supplemented by EC no. 2369/2002 and EC no. 2370/2002, EU no. 1380/2013), the Johannesburg World Summit on Sustainable Development in 2002, the Marine Strategy Framework Directive (EC no. 56/2008 amended by EU no. 845/2007) and, more recently, the United Nations Sustainable Development Goals (SDGs), including SDG 14 of the 2030 Agenda (A/RES/70/1 of the United Nations in 2015). For clams, but this is also true for other local stocks of bivalves (scallops, mussels, etc.), stock management is primarily carried out at a sub-European level. It requires knowledge of species biology and the development of indicators, for which the collection and processing of information deals with a variety of sources, often on specific spatial and temporal scales. These elements are supplemented, as much as possible, by knowledge of how these halieutic populations evolve in their environment, focusing on causal relationships between processes.

This paper reviews the current knowledge of Manila clam in France more than 50 years after its intentional introduction in Europe (initially for breeding purposes). It specifies key fishing activities, as well as the main biological and ecological features of its populations along three metropolitan French coasts: the Mediterranean Sea, the Bay of Biscay and the western part of the English Channel. Additionally, current governance arrangements are discussed, with a view to identifying future research prospects of interest.

2. Current French fisheries (2016–2023)

French production of Manila clam takes place on the Atlantic coast, stretching from the western coast of Cotentin in the western part of the English Channel to Arcachon Bay in the southern part of the Bay of Biscay, and along the Mediterranean coast in the Berre lagoon and the Carteau lagoon (Fig. 1). Harvesting is carried out on tidal flats or in shallow areas (less than 5 m deep), depending on whether the areas in question are subject to tides.

2.1. Techniques and numbers of active Fishers

Three types of fishing practices are currently used to harvest Manila clam in France: handpicking/raking during low tides, snorkelling/free-diving fishing, and clam dredging. While the first two are the most common, the third is practiced by only a handful of vessels (Fig. 1). Hand fishing is conducted at low tide or "à la gratte", with part of the body immersed in water. The fisher reaches the fishing area on foot from the shore or by boat. If the seabed consists of soft mud, he/she can move over it using boots, waders or mud pattens. On the sandy-gravel shores of Cotentin, professional and many recreative fishers rake the sediment to collect clams (Beck et al., 2015; Basuyaux et al., 2018). In other parts of the seashore, clams are mainly collected with bare hands, although small hand-operated devices (*e.g.* for Mediterranean regional, hand dredger called "arseillère") are authorised at certain sites. A fishing trip typically lasts 6 h (including 3–4 h of fishing). Freediving fishing is carried out from a boat or directly from the shore in shallow water. In this case, the fisher is equipped with a mask and snorkel. Divers can be weighted down if the depth of the dive requires it, but the use of fins is prohibited. Clams are picked off the sediment by hand; on some sites, a small tool such as a knife or fork may be used to scrape the sediment. In certain locations, fishers can detect siphon pits at the surface of the sediment to collect clams. A fishing trip lasts maximum 5 h. Finally, dredge fishing consists in towing a steel-mesh cage behind a small-scale vessel (length and power smaller than 12 m and 120 kW respectively). The gear used for Manila clam is an adaptation of the cockle dredge; it is operated by a power hydraulic winch. Previously practised in the Gulf of Morbihan and Champeaux (western Cotentin) sector, this type of activity is now only found in one French site, the Bay of Vilaine. A fishing trip lasts 2 h maximum with 2-3-min dredge hauls.

The spatial distribution of these three types of practices is shown in Fig. 1. The technical characteristics currently authorised are presented in the section of this article on regulations (2.3.). Illustrative photos are shown in Fig. 2.

On the western coast of the Cotentin, clams are the primary species targeted by recreational fishers. The average catch has been increasing for the past ten years, reaching between 80 and 100 clams per day and per fisher in 2023 (personal communication, Maxime Spagnol, AVRIL association) according to the fishing sector compared to an average of 44 in 2016 (Basuyaux et al., 2018). Fishing sessions typically last about 2 h, with an average yield of 49 clams per hour per fisher. Overall, amateur shellfish fishing activity accounted for approximately 120000 fishing sessions per year as in 2023 *i.e.* around 96 % of the total fishing sessions.

2.2. Production

The latest compilation of production data from French professional fisheries dates from the mid-2010s, with total production estimated at 1200 t (de Montaudouin et al., 2015). At that time, two production sites predominated: the Gulf of Morbihan and the Arcachon Bay, with around 500 t each. The situation has changed since then, with other sites accounting for a significant proportion of the production. These include the Berre lagoon, where production began in 2018 and reached an estimated 800 t in 2023. On the western coast of the Cotentin, fishers' observations on the intertidal zone and contents of individual baskets make it possible to estimate clam catches by recreative fishers at about 250 t (Personal communication Maxime Spagnol, AVRIL association; Basuyaux et al., 2018). Professionals, based on their declarations, report a strong increase of 86 t in 2023 [11 t to 18 t between 2013 and 2015 (Basuyaux et al., 2018)] (CRPMEM Normandy data). However, these declarative data are subject to discussion. Thus, the total catches in this sector could be estimated between 330 and 400 t per year since the beginning of the 2020'. Currently, the total estimated production is circa 2900 t with around 70% originating from the Atlantic coast and 30% from the Mediterranean coast.

Each professional fisher is required to submit a monthly declaration of his/her catches so productions are theoretically known. Nevertheless, it should be noted that difficulties are encountered when collecting these statistics. These are essentially linked to three aspects that may

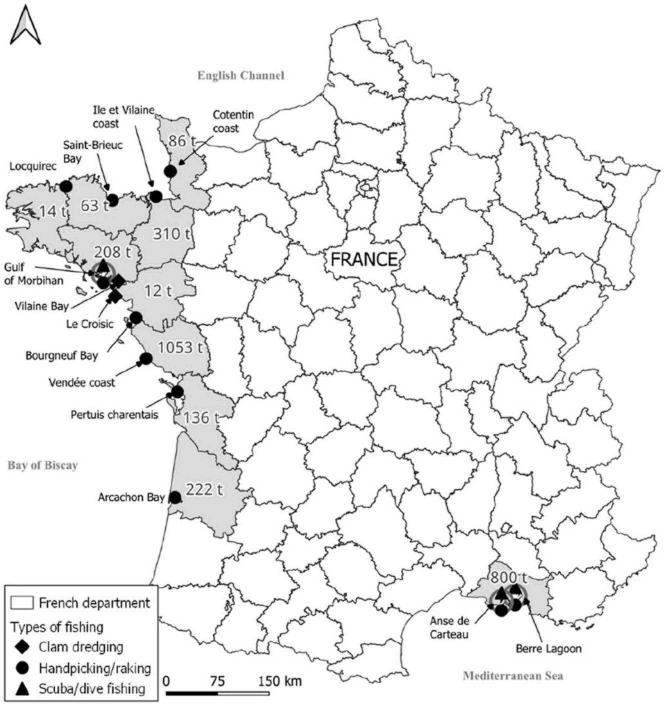


Fig. 1. Map showing Manila clam fishing areas and practices. Production data relate to professional fishing activity. Their sources are CRPMEM Normandy, CDPMEM Morbihan – Télécapêche, (Damour et al., 2022), PNMGP, CRPMEM Nouvelle-Aquitaine, Gipreb.

Fig. 2. Illustrative pictures of the 3 types of Manila clam fishing (©Jean Piel – CDPMEM 56).

introduce some bias. First of all, the data refer to Manila clam catch, but often also those of European clams [*R. decussatus* (Linnaeus, 1758)]. The European clam is currently in scarce supply with a proportion of *R. decussatus* of 1–10% of the abundance of veneridae when the two species cohabit in the same deposit (Beck et al., 2015; Sanchez et al., 2021). In these conditions, it is not worthwhile distinguishing between them when marketing them in the hope of getting a better price. This is

Table 1
Array of measures applied for management of Manila clam deposits in France.

Type of rules	Objective	Measures	Scale
Access regulation to the resource (first and foremost)		National fishing permit for each fisher Designation of site and very regular sanitary quality control	National[a]
Conservation of the resource	Fishing effort reduction	Licenses/stamps contingent ("cockles and Manila clams", "burrowing bivalves" …) Renewal may be subject to a minimum activity level in the previous fishing year, to rules "-2+1" (granting of a new license implies non-renewal of two licenses).	Regional/local[b]
		Opening and closing dates and hours	Regional/local[b]
	Technical measures	Authorized gears and dimensions	Regional/local[b]
		Minimum Conservation Reference Sizes (MCRS), differing between the Atlantic and the Mediterranean	European
		Closed fishing areas	Regional/local[b]
	Catch limitations	Quotas (kg/fisher/day …), size	Regional/local[b]
Conservation of the local environnement	Reduce impacts on habitats	Ban on fishing in certain foreshore habitats	Regional/local[b]

[a] National: State Administration.
[b] Regional/local: stakeholders (fishing sector, State Administration locally with scientists' supports).

called selection bias. Secondly, data is not systematically available on an appropriate spatial scale for such coastal resources. Regulatory obligations require on-foot fishers to make declarations for the sanitary classification zones and on-board fishers for ICES statistical rectangles. ICES rectangles extend about 0.5 and 1° in longitude and latitude, respectively, with an area of approximately 30 nautical square miles. They do not provide very accurate spatial information for local deposits, especially when they are spatially close to one another. This is called "problem of spatial aggregation". Finally, clams are often sold directly (to wholesalers, restaurants, etc.) and few are auctioned. As a result, the quality of the statistics may be affected because there is less opportunity to cross-check the data with other sources such as sales data. This can be viewed as a measurement bias. The fact that some areas benefit from regular surveys and/or are covered by dynamic local fishing authorities improves the quality of statistics.

Although this article deals with professional fishing, it is also worth looking at recreational fishing. There is no obligation to declare catches for this activity, but certain studies provide some idea on catches made. The LIFE-PAP programme provided an estimation of the total clam harvest at French national level at circa 960 t for professional and 2300 t for recreational fishers in 2015 (http://www.aires.marines.fr/Partager/projets-europeeans/LIFE-Peche-a-pied-deloisir; Basuyaux et al., 2018). The global ratio between recreational and professional productions is 2.4. It reached 7 along the Cotentin coast; in this case it is evident that the large number of recreational fishers and the intense harvesting associated with this activity along the coast are used by economic actors as an attraction for tourists. Nevertheless, it is not easy to characterize recreational fishing at sea on a national scale; it is essentially based on surveys. To improve data collection on this activity, Bellanger and Levrel (2017) reiterated the benefits of a complete register of recreational fishers. Such a register already exists for freshwater recreational fishing due to the permit system in force.

2.3. Management and health measures

In France, the management measures of Manila clam exploitation are governed by three types of rules (access regulation to the resource, conservation of the resource and of the local environment) and relate to three scales of regulation (European, national and regional even local) (Table 1).

First and foremost, a national fishing permit is mandatory for each fisher to access the resource. This permit is issued at the state-widescale, with French legislation requiring the registration of fishing licenses since 2010 (Decree n° 2010–1653 December 28, 2010). In 2024, 1300 fishing permits were attributed.

Additionally, each fisher must hold a local license to access a specific deposit. This measure, which falls under resource conservation measures, is administrated by regional or local actors. It allows for the control of fishing efforts and may be completed by the designation of areas where fishing is prohibited. Technical measures and catch limitations supplement this array of rules regarding resource conservation. These include the regulation of authorized fishing gears and their dimensions, the opening and closure time of the fishing period (mainly defined by dates, rarely by hours), and the Minimum Conservation Reference Size (MCRS). While the first two are established at regional or local scales, the MCRS in force in France is set by European legislation. Currently, the MCRS is set to 35 mm shell length for the North Atlantic, the English Channel and the North Sea, with the exception of Skagerrak/Kattergat (North Sea) and 25 mm for the Mediterranean Sea. Furthermore, resource conservation can also be permitted by the establishment of quotas, which set catch limits per fisher and per time units per area (day, fishing season). Local minimum size (above MCRS) can also be established at regional/local levels (*e.g.* 40 mm for the English Channel and 30 mm for Berre lagoon with prefectoral orders that overrules the European text).

Regarding the conservation of local habitats, fishing bans on certain foreshore habitats are enforced to reduce the impact of fisheries on these environments. For example, there is an interdiction on fishing in the vicinity of the intertidal honeycomb *Sabellaria alveolata* (Linnaeus, 1767) reefs, established through the creation of a Special Conservation Zone with a Natural Habitat Protection order the Champeaux and Saint-Anne sectors in the Norman-Breton Gulf, implemented by local authorities (DREAL, DDTM). This type of measure is more recent than the others, dating from the 2010s.

Manila clams are subject to specific health regulations like most other shellfish to protect consumers from potential health risks associated with shellfish consumption. This results in a sanitary classification of production zones. For instance, if the area is classified as B, the collected clams must pass through purification tanks before being marketed. When sanitary shellfish analysis reveals an unfavourable sanitary situation, and the shellfish are deemed unfit for human consumption, marketing restrictions or bans are imposed by a Prefectural decision (prefectural orders). Episodes of shellfish contamination (bacteria, phycotoxins or viruses) or mortality (parasitic infection) most often occur in spring. In addition, as aquatic animals, clams are covered by the Animal Health Law [Regulation (EU) 2016/429 of the European Parliament and of the Council of March 9, 2016 on transmissible animal diseases and amending and repealing certain acts in the area of animal health]. In this frame, any suspicion of emerging diseases, notably abnormal mortality, must be reported and investigated. Although *R. philippinarum* is currently not listed as susceptible to any pathogen regulated by EU rules, it is in the list of host species of the parasite *Perkinsus olseni* (R.J.G. Lester & G.H.G. Davis), notifiable to the Word Organisation for Animal Health (WOAH). In France, mortality of marine molluscs including clams shall be notified through the REPAMO (Réseau de Pathologies des Mollusques), a network dedicated to the surveillance of mollusc diseases (www.repamo.fr). Movements of animals must be suspended during the occurrence of the mortality event and until the presence of an emerging and or regulated pathogen is discarded.

2.4. Regional/local measures and mobilized knowledge

Regulations at the regional and local scales (*i.e.* regarding fishing effort, technical measures except for MCRS, catch limitation and fishing impact on habitats) are decided by professional organizations (Regional Committees Marine Fisheries and Aquaculture in connection with their local offices) and are implemented by prefectural orders - *i.e.* by a 'state-in-the-region' representative (Caill-Milly. et al., 2021). Appendix 1 provides the latest measures according to various deposits. They are adjustable over time based on scientific advice. For certain deposits, these regulations rely on regular or occasional resource assessment surveys (Damour et al., 2022; Sanchez et al., 2021; Bouché and D'Hardivillé, 2023; Mahé, 2022; Patrissi et al., 2023). These surveys provide standardized indicators such as abundance, density, size-distribution and spatial distribution. The most critical factor is the evolution of these indicators other time, rather than the absolute values. Surveys are conducted by scientific organizations or co-conducted by local fishing authorities and scientific bodies. To complement these snap-shot representations of populations, research programs may be implemented to provide additional knowledge. These programs help understand the dynamics of the exploited population in its environment between two "snapshots". At some sites, only commission deposit visits are organised by either a professional organisation or administration. In some sectors, no fishing zones are implemented to preserve specific areas (for example in the Ille-et-Vilaine Department, in Arcachon Bay). In other cases, scientific reserves were created, such as on the western coast of Cotentin at the Agon cape, Manche Department, where the fishing of burrowing bivalves, including clams, has been banned for 5 years in an overexploited sector (Basuyaux et al., 2023). However, the results of this experiment are mixed. While fishers' acceptance of this ban has been generally positive, the recovery of clams has been inconsistent, with some high-density areas being overfished as soon as they are reopened, and other areas where clams have not re-established (Basuyaux et al., 2023).

To define and adapt these measures, various issues regarding the functioning of these populations are raised. They include population abundance and distribution, life-history traits, connectivity and dispersal between functional habitats, the impact of fishing, and more. These issues are related to biological and ecological processes (Mullin, 2013; Gard, 2012; Bœuf, 2010) which need to be understood and addressed. In these cases, the focus is on: population dynamics; habitat considerations; reproduction and spawning; biotic interactions and infectious diseases. The reminder of this article reviews knowledge acquired about French Manila clam deposits.

3. Key issues regarding biological and ecological processes for the French deposits

3.1. Regarding population dynamics

Population dynamics is a fundamental area of ecology that examines variations in the size and density of populations over time and space, whether for one or more species (Begon et al., 1990; Hastings, 2001). Practically, it encompasses two main components: first, the quantitative description of changes in population abundance and the patterns of population growth or decline; second, the understanding of the biological and physical processes driving these changes (Beck et al., 2015; Basuyaux et al., 2018; Dauvin et al., 2024). To achieve this, physical properties of a population are observed through key characteristics such as size, density, dispersion, sex, and age distribution. Critical factors in population dynamics include reproduction rates, mortality and migration. Appropriate data collection, statistical analysis, and modelling are employed to quantify trends, understand interactions, but also forecast future changes.

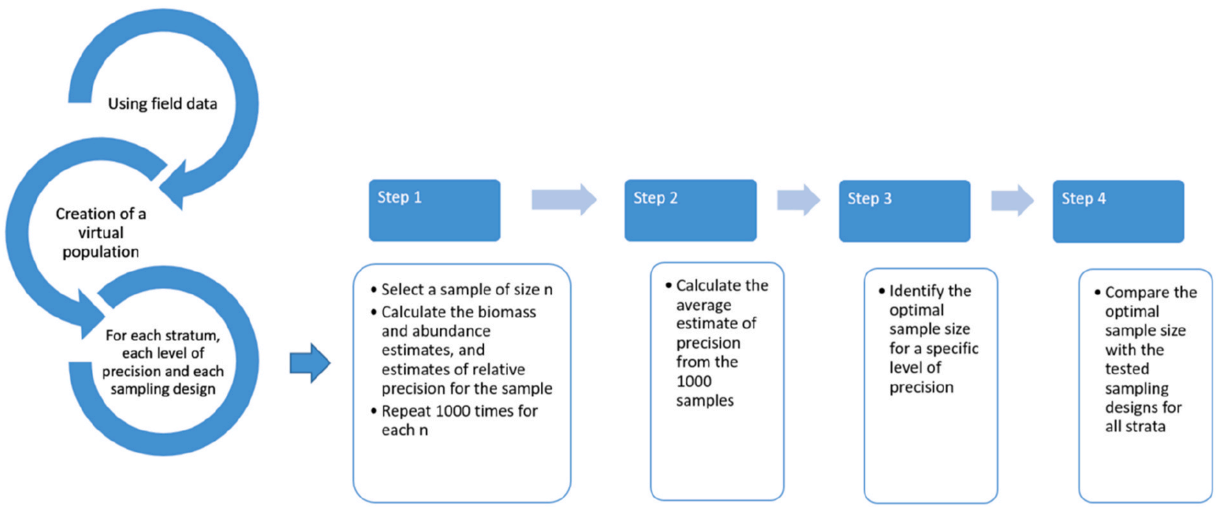


Fig. 3. Methodology used to assess the performance of protocols applied to the Manila clam population in the Arcachon Bay.

3.1.1. *Construction of abundance indices*

As with many local deposits, obtaining abundance indices for clam populations typically relies on a spatial sampling protocol, specifically stratified random sampling (StRS) (Sanchez et al., 2021; Bouché and D'Hardivillé, 2023; Gillespie and Kronlund, 1999; Gray et al., 2014; Norgard et al., 2010; Pitel et al., 2004). StRS offers advantages such as a greater precision of means compared to simple random sampling, ease of implementation and flexibility (Smith et al., 2017). However, the random selection and positioning of stations within a stratum can result in clusters of sampling points or, conversely, areas without any sampling points, potentially leading to missed spatial patterns (Stevens and Olsen, 2004; Christianson and Kaufman, 2016) even when such patterns are present (Yu et al., 2012). In cases where spatial patterns are important, other protocols - spatially balanced protocols - are of interest, as they account for spatial heterogeneity and auto-correlation in the construction of estimators (Stevens and Olsen, 2004; Theobald et al., 2007; Grafström, 2012; Grafström et al., 2012; Grafström et al., 2013; Robertson et al., 2013; Wang et al., 2012; Haining, 2003). These protocols have been developed since the 2000s and include methods such as Generalized Random Tessellation Stratified (GRTS) (Stevens and Olsen, 2004), Balance Acceptance Sampling (BAS) (Robertson et al., 2013; Brown et al., 2015), Local Pivot Method (LPM) (Grafström et al., 2012), Spatially Correlated Poisson Sampling (SCPS) (Grafström et al., 2012).

• Design of optimal scientific data collection protocols

In Arcachon Bay (South-West of France), clam population using a StRS has been in place since 2003. Approximately 500 points are surveyed every other years, requiring a team of 5–6 people working for 15 days (Sanchez et al., 2021). However, securing the necessary funding has been challenging, and in some years (2016, 2017, 2023), it was difficult, if not impossible, to carry out the survey. In this context, the potential contribution of spatially balanced protocols to improve existing monitoring efforts was explored. Initially, a review of the implementation of spatially balanced sampling protocols in environmental monitoring was conducted (Kermorvant, 2019; Kermorvant et al., 2019a). Following this, a sequential procedure was developed to evaluate and select the most effective protocol based on the number of statistical units required to achieve the desired precision in estimation results (Fig. 3).

Kermorvant et al., 2017, 2019b conducted mathematical simulations to reconstruct past intra-basin clam populations (from 2003 to 2016), testing three algorithms for selecting monitoring points (StRS, GRTS, BAS). Among the best performing protocols identified, GRTS was first field-tested in 2018 and 2021 using the same sampling effort. The analysis of these results allowed for adjustment in the 2024 monitoring effort. Specifically, the number of monitoring points in strata where the results exceeded the target accuracy (coefficient of variation of the abundance estimator 0.20) was reduced. Conversely, the resources saved in this first year of protocol change were utilized, following validation by the clam Working Group (involving scientists, professionals and the administration), to survey areas not included in the initial reference strata. The work also integrated economic considerations and generalized the method by accounting for different properties of the statistical population (Kermorvant et al., 2020). Based on a simulation study similar to that described by Zurell et al. (2010), various strategies (sampling plan/number of samples/desired accuracy) can be tested, with an acceptable calculation time of around 20 days maximum per protocol in our case study.

• Test of different sampling units to estimate clam density

Another challenge in sampling a population is identifying the most appropriate sampling techniques to a specific site. Along the western coast of Cotentin Peninsula, Manila clam has successfully colonized a large variety of sediment habitats with densities of less than 20 ind.m^{-2}. Because the intertidal zone is extensive and the species is dispersed, it was worth exploring the possible improvement of the method to estimate the densities. A study carried out on 4 target sites tested several sample unit areas, *i.e.* 1/32, 0.09, 1 and 10 m^2, to evaluate the clam density (Basuyaux et al., 2018). Considering precision and cost, it concluded that it is better to continue using a quadrat area of 1 m^2 for a large number of random sampling points ($\geq$400) to estimate with the greatest possible spatial precision the local and regional abundance of such low-density populations.

At the scale of the 30 km of the Cotentin coast (from Geffosses to the North and Saint-Martin-de-Bréhal to the South), a comprehensive sampling effort was conducted (Basuyaux et al., 2018). The coastline was first divided into 1 km sectors of latitude. On each sector, the geographical coordinates of 10 points were randomly selected. In a subsequent phase, additional points were randomly added in four sectors where clam abundances were the highest. At each point, a 1 m $\times$ 1 m square PVC quadrat was used for sampling, with sediment raked to a depth of 0.15 m and then sieved through a 5 mm mesh to collect all clams. In total, 596 points were covered from February to May 2015. Clams were observed in 177 of the 596 one-square quadrats. The maximum number of clams per m^2 was 52, while for marketable clams (>40 mm), the maximum was 23. When considering only the quadrats that contained clams, the mean abundance was 5.1 $\pm$ 7.0 clams.m^{-2} and 2.5 $\pm$ 2.9 clams.m^{-2} having a size > 40 mm. If all 596 quadrats are

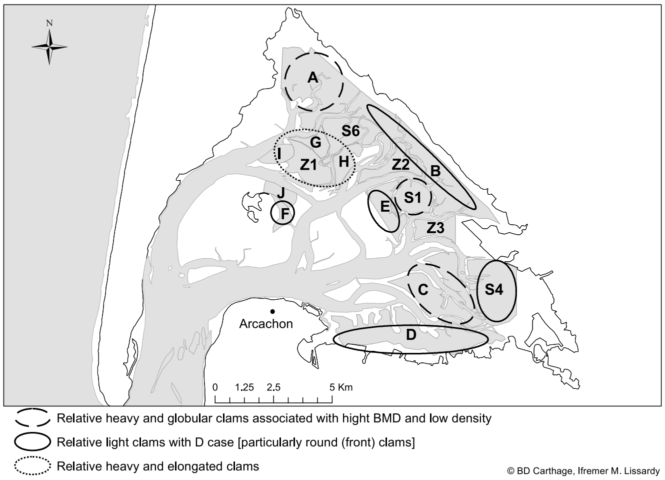


Fig. 4. Spatial vizualisation of the allometry patterns of Manila clam related to density and disease (Caill-Milly et al., 2012).

included, the mean abundance was 1.5 ± 4.5 clams.m^{-2}, with 0.5 ± 1.6 clams.m^{-2} exceeding 40 mm in size.

- Short-term changes of clam density

To identify short-term changes (14–69 days) in the adult abundance of the Manila clam, observations and displacement (movement of clams on the intertidal zone) assessments were observed during the 2014–2018 period to estimate the natural displacement in a high-energy hydrodynamic tidal regime in the western coast of the Cotentin (Dauvin et al., 2024). The mean abundance displacement derived from all the observations carried out in 2014, 2016 and 2018 is estimated at 1.8 ind. m^{-2}.mo^{-1}, a value that should be compared with the mean density of between 2.0 and 12.5 ind.m^{-2} along the western coast of Cotentin. During the experiments, most of the clams show a moderate displacement being less than 2 m in 2017 (Dauvin et al., 2024).

3.1.2. Growth parameters and their dynamics

Understanding population dynamics requires knowledge of individual growth patterns. In bivalves, the most frequently used criterion for measuring growth is the greatest dimension, the length, which corresponds to the anteroposterior measurement of the valves (Gosling, 2003). However, this measurement alone may be insufficient, as it provides information on only one axis of growth, whereas growth can occur along multiple dimensions. Additionally, most bivalves undergo changes in shape during their development (Fan et al., 2007). These progressive allometric changes are primarily controlled by the genotype of the individuals and occur throughout ontogeny (Gosling, 2003; Hoffman, 1978). For many species, the influence of environmental conditions on growth has also been demonstrated (Ohba, 1959; Seed, 1968; Rosenberg, 1972; Brown et al., 1976; Gérard, 1978; Lucas, 1981; Eagar et al., 1984; Stirling and Okumus, 1994; Kwon et al., 1999; Costa et al., 2008), leading to the expression of various phenotypes. Identifying these groups of individuals on both inter- and intra-site scales provides valuable additional insights into understanding stock dynamics.

In Berre lagoon, in order to understand the population dynamics, long-term field monitoring (*in situ* cages coupled with sclerochronology) was performed to estimate the growth rate and the mortality. Von Bertalanffy growth function parameters show a high growth rate (K = 1.42 yr^{-1}) with a small L_∞ (35.70 mm). This means that clams need 1.5 yr to reach 30 mm in length: the minimum catch size for the fishery in this site.

A growth model in length was developed for the Manila clam population in Arcachon Bay using the Von Bertalanffy method (Dang, 2009). Compared to other studies, the growth performance of this population is relatively poor within the lagoon. This site's unique characteristics were later confirmed (Caill-Milly, 2012; Binias, 2013; de Montaudouin et al., 2016b). The growth patterns of individuals in this sedentary and isolated stock differ greatly from those in other areas, with growth slowing down at around 30 mm (Dang, 2009; Dang et al., 2010a). Beyond this size, it appears that growth occurs more in width than in length, resulting in a globular shape. At the scale of Arcachon Bay, three main morphological groups were identified among adult clams and for the first time, relationships between shell shape, density and disease were demonstrated (Caill-Milly et al., 2012). This analysis identified areas where growth conditions are more favourable than others (Fig. 4). When comparing four Manila clam populations along the French Atlantic coast (Banc du Guer, Arcachon Bay, Gulf of Morbihan and Bellevue), three ratios were found to discriminate between these four deposits: H/L (elongation index), SM/Av (a valve density index) and SM/L (an index representing the weight of the valve relative to its anteroposterior length).

The dependence of each discriminant ratio on environmental variables from monitoring networks (REPHY and ARCHYD) (Belin et al., 2013) was analysed using the process described by Bliese (2012). Significant relationships were found between these ratios and chlorophyll *a* concentration, as well as one ratio and seawater temperature ranging from 12 to 20 °C. Potential causes for these relationships were hypothesized (Caill-Milly et al., 2014). The analysis not only highlighted species-level differences in shell morphology but also revealed morphometric specificities on an intraspecific scale, with trends linked to latitude and the influence of other factors.

Fig. 5. Illustration of hatchery spat tagged at T0 (June 17, 2015) and after 9 months.

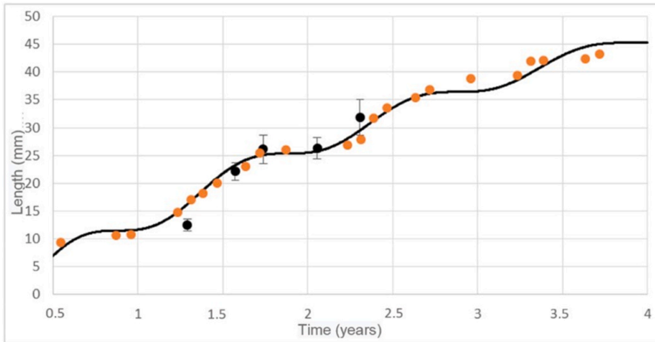


Fig. 6. Modelling of clam growth in the Gouville-sur-Mer (Manche Department). In orange the data from natural populations, and in black the data from the hatchery spat reimplanted (unpublished data). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

On the western coast of the Cotentin, growth parameters were determined through monthly monitoring of natural populations over a 13-month period in 2015–2016 (across 6 stations, with 3 replicates of 0.25 m^2 per station). Cohort analysis was performed on the entire dataset, using Bhattacharya's method (Bhattacharya, 1967) and the FISATII software. By tracking the individual growth of each cohort, it was possible to model growth using a seasonalized Von Bertalanffy model. Additionally, hatchery-reared clams, identified with marking tags on their shells (Fig. 5) were monitored every 3 months. This data helped validate the growth model. The findings indicate that clam growth in this region is seasonal, with growth ceasing during winter. It takes 3 years and 4 months for a clam to reach the local legal catch size of 40 mm (Fig. 6).

3.1.3. Species identification, genetic diversity and population structure

Due to their morphological similarities, distinguishing *R. philippinarum* from *R. decussatus* based on shell characteristics alone is challenging: on the contrary, genetic identification based on nuclear and/or mitochondrial markers alone casts no doubt about the species identification (Hurtado et al., 2011; Habtemariam et al., 2015). For instance, Painblanc (2023) analysed 317 clams sampled along nine French sites using morphological characteristics (shell length, height, width and weight) and two genetic markers (ITS2 and mtCOI). Taxonomic identification was first based on genetic markers and then compared to morphological identification: while the elongation index [the height/length ratio (Caill-Milly et al., 2014),] was the most discriminatory metric between the two species at a given site, a high variance was observed within (a) species across different sites. This suggests that i) shell shape is largely "site-dependent" and ii) shell-based criteria should be used with caution when differentiating species across varying locations (Fig. 7A).

In addition to species identification, genetic analysis is crucial for examining the genetic diversity and population structure of the Manila clam. According to Flassch and Leborgne (1992), the European population originated from a small pool of individuals −500000 spat and 1000 adults from the Pacific coast of North America, representing approximately 70 kg of total biomass-resulting in a limited founder population that has likely caused a strong genetic bottleneck in Europe (Chiesa et al., 2011, 2014, 2017; Cordero et al., 2017), including in France. Indeed, in the native range, three lineages have been identified (Cordero et al., 2017; Mao et al., 2011), whereas only two lineages have been observed in France, but with higher haplotype diversity based on the mtCOI marker. This suggests a genetic bottleneck, yet also indicates a relatively limited loss of genetic diversity (Riquet et al., In prep). Genetic analysis thus allows for a deeper understanding of the Manila clam demographic processes following its introduction, as well as intraspecific diversity and connectivity by identifying multiple haplotypes within each species (Fig. 7B).

Despite its well-established status as a non-indigenous species, a demographical decline is currently occurring in certain areas along the French coastline, for example in the Fier d'Ars area on the isle of Ré, a strong decrease in Manila clam density and quantities harvested has been observed since 2018. In the Mediterranean lagoons the situation is different with *R. decussatus* fishing having long been a traditional activity, notably in the Thau and Berre lagoons. After a peak of harvests in 1979 and 1985, with approximately 475 t collected (Mazouni et al., 1999), recent observations indicate that almost no clams have been harvested in the Thau lagoon over the past decade (Patrissi et al., 2023). Following an observation along these lines in the Berre lagoon, the Manila clam was introduced and has been harvested since 2018. A crucial first step in such cases is to estimate the marketable clam stock and identify the species present. Although adult specimens of *R. decussatus* and *R. philippinarum* can be distinguished morphologically within a site, this process often presents difficulties. Identifying juvenile or smaller specimens is even more challenging, requiring dissection to observe soft tissue and/or undertake genetic analyses for accurate identification, which is both time-consuming and invasive for the sampled individuals.

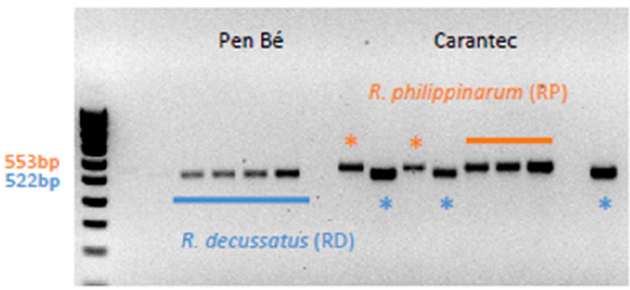
A recent study showed that among 12 French Mediterranean lagoons sampled, *R. philippinarum* was present in only two, while the indigenous species was observed in the other 10 (Mahé et al., 2022). Consequently, alongside the 2023 stock estimate (Patrissi et al., 2023), a genetic analysis based on eDNA was conducted to easily detect the presence of both species in the Thau and Berre lagoons (Fortunato, 2024). A metabarcoding approach was employed using a mitochondrial primer initially developed for freshwater Venerida (Prié et al., 2021). After initial tests in aquaria, which confirmed the effectiveness of this marker in detecting and quantifying both species, it was applied at several sites within the Berre and Thau lagoons. In the Berre lagoon, *R. philippinarum* was confirmed as the dominant species, while in the Thau lagoon, *Polititapes aureus* (Gmelin, 1791), the Golden carpet shell, was primarily detected, with a few *R. decussatus* present, and no *R. philippinarum*. These findings were corroborated by genetic analyses of clam tissues. This tool shows promise for characterizing clam biodiversity in Europe and monitoring its evolution, particularly in regions where both *R. philippinarum* and *R. decussatus* coexist (Fig. 7C).

3.1.4. Modelling the dynamics of a harvested population in relation to its environment

Clam resource management in Arcachon Bay employs a co-management approach that involves both scientists and managers in conjunction with maritime officials. To define, evaluate and test the effectiveness of various management strategies, a specific analytical model has been developed (deterministic compartimental model constructed according to the paradigm of dynamic systems) (Forrester, 1973) and implemented for Arcachon Bay (Bald et al., 2009; Caill-Milly et al., 2022). This simulation tool reproduces the dynamic interactions between biological and physical processes and helps determine the action needed based on the current state of the system (Goffinet, 2003). In addition to serving as a decision-making tool, the model has enhanced our understanding of population dynamics because it can describe processes based on a hierarchical integration of biological, physical, and social knowledge. Recent updates to the model have incorporated new data on life-history traits, local environmental parameters, and more detailed information on fishing activities and their control parameters. The model also includes new process formulations, followed by a performance analysis and initial sensitivity testing based on Banos-Gonzalez et al. (2018). The outcome (Caill-Milly et al., 2022) is a model calibrated with parameters that closely reflect the specific characteristics of the stock in question (Fig. 8).

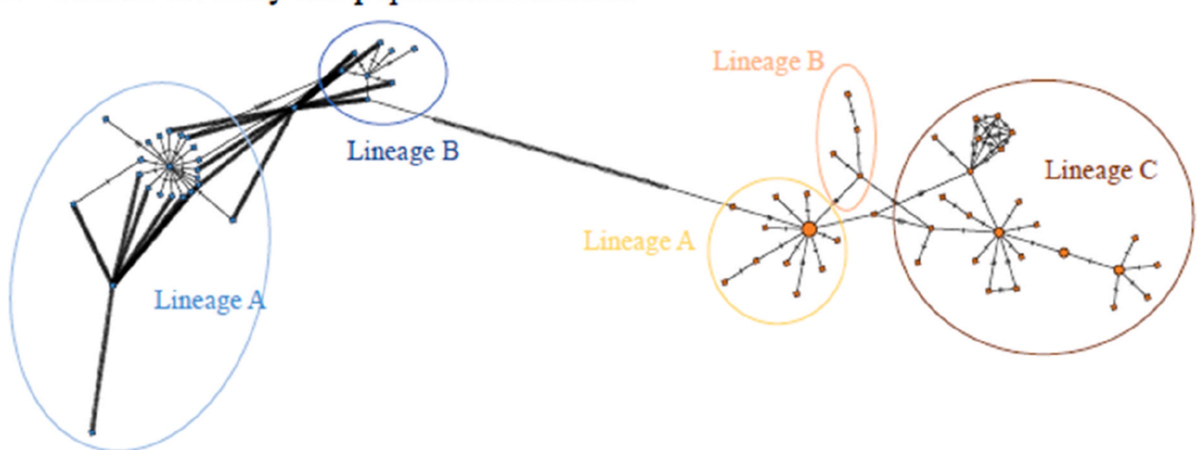
In Berre lagoon, a dynamic energy budget (DEB) model was developed. It dynamically describes the aspects of metabolism at the individual level and, combined with life-history traits (*e.g.* growth and

A- Species discrimination



species	Site	Elongation index	Compactness index	Convexity index
RD	Pen Bé	0.875 ± 0.029	0.530 ± 0.058	0.604 ± 0.050
	Carantec	0.809 ± 0.033	0.501 ± 0.023	0.619 ± 0.030
	Total (N=84)	0.797 ± 0.074	0.480 ± 0.038	0.605 ± 0.045
RP	Pen Bé	0.879 ± 0.024	0.550 ± 0.030	0.626 ± 0.027
	Carantec	0.783 ± 0.047	0.551 ± 0.036	0.705 ± 0.060
	Total (N=233)	0.825 ± 0.064	0.548 ± 0.037	0.667 ± 0.062

B- Genetic diversity and population structure



C- Monitoring clam population based on eDNA

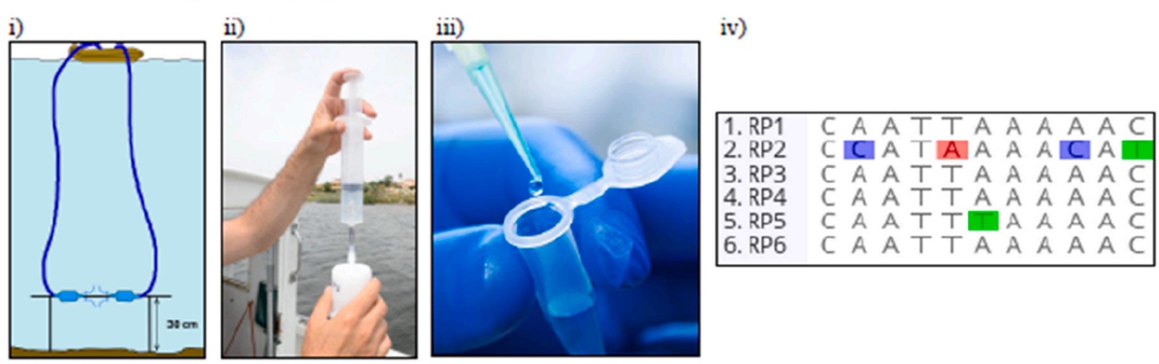


Fig. 7. Three distinct applications of genetics in the Manila clam *R. philippinarum*: A. Species discrimination using amplified PCR products from the 16S mitochondrial marker, showing characteristic bands for *R. decussatus* (in blue, 522 bp expected size on a 2% agarose gel) and *R. philippinarum* (in orange, 522 bp expected size on a 2% agarose gel) across two French populations (Pen Bé and Carantec; left panel). The right panel illustrates species differentiation based on morphometric variables following the methodology of Caill-Milly et al. (2014) for the same two populations (mean ± SD). B. Haplotype network of mitochondrial COI sequences for *R. decussatus* [N = 32, in blue, NCBI accession numbers: JX051518 - JX051549 (Cordero et al., 2014)]; and *R. philippinarum* [N = 47, in orange, NCBI accession numbers: LT600424 – LT600470 (Cordero et al., 2017)]. Circle sizes indicate the frequency of each haplotype, and shaded circles highlight lineages within each species. C. eDNA sampling methodology in Mediterranean lagoons: (i) sample collection, (ii) filtration using Waterra capsules and the Argaly filtering system, (iii) molecular analysis in the laboratory, and (iv) bioinformatic processing to characterize clam sequences. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

mortality rates), it helps the local authority to manage the regulation by simulating the long-term clam population in interaction with different regulations (Mahé, 2022). For example, it shows that the clam's recovery time for Manila clam in this lagoon can be relatively fast only if the environment becomes favourable and the anoxic conditions are absent.

An individual-based model was also produced to investigate biological and environmental interactions that influence the prevalence and intensity of a disease caused by the bacterial pathogen, *Vibrio tapetis* (Borrego et al., 1996), in the Manila clam (Flye-Sainte-Marie et al., 2007; Paillard et al., 2014). It was implemented using environmental observations from sites in Brittany, France, where Manila clams

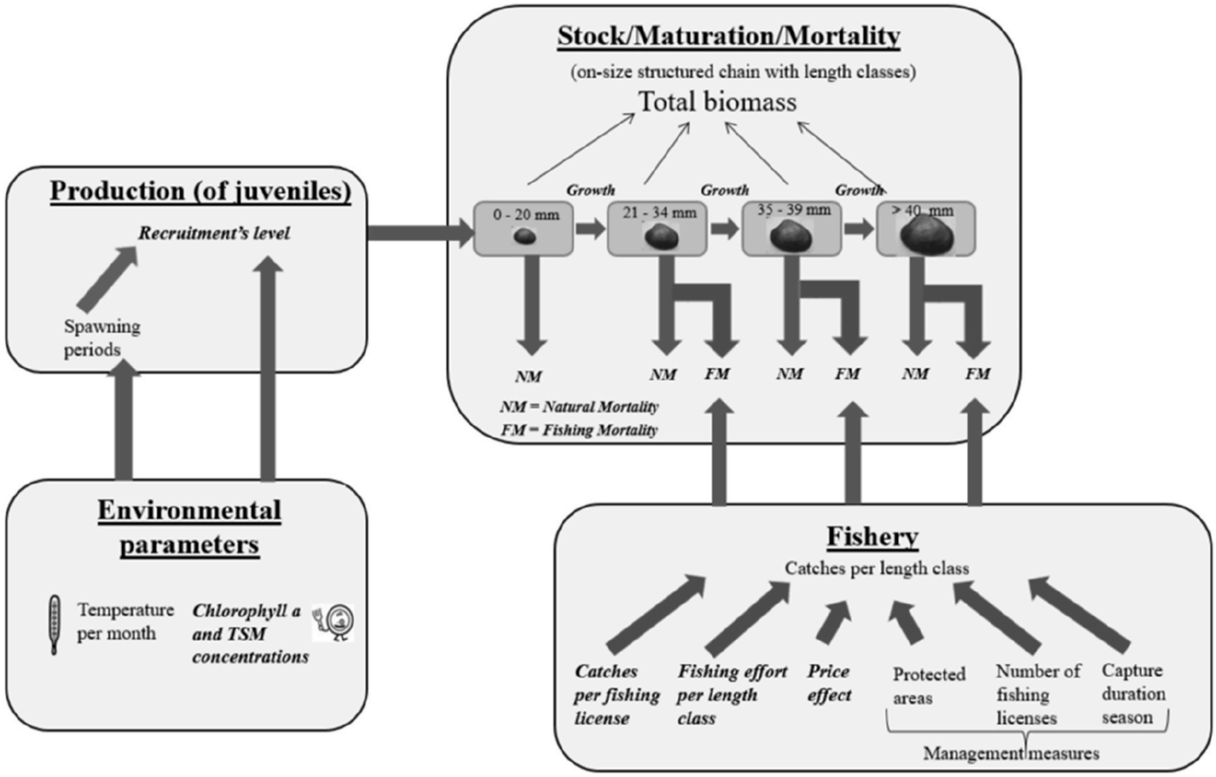


Fig. 8. Diagram of the model developed for the Manila clam, illustrating the four blocks and the interactions between them. Improvements made since the first version of the model are in bold italics (Caill-Milly et al., 2022).

routinely undergo the pathology. Simulations with temperature increases favor disease development and potential spread. It also showed that the modeled hemocyte activity is a major intrinsic determinant of clam recovery.

In some areas, such models can not be used to asses management strategies as some biological data are unavailable (such as growth parameters). In these cases, management strategies are developed based on the combination of simple indicators such as Manila clam abundance estimate, proportion exploited, CPUEs, proportion of stations sampled having high densities (as these represent areas of interest for fishers). Contextual information on environmental factors are also collected to better understand Manila clam population's variations. This type of management is done in Charente Maritime or in the Gulf of Morbihan.

3.2. Regarding reproduction and spawning

To date, there have been few studies on reproduction of *R. philippinarum* in French populations, with most of them conducted in Arcachon Bay and Berre Lagoon. For Arcachon, these studies aimed to address the specific features of the lagoon and to respond to a formal request from the European Commission on the modification of the MCRS. The reproductive cycle of *R. philippinarum* in Arcachon Bay is similar to that reported from other French sites (Laruelle et al., 1994; Maitre-Allain, 1983; Mahé et al., 2024). Dang (2009) provided a detailed description of the reproductive cycle in Arcachon Bay, based on observations from 2006 to 2007: gametogenesis begins in March, gonad maturation starts in April–May, and spawning occurs between May and October. Gonad maturation and spawning periods can vary by site and

Table 2
Methodological elements used to estimate the SL_{50} of *R. philippinarum* according to the deposits considered (F = Females; M = Males; T = Total).

Location	Sample size	Size of the individuals (mm)	Maturity stages	Population	Estimated SL_{50} (mm)	Reference
Portugal – Tage estuary	88	23.9–38.6	3 and 4	T	29.4	Moura et al. (2018)
Portugal – Rio de Aveiro	305	13.6–55.1	3, 4 and 5	F and M	20 F: 19.9 M: 20	Maia et al. (2025)
France – Berre Lagoon	122	11.9–34.9	3 and 4	T	23.6	Mahé et al. (2024)
France - Arcachon Bay	1238	17–41	3, 4 and 5	F and M	26.7 F: 24.5 M: 21.6	Caill-Milly et al. (2023)
South Korea - Komso Bay	216 (102 males and 114 females)	8.4–54.6	« Late active » to « Spent/ Inactive stage	F and M	F: 15.1–20.0 M: 15.1–20.0	Chung et al. (2001)
South Korea - Simpo Jollabuk-do	135 males	8.4–54.6	« Late active » to « Spent/ Inactive stage)	M	M: 17.16	Chung et al. (2013)
South Korea - Simpo	210 females	8.4–54.6	« Late active » to « Spent/ Inactive stage	F	F: 17.83	Choi et al. (2005)
Japan - Mutsu Bay	169 (58 females, 67 males et 44 indeterminate)	7.97–40.58	Individuals with stage 3, 4 or 5 germinal acini	F and M	F: 21.1 M: 18.5	Sugiura and Kikuya (2022)

year. In 2006 and 2007, most individuals were mature for three months, from May to July and June to August, depending on the site. Spawning periods also varied within the bay, with a minimum of one-month delay among the sites depending on their locations (Dang, 2009).

Based on these observations, we assessed the size at first sexual maturity (SL_{50}), by conducting sampling in June, July and August 2021 at the four intra-basin sites previously described, which represent different environmental conditions (Dang, 2009; Caill-Milly et al., 2023). With regard to the selection of individuals (linked to sex, size), maturity stages and calculation methods used to estimate SL_{50}, we noted a lack of harmonisation in practices related to clams (Table 2) but also more broadly for bivalves. While ICES has promoted harmonisation efforts for several years for demersal and pelagic fish, certain cephalopods and crustaceans (local stocks with strong local and regional management components) often face different challenges. After reviewing various methods, we chose the six stages of gamete development outlined by Drummond et al. (2006) and Moura et al. (2018). These stages also align with those used for *Chamelea gallina* (Linnaeus, 1758) in the Adriatic Sea (Bargione et al., 2021). They allow for comparison with other European deposits of Manila clams (Moura et al., 2018; Maia et al., 2025).

For *R. philippinarum* in Arcachon Bay, SL_{50} was estimated at 26.7 mm (26.2–27.2 mm), with moderate spatial variability [detailed in (Caill-Milly et al., 2023)]. Despite some methodological differences, these results are consistent with SL_{50} estimates reported in the literature. However, this indicator sometimes can vary among populations of the same species (Galimany et al., 2015).

On the western coast of the Cotentin, the period of gamete emission was estimated using the condition index of Walne and Barnes, (1975), based on monthly samples from clams larger than 40 mm, with increased sampling frequency every 15 days during the summers. This study, conducted over a 7-year period, found that gametes were produced in the first half of July. However, in some years, a second period of gamete production appeared to occur in August. The clam size at first maturity was not investigated in this study (O. Basuyaux, unpublished data).

3.3. Regarding habitats

3.3.1. Effect of clam rake harvesting on habitats

Beck et al. (2015) investigated the impact of using a clam rake on clam populations, *i.e.* examining effects on abundance, size classes, and the macrofauna biodiversity associated with the *Ruditapes* habitat. Sampling was conducted at three sites, each with three stations (sand, gravelly, and deep gravelly in a mixed gravelly and rocky habitat). Professional fishers used the clam rake at these sites to harvest clams. Infaunal species were sampled before and 1 month after raking, during February–March 2014, using a 0.20 m diameter stainless steel hand-cover with 1/32 m^2 area, with a random strategy. Sampling depth was approximately 0.15 m. Eight replicates were taken at each station, totalling a sampled area of 0.25 m^2. Core samples were passed through a 1-mm mesh sieve, preserved in 5% formaldehyde, and stained with Pink Bengal dye to aid sorting. Species were then identified and stored in 70% alcohol. A total of 83 taxa were identified across the three habitats sampled, with polychaetes (46 taxa) and molluscs (18 taxa) being the most dominant. Polychaetes were numerically predominant, comprising between 51% and 96% of total abundance. No significant differences were observed in the total number of individuals or taxa between the two sampling dates at the raking stations. The relatively weak effects of rake fishing in this intertidal zone may be attributed to high sediment transit and the drifting of organisms between sampling dates in this high-energy environment (Beck et al., 2015).

3.3.2. Test of larval source for a population using hydrodynamical models

Since its introduction to the Chausey Islands (western English Channel) in the late 1980s, the Manila clam *R. philippinarum* has significantly increased in population along the western coast of Cotentin (Beck et al., 2015; Basuyaux et al., 2018). Basuyaux et al., (2025) tested several hypotheses regarding the larval source for the Cotentin population in the Normano-Breton Gulf. They simulated larval dispersal using the MARS 3D Lagrangian transport model, which tracks particles moving passively with ocean currents. This model was coupled with a regional current circulation model that incorporates bathymetry, tide, wind, marine turbulence, and temperature effects for the summer of 2019. The Ichthyop particulate transport model was employed to simulate the dispersion of clam larvae, considered as passive particles, after one month of planktonic life. The simulations varied wind conditions and points of larval release during the June–July 2019. The results indicated that while some larvae were transported offshore, the majority were recruited in the western coast of Cotentin. Notably, larvae from the Chausey Islands clam farms contributed to the clam populations throughout the Normano-Breton Gulf. This finding explains the persistence of clam stocks despite heavy annual harvest and supports a viability of a sustainable fishery, even with a low abundance of breeding individuals.

3.4. Regarding infectious diseases

Several pathogens have been reported in clam populations in France including trematodes, protozoan parasites, bacteria and viruses.

- Trematodes

Trematodes that use clams as second intermediate hosts were identified. In a study carried out in Arcachon Bay, *R. philippinarum* exhibited very low abundance of trematodes (<1.1 metacercariae per clam), involving two echinostomatid species. Experimental infestation confirmed that the Manila clam is resistant to cercarial infection (Dang et al., 2009a). Consequently, it was concluded that these parasites likely have no direct impact on clam population dynamics in Arcachon Bay, although they may exacerbate contamination by trace metals such as cadmium (Paul-Pont, 2010; Paul-Pont et al., 2010).

- Protozoan parasites

A range of protozoan parasites have been detected in *R. philippinarum* worldwide including parasites of the genera *Minchinia*, *Mikrocytos*, *Marteilia* or *Perkinsus*. Among these parasites, *Perkinsus olseni* has been regularly detected along the Atlantic and Mediterranean coasts and has been associated with local mortality events, resulting in severe economic loss, especially in Portugal, Spain, and Italy (Ruano et al., 2015).

In France, the presence of *Perkinsus* parasites was initially evaluated using RFTM (Ray's fluid thioglycolate medium) or histology, diagnostic approaches which do not allow identifying parasites at the species scale. *Perkinsus* parasites were detected in main clam producing zones (Garcia et al., 2006; Lassalle et al., 2007; Dang et al., 2010b). In a survey carried out in Arcachon Bay (France), very high prevalence (70–100% of clams) and intensities (130 × 10^3 cells.g wet gill) of *Perkinsus* spp were observed in clams using RFTM (Dang et al., 2010b). The infection was found to have a negative impact on individual clam growth (Dang et al., 2013).

Subsequently, PCR and sequencing analyses revealed that on the Atlantic and Mediterranean coasts, clams were not only infected with *P. olseni* but also with *P. chesapeaki* (McLaughlin et al., 2000) in some locations (Arzul et al., 2012; Itoïz et al., 2022). While *P. olseni* might have been unintentionally introduced into European waters along with its host, the Manila clam (*R. philippinarum*), brought over from Asia in the 1970s for aquaculture purpose (de Montaudouin et al., 2016a), *P. chesapeaki* introduction might have occurred through introduction of susceptible species including *Mya arenaria* (Linnaeus, 1758) or *Mercenaria mercenaria* (Linnaeus, 1758) from North America (Arzul et al., 2012).

The use of a specific duplex quantitative PCR enabled the monitoring of the dynamics of both congeneric species in *R. philippinarum* in Arcachon bay and revealed that *P. olseni* was the most prevalent parasite with high infection intensities (Itoïz, 2021; Itoïz et al., 2021; Itoïz et al., 2024). In contrast, *P. chesapeaki* appeared more cryptic. These results highlight the interest of combining targeted and less targeted diagnostic approaches to get the most accurate epidemiological picture.

- Bacteria

Brown ring disease (BRD), first described in 1987 in Landeda (Finistère, France) (Paillard and Maes, 1990; Paillard, 2016), is caused by a vibrio, *Vibrio tapetis*, which colonizes extrapallial fluids, inhibiting the shell calcification process, and inducing an abnormal brown organic deposit in the internal valves (Paillard et al., 2025). BRD has spread rapidly in Brittany and along European coasts, causing heavy mortalities in clam beds between 1990 and 2010 (with maximum prevalence reaching 60% in winter). In natural populations, BRD prevalence was lower, on the order of 5–20% (1993–2003) in the Gulf of Morbihan (Paillard et al., 2014). But recently (2019–2022), in certain areas of the English Channel, the prevalence of BRD could reach, in winter, 50% in the clam beds of Chausey and 40% in the natural populations of Blainville-sur-Mer (O. Basuyaux, personal observation). Moreover, typical BRD symptoms are still visible in clams, with some changes in compartment location, with some extent in the central compartment, particularly in moribund clams. At seven stations in the Gulf of Morbihan, we have shown that sediment granulometry has an impact on BRD development, with an abundance of large particles in the sediment increasing the probability of infection and pathogenicity in the extrapallial compartment (Flye-Sainte-Marie et al., 2008). BRD and the *V. tapetis* pathogen were identified in calcified archives of clams harvested before the epizootic (Paillard et al., 2019; Der Sarkissian et al., 2017). In this way, shellfish archives can be used as epidemiological tracers of the disease, and also to identify pathogen strains and their evolution.

- Viruses: OsHV-1 and BMD virus-like particles

The ostreid herpesvirus type 1 (OsHV-1) is one of the few viruses reported in marine molluscs which have been fully characterized (Davison et al., 2005). Although this virus is primarily infecting the Pacific cupped oyster *Magallana gigas* (Thunberg, 1793), it has been associated with mortality in larvae of *R. philippinarum* and *R. decussatus* produced in hatchery (Renault and Arzul, 2001; Arzul et al., 2001). This member of Malacoherpesviridae family can thus present a threat for the production and fishery of Manila clam.

In 2005, a new disease named Brown Muscle Disease (BMD) was discovered in Arcachon Bay (Dang et al., 2008) and associated with the presence of Virus-Like Particles (Dang et al., 2009b). BMD quickly became associated with high mortality rates in adult Manila clams in the area. The disease affected 62% of the Manila clam habitat surface (Dang and de Montaudouin, 2009), with prevalence reaching up to 30% in some areas among adult specimens. At the individual level, the condition index of Manila clams affected by BMD was reduced by 37%. The disease primarily targets the posterior adductor muscle, which becomes infused with conchiolin and gradually calcifies. However, a recent study suggests that muscle atrophy is a latter sign of the pathology and it is the nervous system which could instead be a primary target of the BMD agent (Pierron et al., 2019). Clams found at the surface showed an infection rate three times higher than that of buried (*i.e.* normal position) sympatric clams. Laboratory trials further revealed that surfaced clams had significantly higher mortality rates after 15 days compared to buried individuals (82% versus 12%). In a subsequent study, significant stress responses were observed in BMD-infected clams across various biological scales. These responses included a noticeable reduction in the condition index, alterations in immune parameters, and changes in the expression of stress-related genes (Binias et al., 2014). While this comprehensive stress response highlights the severe impact of BMD on the overall health and physiological functioning of the affected clams, the apparent restricted distribution of this disease raises several questions including the potential role of environmental factors or of genetic factors specific to Arcachon clam populations in BMD development.

4. General discussion and conclusion

When data is available and/or of sufficient quality, time series relating to stock monitoring indicators (such as abundance indices, demographic structure, etc.) are typically calculated to track their evolution over time (variations in abundance) and to adapt exploitation practices as needed. In all cases, the methods used must be reliable, not

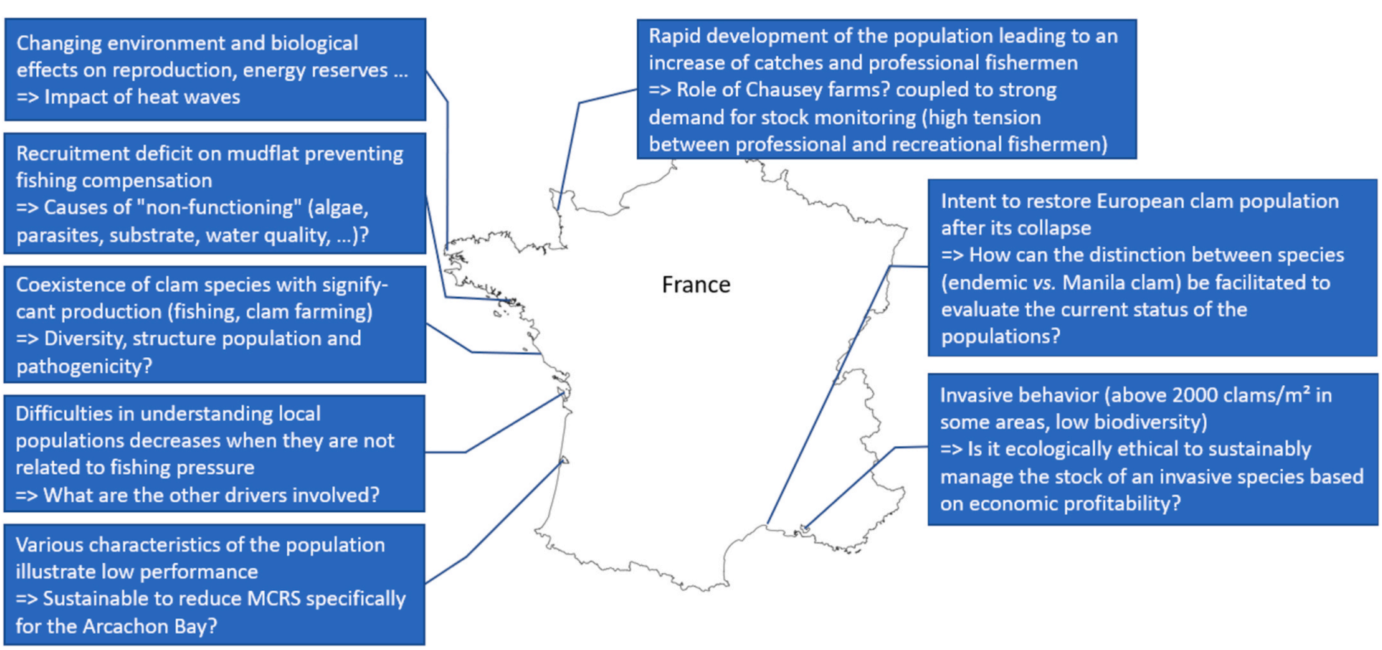


Fig. 9. Current or recent main issues that have been identified on the French Manila clam populations.

overly data-intensive and relatively straightforward to implement. This ensures that indicators can be generated effectively to inform appropriate management measures for the stocks.

4.1. Use of this knowledge for management purposes

4.1.1. To contribute to area selection criteria (growth patterns)

Highlighted morphometric specificities at both intra and interspecific scales offer valuable knowledge that can influence the selection of appropriate management measures for the studied population. This information supports spatially explicit management approaches, which are particularly effective for species that are either not very mobile or are sedentary yet highly dispersive (Caddy and Defeo, 2003). In Arcachon Bay and Gulf of Morbihan, such insights are incorporated into the criteria for selecting protected areas.

4.1.2. To consider the suitability of MCRS for certain zones

To revise any MCRS, it is necessary to consider biological features, primarily focusing on sexual maturity, individual growth and natural mortality. In the case of Arcachon Bay, it is professional fishers who have collectively requested that a specific MCRS of 32 mm be set for Arcachon deposit. A synthesis of available knowledge was compiled (Caill-Milly et al., 2023) and provided to the European Commission. It concluded that, based on available information, reducing the MCRS to the requested size for this site would not be an issue for the population viability. However, it was pointed out that this measure could not be considered on its own; it should be considered in conjunction with other management measures already in place, such as the establishment of protected areas and the limitation of fishing effort (*e.g.* number of licenses, authorized catch periods, quotas, etc.).

4.1.3. To test management scenarios (model implementation)

The management model specifically developed for the Manila clam in Arcachon Bay aims to enhance stock management through a robust, science-based decision-making process. Recent improvements to the model enable the testing of various management strategies (number of fishing licences, quota per licence, length of fishing season and area of fishing reserve) as well as environmental changes on the total biomass. The findings suggest that adopting a combination of management measures is more effective than making significant changes to a single measure. These combined measures form part of a range of measures that have been in place since 2008–2009 (Caill-Milly et al., 2022). They have also been used for this species in other European coastal systems (Coelho et al., 2021). The co-management approach for this local exploited stock is therefore attentive to the legitimacy of such measures. This is why it has been important to continue to work with local fisheries' committees when elaborating the contents of measures to be adopted.

4.2. Identification of knowledge shortfalls

Although not exhaustive, Fig. 9 illustrates current main issues that have been identified on the French populations by the co-authors of this paper. Issues range from the individual to the population level, with questioning very often linked to environmental effects. For example, a "one health" approach is being proposed in the Bay of Brest to assess the physiology modification of Manila clam, the associated microorganisms' dynamics and the evolution of BRD linked to environmental changes. In the Gulf of Morbihan, the Pertuis Charentais and the Cotentin, the effect of factors (other than fishing) influencing recruitment is being investigated.

Other questions also remain, for example on interactions with other bivalves: Is the European clam replaced by the Manila clam when the two species cohabit? What are the consequences of interactions with Asian mussels such *Arcuatula senhousia* (W. H. Benson, 1842)? It is essential to maintain vigilance about the risks of the pathogens or predators (such as blue crabs) emerging, these risks being amplified in a context of climate change. In any case, the importance of monitoring and raising awareness among professionals is crucial. It allows for a full reporting of abnormal mortality events, as this is currently one of the only warning signs of an outbreak.

As has been presented, the sustainability of the Manila clam fishery has not only depended upon a continued investment by scientists to produce up-to-date biological knowledge about stock status and health, but also on how this 'science' has been mobilized to influence the 'politics' governing the fishery. A deeper understanding of how this came about - and at different scales of governance (local, regional, European) - would contribute much needed new knowledge on decisional processes transforming small-scale fisheries more generally (Carter and Caill-Milly, 2024). This matters especially at a time when challenges to the sustainability of small-scale fisheries have been highlighted in international and European Union policy strategies (SFF Guidelines, 2015). In Europe, and despite the regionalization of the CFP, it is by no means straightforward to change common rules to adapt them to the specificities of complex, and evolving, interactions between shellfish and ecosystems. This is particularly true for small-scale fisheries, whose representatives have weak bargaining power (Said et al., 2020) and in the French context, where shellfish gatherers tend to be underrepresented in decisional fisheries' committees (Frangoudes et al., 2020). A targeted analytical focus on political processes would also produce new understandings on how policies 'outside' the CFP can support any future transformations of this fishery, including fishers' income diversification strategies (Carter and Caill-Milly, 2024).

CRediT authorship contribution statement

Nathalie Caill-Milly: Writing – original draft, Resources, Investigation, Conceptualization. **Florence Sanchez:** Writing – review & editing, Resources, Investigation. **Muriel Lissardy:** Writing – review & editing, Resources. **Noëlle Bru:** Writing – review & editing. **Claire Kermorvant:** Writing – review & editing, Resources, Investigation. **Xavier de Montaudouin:** Writing – review & editing, Resources, Investigation. **Sylvie Lapègue:** Writing – review & editing, Resources, Investigation. **Florentine Riquet:** Writing – review & editing, Resources, Investigation. **Ludovic Bouché:** Writing – review & editing, Resources. **Céline D'Hardivillé:** Writing – review & editing, Resources, Investigation. **Franck Lagarde:** Writing – review & editing, Resources, Investigation. **Aurélie Chambouvet:** Writing – review & editing, Resources, Investigation. **Nicolas Mayot:** Writing – review & editing, Resources, Investigation. **Jean-Claude Dauvin:** Writing – review & editing, Resources, Investigation. **Jean-Philippe Pezy:** Writing – review & editing, Resources. **Olivier Basuyaux:** Writing – review & editing, Resources, Investigation. **Anthony Guéguen:** Writing – review & editing, Resources, Investigation. **Yohan Weiller:** Writing – review & editing, Resources, Investigation. **Isabelle Arzul:** Writing – review & editing, Resources, Investigation. **Christine Paillard:** Writing – review & editing, Resources, Investigation. **Caitriona Carter:** Writing – review & editing, Resources, Investigation.

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.

Acknowledgments

We would like to thank the National Institute of Fisheries Science (NIFS) for supporting N. Caill-Milly's attendance at the 5th international Manila Clam symposium in Gunsan (Korea) in June 2024 as a guest researcher. This opportunity was at the origin of this review. Thanks are also addressed to the two anonymous reviewers and the editor for their useful comments on the submitted manuscript.

This synthesis is not specifically funded, but is based on the results of a large number of funded projects. For precise funding details, please refer to the articles cited in the bibliography.

Appendix 1

Latest measures taken at regional/local levels according to various Manila clam deposits.

Sites	Fishing effort reduction		Technical measures		Catch limitations	Reduce impacts on habitats
	Licenses/stamps contingent	Opening and closing dates and hours	Authorized gears and dimensions	Closed fishing areas	Quotas (kg/fisher/day …)	Ban on fishing in certain foreshore habitats
Manche (Cotentin from Bréhal to Pirou)	100 licenses				60 kg/fisher/day	
Gulf of Morbihan (Morbihan)	112 licenses in 2024	Between mid-June and mid-September	By hand, on foot or snorkel	Fishing area rotation	60 kg/fisher/fishing trip. Truscat zone: quota of 100 tonnes for the entire fishing season	Mud pattens on mudflats Snorkelling means less support on the ground
Other Morbihan (Morbihan)	112 licenses in 2024	All the year	By hand, on foot or snorkel	Fishing area rotation	60 kg/fisher/fishing trip	Mud pattens on mudflats
Charente-Maritime	34 licenses	Different in each deposit of the departement	True	Closed fishing areas for *Zostera noltei* conservation	70 kg (until 80 kg)/ fisher/day	Marine eelgrasses must be avoided during summer, some areas of eelgrass are closed to fishing between April and September.
Arcachon Bay	39 vessel owners with a maximum of 2 employees each	Almost opened everywhere, and opened during the day	True	2 areas banned by pref. orders and 1 by the National Nature Reserve (NNR)	Free of quotas	Marine eelgrasses should be preserved with using authorized gears
Berre Lagoon	78 licenses	5 days per week from March to December			50 kg (until 80 kg)/ fisher/day	

Data availability

If available, data will be sent on request

References

Arzul, I., Renault, T., Lipart, C., Davison, A.J., 2001. Evidence for interspecies transmission of oyster herpesvirus in marine bivalve. J. Gen. Virol. 2 82 (4), 865–870. https://doi.org/10.1099/0022-1317-82-4-865.

Arzul, I., Chollet, B., Michel, J., Robert, M., Garcia, C., Joly, J.-P., François, C., Miossec, L., 2012. One *Perkinsus* species may hide another: characterization of Perkinsus species present in clam production areas of France. Parasitology 139, 1757–1771. https://doi.org/10.1017/S0031182012001047.

Bald, J., Sinquin, A., Borja, A., Caill-Milly, N., Duclercq, B., Dang, C., de Montaudouin, X., 2009. A system dynamics model for the management of the Manila clam, *Ruditapes philippinarum* (Adams and Reeve, 1850) in the Bay of Arcachon (France). Ecol. Model. 220 (21), 2828–2837. https://doi.org/10.1016/j.ecolmodel.2009.03.031.

Banos-Gonzalez, I., Martínez-Fernández, J., Esteve-Selma, M.Á., Esteve-Guirao, P., 2018. Sensitivity analysis in socio-ecological models as a tool in environmental policy for sustainability. Sustainability 10, 2928. https://doi.org/10.3390/su10082928.

Bargione, G., Donato, F., Barone, G., Virgili, M., Penna, P., Lucchetti, A., 2021. *Chamelea gallina* reproductive biology and minimum conservation reference size: implications for fishery management in the Adriatic Sea. BMC Zoology 6 (32), 1–16.

Basuyaux, O., Bennis, A.C., Amji, S., Croguennec, G., Boutet, M., Lefebvre, V., Basuyaux, Y., Dauvin, J.-C. 2025. Multidisciplinary study of the population dynamics of the Non-Indigenous Manila Clam *Ruditapes philippinarum* along the western coast of Cotentin, France. Proceedings of the Coast Caen 2023 Conference, Springer Nature.

Basuyaux, O., Beck, F., Pezy, J.-P., Baffreau, A., Joncourt, Y., Tétard, X., Dauvin, J.-C., 2018. Evaluation of *Ruditapes spp.* clam stock on the western coast of Cotentin (English channel). J. Mar. Biol. Oceanogr. 7 (1). https://doi.org/10.4172/2324-8661.1000186.

Basuyaux, O., Arrenoux, G., Baffreau, A., Bennis, A.-C., Boutet, M., Brieau, L., Champolivier, L., Croguennec, G., Dauvin, J.-C., Charrier, G., Desfeux-Mezière, V., Garcia, A., Haitz, F., Huet, M., Jolly, G., Joncourt, Y., Lehuen, A., Lefebvre, J., Legrand, A., Michel, J., Paillard, C., Lefebvre, V., Laisney, N., Laplace-Dolonde, A., Lemoine, A., Moal, A., Ollivier, E., Sahnoun-Ajmi, S., Spagnol, M., Timsit, O., Carreira Pinto Vierra, M., Vigoureux, P., Zablocki Thomas, L., 2023. Reconstitution d'un Stock de bivalves, Indicateur de Stocks et Vigie des havres. Rapport de synthèse final 253. https://www.gemel-normandie.org/nos-publications/rapports/.

Bœuf, coord, 2010. Biodiversité en environnement marin Synthèse et recommandations en sciences environnementale et sociale. Rapport à l'Ifremer de l'expertise collective en biodiversité marine, p. 139. Version au 25 août 2010.

Beck, F., Pezy, J.-P., Baffreau, A., Dauvin, J.-C., 2015. Effects of clam rake harvesting on the intertidal *Ruditapes* habitat of the English Channel. ICES J. Mar. Sci. https://doi.org/10.1093/icesjms/fsv137.

Begon, M., Harper, J.L., Townsend, C.R., 1990. Ecology: Individuals, Populations, and Communities, vol. 2. Blackwell Scientific Publications, Boston MA.

Belin, C., Claisse, D., Daniel, A., Fleury, E., Le Mao, P., Amouroux, I., Miossec, L., Boisseaux, A., Lamoureux, A., Soudant, D., 2013. Qualité du milieu marin littoral: synthèse nationale de la surveillance 2012, édition 2013. Ifremer, p. 80. Available at: https://envlit.ifremer.fr.

Bellanger, M., Levrel, H., 2017. A cost-effectiveness analysis of alternative survey methods used for the monitoring of marine recreational fishing in France. Ocean Coast. Manage. 138, 19–28.

Bhattacharya, C.G., 1967. A simple method of resolution of a distribution into Gaussian components. Biometrics 23, 115–135.

Binias, C., 2013. Epizootiologie et contribution à la caractérisation de l'agent infectieux de la maladie du muscle marron, une pathologie émergente de la palourde japonaise, *Venerupis philippinarum*. PhD thesis. University of Bordeaux, France.

Binias, C., Gonzalez, P., Provost, M., Lambert, C., de Montaudouin, X., 2014. Brown muscle disease: impact on Manila clam *Venerupis* (=*Ruditapes) philippinarum* biology. Fish Shellfish Immunol. 36, 510–518. https://doi.org/10.1016/j.fsi.2013.12.009.

Bliese, P., 2012. Multilevel Modeling in R (2.4): a Brief Introduction to R, the Multilevel Package and the Nlme Package. www.cran.r-project.org/doc/contrib/Bliese.Multilevel.pdf.

Borrego, J.J., Castro, D., Luque, A., Paillard, C., Maes, P., Garcia, M.T., Ventosa, A., 1996. *Vibrio tapetis* sp.nov., the causative agent of the Brown Ring Disease affecting cultured clams. Int. J. Syst. Bacteriol. 480–484. https://doi.org/10.1099/00207713-46-2-480.

Bouché, L., D'Hardivillé, C., 2023. Campagne d'évaluation du stock de palourdes du golfe du Morbihan. CDPMEM 56 - Comité Départemental des Pêches Maritimes et des Élevages Marins du Morbihan, Ref. LTBH/LO, 41p 15, 16, 17 et 20 mars 2023.

Brown, R.A., Seed, R., O'Connor, R.J.O., 1976. A comparison of relative growth in *Cerastoderma* (= Cardium) *edule, Modiolus modiolus* and *Mytilus edulis* (Mollusca: Bivalvia). J. Zool. Soc. Lond. 179, 297–315. https://doi.org/10.1111/j.1469-7998.1976.tb02298.x.

Brown, J.A., Robertson, B.L., McDonald, T., 2015. Spatially balanced sampling: application to environmental surveys. Spat Stat Conf 27, 6–9. https://doi.org/10.1016/j.proenv.2015.07.108, 2015.

Caddy, J.F., Defeo, O., 2003. Enhancing or restoring the productivity of natural populations of shellfish and other marine invertebrate resources. FAO Fisheries Technical Paper 448. FAO, Rome, p. 159.

Caill-Milly, N., 2012. Relations entre l'état d'une ressource et son exploitation via la compréhension et la formalisation des interactions de socio-écosystèmes. Application à la palourde japonaise (*Venerupis philippinarum*) du bassin d'Arcachon. University of Pau and Pays de l'Adour, France. PhD thesis.

Caill-Milly, N., Bru, N., Mahé, K., Borie, C., D'Amico, F., 2012. Shell shape analysis and spatial allometry patterns of manila clam (*Ruditapes philippinarum*) in a mesotidal coastal lagoon. J. Mar. Sci. 2012 (ID 281206), 1–11. https://doi.org/10.1155/2012/281206.

Caill-Milly, N., Bru, N., Barranger, M., Gallon, L., D'Amico, F., 2014. Morphological trends of four manila clam populations (*Venerupis philippinarum*) on the French atlantic coast: identified spatial patterns and their relationship to environmental variability. J. Shellfish Res. 33 (2), 355–372. https://doi.org/10.2983/035.033.0205.

Caill-Milly, N., Sanchez, F., Lissardy, M., de Montaudouin, X., Bru, N., Kermorvant, C., Ganthy, F., 2021. Drawing lessons from a pluridisciplinary approach associating stakeholders for a better management of a bivalve population (French Atlantic coast)? Estuar. Coast Shelf Sci. 251, 107194. https://doi.org/10.1016/j.ecss.2021.107194, 12pp.

Caill-Milly, N., Garmendia, J.B., D'Amico, F., Guyader, O., Dang, C., Bru, N., 2022. Adapting a dynamic system model using life traits and local fishery knowledge — application to a population of exploited marine bivalves (*Ruditapes philippinarum*) in a mesotidal coastal lagoon. Ecol. Model. 470 (15p), 110034. https://doi.org/10.1016/j.ecolmodel.2022.110034.

Caill-Milly, N., Sanchez, F., Benito, D., Ruiz, P., Izagirre, U., Briaudeau, T., 2023. Assessment of size at first maturity for *Ruditapes philippinarum* from Arcachon Bay (French Atlantic coast): new insights for fishery management. Estuar. Coast Shelf Sci. https://doi.org/10.1016/j.ecss.2023.108321.

Carter, C., Caill-Milly, N., 2024. Coupling 'science' and 'decision-making' to transform small-scale fisheries: the surprising case of the Manila clam (Arcachon Bay, SW France). paper under preparation.

Chiesa, S., Nonnis Marzano, F., Minervini, G., De Lucrezia, D., Baccarani, G., Bordignon, G., Poli, I., Ravagnan, G., Argese, E., 2011. The invasive Manila clam *Ruditapes philippinarum* (Adams and Reeve, 1850) in Northern Adriatic Sea: population genetics assessed by an integrated molecular approach. Fish. Res. 110 (2), 259–267. https://doi.org/10.1016/j.fishres.2011.04.013.

Chiesa, S., Lucentini, L., Freitas, R., Nonnis Marzano, F., Minello, F., Ferrari, C., Filonzi, L., Figueira, E., Breda, S., Baccarani, G., Argese, E., 2014. Genetic diversity of introduced Manila clam *Ruditapes philippinarum* populations inferred by 16S rDNA. Biochem. Syst. Ecol. 57, 52–59. https://doi.org/10.1016/j.bse.2014.07.008.

Chiesa, S., Lucentini, L., Freitas, R., Marzano, F.N., Breda, S., Figueira, E., Caill-Milly, N., Herbert, R.J.H., Soares, A.M.V.M., Argese, E., 2017. A history of invasion: COI phylogeny of Manila clam *Ruditapes philippinarum* in Europe. Fish. Res. 186, 25–35. https://doi.org/10.1016/j.fishres.2016.07.024.

Choi, K.H., Park, G.M., Chung, E.Y., 2005. Ovarian maturation in female *Ruditapes philippinarum* on the west coast of korea. Dev. Reprod. 9 (2), 123–134.

Christianson, D.S., Kaufman, C.G., 2016. Effects of sample design and landscape features on a measure of environmental heterogeneity. Methods Ecol. Evol. 7, 770–782. https://doi.org/10.1111/2041-210X.12539.

Chung, E.Y., Hur, S.B., Hur, Y.-B., Lee, J.S., 2001. Gonad maturation and artificial spawning of the manila clam, *Ruditapes philippinarum* (Bivalvia: veneridae) in komso bay, korea. J. Fish. Sci. Technol. 4 (4), 208–218.

Chung, E.Y., Chung, J.S., Lee, K.Y., 2013. Gametogenic cycle, the spawning season, first sexual maturity, and the biological minimum size in male *Ruditapes philippinarum* (Bivalvia: veneridae) in western korea. J. Life Sci. 7 (6), 613–622.

Coelho, P., Carvalho, F., Goulding, T.A., Chainho, P., Guerreiro, J., 2021. Management models of the Manila Clam (*Ruditapes philippinarum*) fisheries in invaded European coastal systems. Front. Mar. Sci. 8, 685307. https://doi.org/10.3389/fmars.2021.68530.

Cordero, D., Pena, J.B., Saavedra, C., 2014. Phylogeographic analysis of introns and mitochondrial DNA in the clam *Ruditapes decussatus* uncovers the effects of Pleistocene glaciations and endogenous barriers to gene flow. Mol. Phylogenet. Evol. 71, 274–287. https://doi.org/10.1016/j.ympev.2013.11.003.

Cordero, D., Delgado, M., Liu, B., Ruesink, J., Saavedra, C., 2017. Population genetics of the manila clam (*Ruditapes philippinarum*) introduced in North America and Europe. Sci. Rep. 7 (1). https://doi.org/10.1038/srep39745. Article 1.

Costa, C., Aguzzi, J., Menesatti, P., Antonucci, F., Rimatori, V., Mattoccia, M., 2008. Shape analysis of different populations of clams in relation to their geographical structure. J. Zool. 276, 71–80. https://doi.org/10.1111/j.1469-7998.2008.00469.x.

Damour, A., Weiller, Y., Meslin, S., 2022. OFB. Diagnostic de l'exploitation des gisements de palourdes du Parc naturel marin de l'estuaire de la Gironde et de la mer des Pertuis, p. 74. http://plan-gestion.parc-marin-gironde-pertuis.fr/drupal/sites/default/files/2024-07/Rapport_combin%C3%A9_Diagnostic_palourdes_VF.pdf.

Dang, C., 2009. Dynamique des populations de palourdes japonaises (*Ruditapes philippinarum*) dans le bassin d'Arcachon, conséquences sur la gestion des populations exploitées. University of Bordeaux I, France. PhD thesis.

Dang, C., de Montaudouin, X., 2009. Brown muscle disease and manila clam *Ruditapes philippinarum* dynamics in Arcachon bay, France. J. Shellfish Res. 28, 355–362.

Dang, C., de Montaudouin, X., Gonzalez, P., Mesmer Duldons, N., Caill-Milly, N., 2008. Brown muscle disease (BMD), an emergent pathology affecting Manila clam *Ruditapes philippinarum* in Arcachon Bay (SW France). Dis. Aquat. Org. 80 (3), 219–228. https://doi.org/10.3354/dao01941.

Dang, C., de Montaudouin, X., Bald, J., Jude, F., Raymond, N., Lanceleur, L., Paul-Pont, I., Caill-Milly, N., 2009a. Testing the enemy release hypothesis: trematode parasites in the non-indigenous Manila clam *Ruditapes philippinarum*. Hydrobiologia 630 (1), 139–148. https://doi.org/10.1007/s10750-009-9786-9.

Dang, C., Gonzalez, P., Mesmer-Dudons, N., Bonami, J.-R., Caill-Milly, N., de Montaudouin, X., 2009b. Virus-like particles associated with brown muscle disease in Manila clam, *Ruditapes philippinarum*, in Arcachon Bay (France). J. Fish. Dis. 32 (7), 577–584. https://doi.org/10.1111/j.1365-2761.2009.01019.x.

Dang, C., de Montaudouin, X., Gam, M., Paroissin, C., Bru, N., Caill-Milly, N., 2010a. The Manila clam population in Arcachon Bay (SW France): can it be kept sustainable? J. Sea Res. 63 (2), 108–118. https://doi.org/10.1016/j.seares.2009.11.003.

Dang, C., de Montaudouin, X., Caill-Milly, N., Trumbic, Z., 2010b. Spatio-temporal patterns of perkinsosis in the manila clam *Ruditapes philippinarum* from Arcachon bay (SW France). Dis. Aquat. Org. 91 (2), 151–159. https://doi.org/10.3354/dao02243.

Dang, C., de Montaudouin, X., Binias, C., Salvo, F., Caill-Milly, N., Bald, J., Soudant, P., 2013. Correlation between perkinsosis and growth in clams *Ruditapes spp*. Dis. Aquat. Org. 106 (3), 255–265. https://doi.org/10.3354/dao02640.

Dauvin, J.-C., Basuyaux, O., Pezy, J.-P., 2024. Sediment types with alternation of sandy and rocky shores influence the distribution of clams in an area characterized by high-energy hydrodynamic conditions. J. Mar. Cci. Eng. 12, 1488. https://doi.org/10.3390/jmse12091488.

Davison, A.J., Trus, B.L., Cheng, N., Steven, A.C., Watson, M.S., Cunningham, C., Deuff, R.L., Renault, T., 2005. A novel class of herpesvirus with bivalve hosts. J. Gen. Virol. Jan 86 (Pt 1), 41–53. https://doi.org/10.1099/vir.0.80382-0.

de Montaudouin, X., Arzul, I., Caill-Milly, N., Goulletquer, P., Paillard, C., Soudant, P., Khayati, A., Labrousse, J.-M., Lafitte, C., 2015. Asari clam in France (1972-2015). Third Manila Clam World Symposium, 1-3 June, Tsu, Japan.

de Montaudouin, X., Arzul, I., Caill-Milly, N., Khayati, A., Labrousse, J.-M., Lafitte, C., Paillard, C., Soudant, P., Goulletquer, P., 2016a. Asari clam (*Ruditapes philippinarum*) in France: history of an exotic species 1972 – 2015. Bull. Jap. Fish. Res. Edu. Agen. 42, 35–42.

de Montaudouin, X., Lucia, M., Binias, C., Lassudrie, M., Baudrimont, M., Legeay, A., Raymond, N., Jude-Lemeilleur, F., Lambert, C., Le Goic, N., Garabetian, F., Gonzalez, P., Hegaret, H., Lassus, P., Mehdioub, W., Bourasseau, L., Daffe, G., Paul-Pont, I., Plus, M., Do, V.T., Meisterhans, G., Mesmer-Dudons, N., Caill-Milly, N., Sanchez, F., Soudant, P., 2016b. Why is Asari (= Manila) clam *Ruditapes philippinarum* fitness poor in Arcachon Bay: a meta-analysis to answer? Estuar. Coast Shelf Sci. 179, 226–235. https://doi.org/10.1016/j.ecss.2015.09.009.

Der Sarkissian, C., Pichereau, V., Dupont, C., Ilsøe, P.C., Perrigault, M., Butler, P., Chauvaud, L., Eiríksson, J., Scourse, J., Paillard, C., Orlando, L., 2017. Ancient DNA reveals marine mollusc shells as new metagenomic archives of the past. Mol. Ecol. Resour 17, 835–853. https://doi.org/10.1111/1755-0998.12679.

Drummond, L., Mulcahy, M., Culloty, S., 2006. The reproductive biology of the Manila clam, *Ruditapes philippinarum*, from the North-West of Ireland. Aquaculture 254, 326–340. https://doi.org/10.1016/j.aquaculture.2005.10.052.

Eagar, R.M.C., Stone, N.M., Dickson, P.A., 1984. Correlations between shape, weight and thickness of shell in four populations of *Venerupis romboides* (Pennant). J. Molluscan Stud. 50, 19–38.

EUMOFA, 2019. Species Analyses, 2018 edition, p. 115. https://doi.org/10.2771/01920. 2014.

Fan, D., Zhang, A., Yang, Z., Sun, X., 2007. Observations on shell growth and morphology of bivalve *Ruditapes philippinarum*. Chin. J. Oceanol. Limnol. 25 (3), 322–329. https://doi.org/10.1007/s00343-007-0322-3.

Flassch, J.-P., Leborgne, Y., 1992. Introduction in Europe, from 1972 to 1980, of the Japanese Manila Clam (*Tapes philippinarum*) and the Effects on Aquaculture Production and Natural Settlement, vol. 194, pp. 92–96. https://archimer.ifremer.fr/doc/00037/14871/.

Flye-Sainte-Marie, J., Pouvreau, S., Paillard, C., Jean, F., 2007. Impact of Brown ring disease on the energy budget of the manila clam *Ruditapes philippinarum*. J. Exp. Mar. Biol. Ecol. 349 (2), 378–389. https://doi.org/10.1016/j.jembe.2007.05.029.

Flye-Sainte-Marie, J., Jean, F., Ford, S.E., Paillard, C., 2008. Effect of sediment grain-size on development of brown ring disease in the Manila clam *Ruditapes philippinarum*. Aquaculture 278, 184–187.

Forrester, J.W., 1973. Confidence in Models of Social Behavior – with Emphasis on System Dynamics Group. Sloan School of Management. MIT.

Fortunato, H., 2024. Caractérisation de la diversité génétique des palourdes présentes dans plusieurs lagunes françaises. In: Rapport Master, vol. 2. Caen Normandie University.

FranceAgriMer, 2018. Étude sur l'évaluation de l'activité de pêche de loisirs en France métropolitaine (dont la Corse) - Synthèse est une publication de FranceAgriMer, p. 14.

Frangoudes, K., Bellanger, M., Curtil, O., Guyader, O., 2020. Small-scale fisheries in France: activities and governance issues'. In: Pascual-Fernández, J.J., Pita, C., Bavinck, M. (Eds.), Small-scale Fisheries in Europe: Status, Resilience and Governance. Springer, Cham, pp. 231–252.

Galimany, E., Baeta, M., Durfort, M., Lleonart, J., Ramón, M., 2015. Reproduction and size at first maturity in a Mediterranean exploited *Callista chione* bivalve bed. Sci. Mar. 79, 233–242.

Garcia, C., Arzul, I., Chollet, B., François, C., Goubet, A., Joly, J.P., Miossec, L., Robert, M., 2006. Bilan 2005 du réseau REPAMO. Rapport Ifremer, LGP, La Tremblade. France.

Gard, B., 2012. Processus écologiques et évolutifs influençant la colonisation de l'ambroisie à feuilles d'armoise (*Ambrosia artemisiifolia* L.) en France. University of Bourgogne, France. PhD thesis.

Gérard, G., 1978. Recherches sur la variabilité de diverses populations de *Ruditapes decussatus* et *Ruditapes philippinarum* (Veneridae, Bivalvia). Université de Bretagne Occidentale, France. PhD thesis.

Gillespie, G., Kronlund, A.L., 1999. A manual for intertidal clam surveys. Can. Rep. Fish. Aquat. Sci. 2270, 144.

Goffinet, B. (Coordinateur), 2003. La modélisation à l'Inra. Groupe de réflexion Modélisation, non paginé. Consultable sur : http://www.inra.fr/mia/doc/rapport_modelisation_VO.pdf.

Gosling, E., 2003. Bivalve Molluscs – Biology, Ecology and Culture. Fishing News Books, p. 443.

Grafström, A., 2012. Spatially correlated Poisson sampling. J. Stat. Plann. Inference 142, 139–147. https://doi.org/10.1016/j.jspi.2011.07.003.

Grafström, A., Lundstrëm, N.L., Schelin, L., 2012. Spatially balanced sampling through the pivotai method. Biometrics 68, 514–520.

Grafström, A., Lundstrëm, N.L., 2013. Why well spread probability samples are balanced. Open J. Stat. 3 (1), 36–41. https://doi.org/10.4236/ojs.2013.31005.

Gray, C.A., Johnson, D.D., Reynolds, D., Rotherham, D., 2014. Development of rapid sampling procedures for an exploited bivalve in the swash zone on exposed ocean beaches. Fish. Res. 154, 205–212. https://doi.org/10.1016/j.fishres.2014.02.027.

Habtemariam, B.T., Arias, A., García-Vázquez, E., Borrell, Y.J., 2015. Impacts of supplementation aquaculture on the genetic diversity of wild *Ruditapes decussatus* from northern Spain. Aquac. Environ. Interact. 6 (3), 241–254. https://doi.org/10.3354/aei00128.

Haining, R.P., 2003. Spatial Data Analysis: Theory and Practice. Cambridge University Press.

Hastings, A., 2001. Population dynamics. In: Simon, Asher Levin (Ed.), Encyclopedia of Biodiversity. Elsevier, pp. 769–776. https://doi.org/10.1016/B0-12-226865-2/00352-7, 9780122268656.

Hoffman, A., 1978. Growth allometry in a bivalve *Anadara diluvia* (lamark) from the badenian (miocene) korytnica clays, Poland. Acta Palaeontol. Pol. 23, 41–49.

Hurtado, N.S., Pérez-García, C., Morán, P., Pasantes, J.J., 2011. Genetic and cytological evidence of hybridization between native *Ruditapes decussatus* and introduced *Ruditapes philippinarum* (Mollusca, Bivalvia, Veneridae) in NW Spain. Aquaculture 311 (1), 123–128. https://doi.org/10.1016/j.aquaculture.2010.12.015.

Itoïz, S., 2021. Écologie fonctionnelle des Perkinsozoa (Alveolata) en milieu marin : de la diversité globale à l'étude d'un cas de co-infection entre *Perkinsus olseni* et *Perkinsus chesapeaki*. PhD thesis, Université de Bretagne Occidentale. France.

Itoïz, S., Perennou, M., Mouronvalle, C., Derelle, E., Le Goïc, N., Bidault, A., de Montaudouin, X., Arzul, I., Soudant, P., Chambouvet, A., 2021. Development of duplex TaqMan-based real-time PCR assay for the simultaneous detection of *Perkinsus olseni* and *P. chesapeaki* in host Manila clam tissue samples. J. Invertebr. Pathol. https://doi.org/10.1016/j.jip.2021.107603.

Itoïz, S., Metz, S., Derelle, E., Reñé, A., Garcés, E., Bass, D., Soudant, P., Chambouvet, A., 2022. Emerging parasitic protists: the case of Perkinsea. Front. Microbiol. 12, 735815. https://doi.org/10.3389/fmicb.2021.735815.

Itoïz, S., Mouronvalle, C., Perennou, M., Chailler, E., Smits, M., Derelle, E., Metz, S., Le Goïc, N., Bidault, A., de Montaudouin, X., Arzul, I., Soudant, P., Chambouvet, A., 2024. Co-infection of two eukaryotic pathogens within clam populations in Arcachon Bay. Front. Microbiol. 14. https://doi.org/10.3389/fmicb.2023.1250947.

Kermorvant, K., 2019. Optimisation de protocoles d'échantillonnage appliqués aux suivis de la biodiversité et des ressources. University of Pau and Pays de l'Adour, France. PhD thesis.

Kermorvant, C., Caill-Milly, N., D'Amico, F., Bru, N., Sanchez, F., Lissardy, M., Brown, J., 2017. Optimization of a survey using spatially balanced sampling: a single-year application of clam monitoring in the Arcachon Bay (SW France). Aquat. Living Resour. 30 (11), 1–11. https://doi.org/10.1051/alr/2017036, 37.

Kermorvant, C., D'Amico, F., Bru, N., Caill-Milly, N., Robertson, B., 2019a. Spatially balanced sampling designs for environmental surveys. Environ. Monit. Assess. 191 (8). https://doi.org/10.1007/s10661-019-7666-y, 524, 7pp.

Kermorvant, C., Caill-Milly, N., Bru, N., D'Amico, F., 2019b. Optimizing cost-efficiency of long term monitoring programs by using spatially balanced sampling designs: the case of manila clams in Arcachon bay. Ecol. Inform. 49, 32–39. https://doi.org/10.1016/j.ecoinf.2018.11.005.

Kermorvant, C., Coube, S., D'Amico, F., Bru, N., Caill-Milly, N., 2020. Sequential process to choose efficient sampling design based on partial prior information data and simulations. Spat. Stat 38, 100439. https://doi.org/10.1016/j.spasta.2020.100439, 13pp.

Kwon, J.Y., Park, J.W., Lee, Y.H., Hong, Y.K., Chang, Y.J., 1999. Morphological variation and genetic relationship among populations of shortnecked clam *Ruditapes philippinarum* collected from different habitats. J. Fish. Sci. Technol. 2, 98–104.

Laruelle, F., Guillou, J., Paulet, Y., 1994. Reproductive pattern of the clams, Ruditapes decussatus and R. philippinarum on intertidal flats in Brittany. J. Mar. Biol. Assoc 74, 351–366. U. K.

Lassalle, G., de Montaudouin, X., Soudant, P., Paillard, C., 2007. Parasite co-infection of two sympatric bivalves, the Manila clam (*Ruditapes philippinarum*) and the cockle (*Cerastoderma edule*) along a latitudinal gradient. Aquat. Living Resour. 20, 33–42. https://doi.org/10.1051/alr:2007013.

Lucas, A., 1981. Adaptations écophysiologiques des bivalves aux conditions de culture. Bull. de la Société d'Ecophysiologie 6 (1–2), 27–35.

Lunghi, M., Arnich, N., Lehuédé, F., Dubuisson, C., Thebault, A., 2023. Consumption of bivalve shellfish in French coastal populations: data for acute and chronic exposure assessment. J. Food Prot. 86 (12), 100180. https://doi.org/10.1016/j.jfp.2023.100180.

Mahé, M., 2022. La gestion durable d'une ressource halieutique à l'aide d'un modèle : exemple de *Ruditapes philippinarum* (Adams et Reeve, 1850) dans l'étang de Berre. PhD thesis, University of Aix-Marseille, France.

Mahé, M., Aurelle, D., Poggiale, J.C., Mayot, N., 2022. Assessment of the distribution of *Ruditapes spp.* in northern Mediterranean sites using morphological and genetic data. J. Molluscan Stud. https://doi.org/10.1093/mollus/eyac029, 0: eyac029.

Mahé, M., Camus, L., Marschal, C., Grisel, R., Poggiale, J.-C., Mayot, N., 2024. Population dynamics of *Ruditapes philippinarum* (A. Adams & Reeve, 1850) after the major ecological crisis of 2018 of the Berre lagoon, southern *France, J. Molluscan Stud*, 90(2). https://doi.org/10.1093/mollus/eyae009.

Maia, F., Gaspar, M.B., Barroso, C.M., 2025. Comparative study of *Ruditapes philippinarum* and *Ruditapes decussatus* in Ria de Aveiro, Portugal: Invasive species management and marine resource conservation. Estuar. Coast Shelf Sci 314, 109123. https://doi.org/10.1016/j.ecss.2025.109123.

Maitre-Allain, T., 1983. Suivi d'un essai de repeuplement de palourdes dans l'étang de Thau (Hérault): Croissance, Mortalité, Reproduction. PhD thesis. UPMC, France.

Mao, Y., Gao, T., Yanagimoto, T., Xiao, Y., 2011. Molecular phylogeography of *Ruditapes philippinarum* in the northwestern pacific ocean based on COI gene. J. Exp. Mar. Biol. Ecol. 407 (2), 171–181. https://doi.org/10.1016/j.jembe.2011.06.002.

Mazouni, N., et al., 1999. Gestion d'une ressource naturelle exploitée : Cas de la palourde (*Ruditapes decussatus*) dans la lagune de Thau. Sète (FR) : Programme PALOURDE, 1999. Rapport final 103.

McLaughlin, S.M., Tall, B.D., Shaheen, A., El Sayed, E.E., Faisal, M., 2000. Zoosporulation of a new *Perkinsus* species isolated from the gills of the softshell clam *Mya arenaria*. Parasite 7, 115–122. https://doi.org/10.1051/parasite/2000072115.

Moura, P., Vasconcelos, P., Pereira, F., Chainho, P., Lino Costa, J., Gaspar, M., 2018. Reproductive cycle of the Manila clam (*Ruditapes philippinarum*): an intensively harvested invasive species in the Tagus Estuary (Portugal). J. Mar. Biol. Assoc. U. K. 98 (7), 1645–1657. https://doi.org/10.1017/S0025315417001382.

Mullin, M.M., 2013. Webs & Scales: Physical and Ecological Processes in Marine Fish Recruitment. University of Washington Press, Seattle and London.

Norgard, T., Davies, S., Stanton, L., Gillespie, G.E., 2010. Evaluation of survey methodologies for monitoring Olympia oyster (*Ostrea lurida* Carpenter, 1864) populations in British Columbia. CSAS Research Document 2010/0006 62.

Ohba, S., 1959. Ecological studies in the natural population of a clam, *Tapes japonica*, with special reference to seasonal variations in the size and structure of the population and to individual growth. Biol. J. Okayama Univ. 5, 13–42.

Paillard, C., 2016. An ecological approach to understanding host-pathogen-environment interactions: the case of Brown Ring Disease in clams. In: Oysters and Clams: Cultivation, Habitat Threats and Ecological Impact. Nova Science Publishers, Hauppauge, NY, pp. 97–112, 11788-3619, USA, Inc. (NOVA). Chapter 7. https://novapublishers.com/shop/oysters-and-clams-cultivation-habitat-threats-and-ecological-impact/(hal-01426301.

Paillard, C., Maes, P., 1990. Etiologie de la maladie de l'anneau brun chez *Tapes philippinarum* : pathogénicité d'un Vibrio sp. C. R. Acad. Sci. Paris 310 (Série III), 15–20.

Paillard, C., Jean, F., Ford, S.E., Powell, E.N., Klinck, J.M., Hofmann, E.E., Flye-Sainte-Marie, J., 2014. A theoretical individual-based model of Brown Ring Disease in Manila clams, *Venerupis philippinarum*. J. Sea Res. 91, 15–34. https://doi.org/10.1016/j.seares.2014.03.005.

Paillard, C., Faure, D., Orlando, L., 2019. Le séquençage à haut débit ouvre les archives fossiles de l'ADN ancien, chapitre 7, 78, 258-260, dans 101 secrets de l'ADN. Éditeurs D Faure, D. Joly, S Salamitou. CNRS Éditions, Paris, p. 358, 978-2-271-12323-7.

Paillard, C., Rahmani, A., Bidault, A., Smits, M., Pichereau, V., 2025. Role of the environment in Vibrio−bivalve interactions: development of the brown ring disease model in clams. In: Smolowitz, Roxanna (Ed.), Diseases of Bivalves. Historical and Current Perspectives. Academic Press, pp. 51–64. https://doi.org/10.1016/B978-0-12-820339-2.00012-7, 20250128203390, 9780128203392.

Painblanc, S., 2023. Identifications morphologique et génétique de deux espèces de palourdes, *Ruditapes decussatus* et *R. philippinarum*, le long du littoral français. In: Rapport Master, vol. 1. Le Mans University.

Patrissi, M., Bernard, I., Hugo, F., Limonet, J., Violette, H., Sanchez, F., Caill-Milly, N., Bouvier, C., Lapègue, S., Holley, J.-F., Lagarde, F., 2023. Projet PALTEVA : Diagnostic de l'état de la population de palourdes européennes (*Ruditapes decussatus*) dans la lagune de Thau. Suivi 2023. 47pp. https://archimer.ifremer.fr/doc/00877/98910/.

Paul-Pont, I., 2010. Sensibilité et adaptation de populations de bivalves marins soumis à des stress multiples : infestation parasitaire, contamination microbienne et pollution métallique, vol. 1. University of Bordeaux, France. PhD thesis.

Paul-Pont, I., de Montaudouin, X., Gonzalez, P., Jude, F., Raymond, N., Paillard, C., Baudrimont, M., 2010. Interactive effects of metal contamination and pathogenic organisms on the introduced marine bivalve *Ruditapes philippinarum* in European populations. Environ. Pollut. 158, 3401–3410. https://doi.org/10.1016/j.envpol.2010.07.028.

Pierron, F., Gonzalez, P., Bertucci, A., Mérour, E., Brémont, M., de Montaudouin, X., 2019. Transcriptome-wide analysis of wild Asari (=Manila) clams affected by the Brown Muscle Disease: etiology and impacts of the disease. Fish Shellfish Immunol. 86, 179–185. https://doi.org/10.1016/j.fsi.2018.11.043.

Pitel, M., Savina, M., Fifas, S., Berthou, P., 2004. Evaluations locales des populations de bivalves dans le golfe de normand breton. In: Résultats de la campagne BIVALVES2002 - IFREMER, vols. 6–7.

Prié, V., Valentini, A., Lopes-Lima, M., Froufe, E., Rocle, M., Poulet, N., Taberlet, P., Dejean, T., 2021. Environmental DNA metabarcoding for freshwater bivalves biodiversity assessment: methods and results for the Western Palearctic (European sub-region). Hydrobiologia 848, 2931–2950. https://doi.org/10.1007/s10750-020-04260-8.

Renault, T., Arzul, I., 2001. Herpes-like virus infections in hatchery-reared bivalve larvae in Europe: specific viral DNA detection by PCR. J. Fish. Dis. 24 (3), 161–167. https://doi.org/10.1046/j.1365-2761.2001.00282.x.

Riquet, F., Le Clanche, U., Fortunato, H., Boulaire, E., Heurtebise, S., Ledu, C., Bouvier, C., Lagarde, F., Lapègue, S., Cormier, A. (In prep.) Divergence and Gene Flow in the Endemic and Non-indigenous Clam Species along the French Coastline Revealed by Mitogenome Study.

Robertson, B., Brown, J., McDonald, T., Jaksons, P., 2013. BAS: balanced acceptance sampling of natural resources. Biometrics 69 (3), 776–784. https://doi.org/10.1111/biom.12059.

Rosenberg, G.D., 1972. Patterned growth of the bivalve *Chione undatella* (Sowerby) relative to the environment. Departement of Geology. University of California, United States. PhD thesis.

Ruano, F., Batista, F.M., Arcangeli, G., 2015. *Perkinsosis* in the clams *Ruditapes decussatus* and *R. Philippinarum* in the northeastern atlantic and Mediterranean Sea: a review. J. Invertebr. Pathol. 131, 58–67. https://doi.org/10.1016/j.jip.2015.07.015.

Said, A., Pascual-Fernández, J., Amorim, V.I., Autzen, M.H., Hegland, T.J., Pita, C., Ferretti, J., Penca, J., 2020. Small-scale fisheries access to fishing opportunities in the European Union: is the Common Fisheries Policy the right step to SDG14b? Mar. Policy. 118, 104009.

Sanchez, F., Caill-Milly, N., Lissardy, M., Antajan, E., Meteigner, C., 2021. Suivi de la population de palourde japonaise dans le bassin d'Arcachon - Année 2021. ODE/LITTORAL/LER AR 21, 18. https://archimer.ifremer.fr/doc/00747/85909/.

Seed, R., 1968. Factors influencing shell shape in the mussel. Mytilus edulis L. J. Mar. Biol. Assoc. U. K. 48, 561–584.

SFF Guidelines, 2015. FAO voluntary Guidelines for securing sustainable small-scale fisheries in the context of food security and poverty eradication. Food and Agriculture Organization of the United Nations Rome, 2015.

Smith, A.N., Anderson, M.J., Pawley, M.D., 2017. Could ecologists be more random? Straightforward alternatives to haphazard spatial sampling. Ecography. https://doi.org/10.1111/ecog.02821.

Stevens, D.L., Olsen, A.R., 2004. Spatially balanced sampling of natural resources. J. Am. Stat. Assoc. 99, 262–278.

Stirling, H.P., Okumus, T., 1994. Growth, mortality and shell morphology of cultivated mussel *Mytilus edulis* stocks cross-planted between two Scottish sea lochs. Mar. Biol. 119, 115–124.

Sugiura, D., Kikuya, N., 2022. Cycle of reproduction, oocyte atresia, and maturation size of the Manila clam *Ruditapes philippinarum* on a pebble beach in Mutsu Bay, Northern Japan, Invertebr. Reprod. Dev. 66 (1), 8–15. https://doi.org/10.1080/07924259.2021.1999337.

Theobald, D.M., Stevens Jr., D.L., White, D., Urquhart, N.S., Olsen, A.R., Norman, J.B., 2007. Using GIS to generate spatially balanced random survey designs for natural resource applications. Environ. Manage. 40, 134–146.

Walne, R. Mann, 1975. Growth and biochemical composition in *Ostrea edulis* and *Crassostrea gigas*. In: Barnes, H. (Ed.), Proc. 9th Eur. Mar. Biol. Symp. Aberdeen University Press, Aberdeen, pp. 587–607.

Wang, J.F., Jiang, C.S., Hu, M.G., Cao, Z.D., Guo, Y.S., Li, L.F., Liu, T.J., Meng, B., 2012. Design-based spatial sampling: theory and implementation. Environ. Model. Softw. 40, 280–288. https://doi.org/10.1016/j.envsoft.2012.09.015.

Yu, H., Jiao, Y., Su, Z., Reid, K., 2012. Performance comparison of traditional sampling designs and adaptive sampling designs for fishery-independent surveys: a simulation study. Fish. Res. 113, 173–181.

Zurell, D., Berger, U., Cabral, J.S., Jeltsch, F., Meynard, C.N., Münkemüller, T., Nehrbass, N., Pagel, J., Reineking, B., Schröder, B., 2010. The virtual ecologist approach: simulating data and observers. Oikos 119 (4), 622–635. https://doi.org/10.1111/j.1600-0706.2009.18284.x.