



# Too late for regulatory management on Pacific oysters in European coastal waters?

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## ABSTRACT

This research presents the invasion history as well as an up-to-date distribution of the Pacific oyster *Magallana gigas* in European coastal waters, concluding that this invasive species has spread to large parts of all coastal biotopes. Moreover, the measures and management of the Pacific oyster invasions of coastal and marine ecosystems is discussed including restoration and resilience of invaded ecosystems. When *Magallana gigas* is well established and has reached adjustment phase characterized by firm biogenic reefs, eradication or even decimation is difficult and costly. During the establishment phase and maybe also the expansion phase, where the oyster appear as single individuals spread out on the sediment and yet not forming larger clumps and reefs, it is more realistic to implement mitigation tools. These initiatives cannot be implemented everywhere. They should be reserved especially for protected areas under national or international legislation e.g., Natura2000 areas, where smaller areas can be restored. The present contribution discusses and evaluates known mitigation tools like physical damaging of individual oysters, dredging, small-scale hand picking as well as various fishery concepts. Additionally, this research proposes some novel strategies where triploidity is suggested for implementation to avoid or decimate further spread of the species. As well as some initiatives based on choking and/or starving out the oysters by deploying a thick layer of sand/gravel or food for the competing blue mussels over oyster reefs. The efficiency of the different strategies, as well as the required frequency of follow up initiatives, are evaluated. The major conclusion from this research suggests that decisions to combat the alien oyster are mainly based on political/socioeconomic arguments and less on ecological arguments. This is because reefs of Pacific oysters most likely lead to equal or higher biodiversity as compared to native (e.g., blue mussel) beds and the oysters serve a redundant role in a trophic sense living from same resources as native bivalves. Moreover, oyster reefs serve ecosystem services as protecting shores against erosion and flooding. The most negative impact reported is on some mussel feeding birds that may have a reduced access to food. If eradication/decimation is decided, several mitigation instruments should simultaneously come into play and often repeating treatment strategy is necessary.

## 1. Introduction

### 1.1. Pacific oyster - a dilemma between resource and pest

The invasive marine invertebrate, the Pacific oyster *Magallana gigas* formerly *Crassostrea gigas* (Thunberg, 1793) (Fig. 1) (see Bayne et al., 2017), is classified by the European Union as a beneficial resource for the aquaculture industry as well as a nuisance for several of the member states in EU. According to ‘Council regulation (EC) No 708/2007 of 11 June 2007 concerning use of alien and locally absent species in

aquaculture’, 2022 3) “Aquaculture has benefited economically from the introduction of alien species and translocation of locally absent species in the past (for example rainbow trout and Pacific oyster) and the policy objective for the future is to optimize benefits associated with introductions and translocations while at the same time avoiding alterations to ecosystems, preventing negative biological interaction, including genetic change, with indigenous populations and restricting the spread of non-target species and detrimental impacts on natural habitats.” In Chapter I of the Council regulation nr 708/2007 under Subject matter, scope and definitions, Article 2 entitled ‘Scope’ it is

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Fig. 1. Biogenic reef of the Pacific oyster *Magallana gigas* (Photo by Per Dolmer).

stated: 5) “This Regulation, except for Articles 3 and 4, shall not apply to the species listed in Annex IV. The risk assessment in Article 9 shall not apply to species listed in Annex IV except in cases where Member States wish to take measures to restrict the use of the species concerned in their territory.” Pacific oyster is in fact one out of only 10 species listed in Annex IV. Hence, the Pacific oyster is perceived as an economically beneficial alien species in EU unless a given member state decides otherwise. In the regions where the species is not considered problematic, it is rather of economic interest (McKenzie and Lopez, 1997; McKenzie et al., 1997; Leppäkoski et al., 2002; Escapa et al., 2004). Furthermore, Regulation (EU) No 1143/2014 Of The European Parliament And Of The Council of 22 October 2014 on the prevention and management of the introduction and spread of invasive alien species The European Parliament And The Council Of The European Union, n.d., suggests that the member countries must initiate a control mechanism early on when an invasive species is discovered, and foster cross-border cooperation, particularly with neighboring countries, and coordination between Member States, particularly within the same biogeographical region. But again, the species in annex IV in regulation 708/2007 is not included in the regulation (Article 2.2). Based on data from IMPASSE, DAISIE, FishBase, and FAO-DIAS, Savini et al. (2010) the Pacific oyster is included in the top 27 of alien species introduced to Europe for aquaculture and related activities. However, they also emphasize a serious tradeoff that import of such species for aquaculture has led to co-introduction of several associated non-target species. The authorities in Northern European countries, especially the Nordic EU countries and Norway, consider the species to be harmful but the authorities have, to our knowledge, not implemented efficient actions or intentions trying effectively to control the species (Herbert et al., 2016). Because of the classification as an invasive species, aquaculture of the species in open systems is not permitted.

Invasive species are often known, when reaching high abundances, to cause damage to ecosystems and reduce their resilience. Therefore,

proportionate restoration measures should be conducted to support the ecosystem resilience towards invasions and to enhance the conservation status of habitats. Invasive species are often considered to be threats to native organisms. Some species introduced into new habitats show physiological and ecological advantages in coping with the new conditions as compared to their native environmental and ecological conditions (Nehls et al., 2006). The Pacific oyster originates from north-eastern Asia but has been widely introduced elsewhere for aquaculture purposes. It is rapidly expanding its global distribution across the historical distributions of native oyster taxa, whose reef habitats have faced a large eradication for various reasons (McAfee and Connell, 2021). Although highly variable, the invasiveness of the Pacific oyster has been realized in several countries and it is therefore considered as a pest or a noxious species in such areas (Ashton, 2001; Blake, 2001; Orensanz et al., 2002; Miossec et al., 2009; Holm et al., 2015). In some places this has resulted in transfer restrictions and eradication actions (e.g., in Australia, Ayres, 1992).

## 1.2. Our scientific questions

Our question is if it is ecologically beneficial to implement measures that control the distribution of Pacific oysters and its impact on the ecosystem? Is it at all possible to effectively regulate this alien species? No matter the biological dimension in the answers, if a given government for any reason decides to implement measures against the species there is a variety of relevant appliances available. Here we discuss perspectives in known eradication and decimation actions, and evaluate future possible practical, yet resource demanding strategies for obtaining an effective long-lasting regulation of the species. This review refers to key studies reporting results of a suite of management and regulatory actions and we propose generated ideas supplementing existing tools for obtaining a sustainable ecosystem function after establishment of the invasive Pacific oyster in European coastal waters. The present contribution then discusses current management strategies to accept or regulate the Pacific oyster in European coastal waters and review and identify different local measures and mitigation actions that can control the species. The intentions are to identify important ecological characteristics that should be addressed before deciding if mitigation measures should be activated. Moreover, if so, which mitigation measures that should be included in a management program. This in relation to avoiding negative impact on the ecosystem, and control of the invasive species and/or an efficient habitat restoration, in relation to the cost of the program. The present contribution includes a description of the invasion history of the Pacific oyster and an evaluation of which habitats that are invaded, and which habitats that are at risk of being invaded in the future. To qualify the management decisions, the population dynamic of the species is discussed in relation to the high production potential and the high population resilience of the species. Finally, the different mitigation measures are evaluated, to support the implementation of an optimal management and choice of methods from the mitigation-toolbox.

## 2. The invasion concept applying to Pacific oysters

Invasions by alien species is indeed a controversial subject. It is under debate among scientific experts but also in the mainstream popular press. The latter is according to Riccardi and Ryan (2018) often led by denier’s disregarding any potential harm of invasions on biodiversity and ecosystems regardless of systematic evidence. However, Our question is. Hence, a long and heated debate has been taken place in the scientific community e.g., Davis et al. (2011) arguing for assessing organisms on environmental impact rather than on whether they are natives. The findings of this article has led to a long series of comments in the scientific journal Nature and other media. Boltovskoy et al. (2018) made a well-placed pragmatic statement that the widespread perception that many non-indigenous species are effectively or potentially harmful

is not conflicting with that most have mixed (negative, neutral, and positive) impacts. It is however out of the present contributions scope to refer all arguments from all scientific contributions regarding this. Nevertheless, a recent review by Cassini (2020) addresses the complexity of the subject thoroughly by emphasizing controversial problems with definitions, methodology, data treatment and potential ecologic and social impacts of invasive species. Cassini finalizes his review by stating "Investigating the values that underlie our attitudes towards non-native species could be the first step to reconciling currently confrontational situations".

The Pacific oyster was introduced in Europe purposely approximately 50 years ago for aquaculture production and has, by escaping propagules, established itself often in massive biogenic reefs defined as: "Intertidal or subtidal three-dimensional habitats formed by oysters and/or mussels at high densities" (sensu Gillies et al., 2015). From where they further spread out via potential steppingstone populations inhabiting new territories (see Reise, 1998) (Fig. 2).

Sagoff (2018) recently wrote "If an invasive species is defined as a species that spreads to the detriment of economic interests and public health, however, invasion biology could not be easily distinguished from pest management and public health sciences. If an invasive species is defined in some other way, for example, because of its ecological rather than economic or health effects, invasion biology might not be distinguished from disciplines which deal with ecological dispersal, colonization, succession, disturbance, etc., and which are already well established in the ecological literature". Pacific oyster could therefore fit into both of Sagoff's definitions. However, depending on the stage of invasion (see Reise et al., 2006) it probably firstly acts as an ecological disturbance following general ecological rules, and secondly as an economical challenge and depending on invasion history at a given locality should be treated accordingly. Consequently, economic drivers of a decision-making process are first strong enough when the invasion is well established i.e., in adjustment phase, and then it is very costly to combat the species.

### 2.1. The history of the European invasion by the Pacific oyster

At present (2019) the global wild catch of cupped oyster *Nei* and Pacific oysters was 45,767 tons hereof 39,021 tons Pacific oyster (FAO, 2021). In aquaculture, 5,918,395 tons of cupped oyster *nei* and Pacific oysters was produced globally in 2019 hereof 623,591 tons Pacific oyster (FAO, 2021; McAfee and Connell, 2021). In EU the annual

production (2019) of cupped oysters were 104,861 tons, corresponding to a value of 444 Mio Euro (FAO, 2021). The largest producer of Pacific oysters in EU is France, farming 80% of the EU production in 2018 (FAO, 2021).

### 2.2. Introductions in aquaculture

In Europe, the Pacific oyster was introduced into aquaculture and aquaculture experiments in France, the Netherlands, Cyprus, and the United Kingdom in the 1960's after a period of high mortalities of Portuguese oysters, *Crassostrea unguolata* and European flat oyster, *Ostrea edulis* due to overexploitation, diseases, and severe winters (Walne and Spencer, 1971; Grizel and Héral, 1991; Zibrowius, 1991; Spencer et al., 1994; Drinkwaard, 1999; Steele and Mulcahy, 1999; Wood et al., 2021). In the 1970s the Pacific oyster was introduced in several European countries (see Fig. 3) including Germany, Ireland, Greece, Italy, Malta,



Fig. 3. Distribution of the Pacific oyster *Magallana gigas* in European waters (Yüksek, 1989; Çevik et al., 2001; Skolka and Gomoiu, 2004; Son, 2010; Nehring, 2011; Lallias et al., 2015; Smith et al., 2015; Shelmardine et al., 2017; Krapal et al., 2019; Ewers-Saucedo et al., 2020; Gökçek et al., 2020; Mitov et al., 2020; pers. Com. K. Reise, 2020; Aydin and Gül, 2021; Mortensen et al., 2022).



Fig. 2. Individual Pacific oyster *Magallana gigas* shells (left) and soft parts (right) (Photo by Per Dolmer)

Portugal, Norway, and Denmark (Agius et al., 1978; Kristensen, 1989; Grizel and Héral, 1991; Mortensen, 1993; Drinkwaard, 1999; Huvet et al., 2004; Orban et al., 2004; Jensen and Knudsen, 2005; Nehring, 2006; Troost, 2010; Kochmann et al., 2012; Dolmer et al., 2014; Laugen et al., 2015). In Croatia the Pacific oyster has never been officially introduced into aquaculture but aquaculture experiments are likely to have been conducted in the 1970s (Ezgeta-Balić et al., 2020). In the 1980s the Pacific oyster was introduced in the Black Sea at the Crimean coast, the Channel Islands (UK), Spain and Sweden (Zolotarev, 1996; Iglesias et al., 2012; Dolmer et al., 2014; Strand and Lindegarth, 2014; Laugen et al., 2015). At the Galician coast (Spain), the first introduction of Pacific oysters was unintentional due to *M. gigas* seed mixed up in legally imported European flat oyster seed (Molares et al., 1986 op cit in Iglesias et al., 2012). In the 1990s the Pacific oyster was introduced in Belgium, Ireland, and Scotland (Coutteau et al., 1997; Shelmerdine et al., 2017) and a small-scale trial was conducted at Madeira Island (Kaufmann et al., 1994). At the Romanian coast, the Pacific oyster was produced in aquaculture 2001–2003 (Aydin and Gül, 2021). In 2014, the Icelandic company Víkurskel ehf started a trial production of Pacific oysters in the Skjalfandi bay, Iceland (Viðskiptablaðið, 2014). The first trial production was successful and was sold to Icelandic restaurants in 2018 (Iceland review, 2018). However, in 2019 the Icelandic environmental agency did not give the company permission to import spat from Spain for continued commercial production (MBL.IS, 2019). It is unknown whether the four years of trial production has resulted in establishment of a feral population, but due to the water temperature at latitude 66°N it is not likely. In 2022, a Danish two-year trial production has been initiated in the Limfjord (pers. comm. B. Vismann). From many of the above-mentioned producing areas, Pacific oyster larvae have dispersed and established feral self-sustaining populations (see Fig. 3). Even when productions (or trials) were terminated, Pacific oyster dispersal might continue because in most cases the oysters were abandoned.

### 2.3. Distribution in the Wadden Sea

In 1975 and 1976, massive spawning events occurred and resulted in settlement of millions of Pacific oysters in the Oosterschelde estuary, Netherland (Drinkwaard, 1999; Smaal et al., 2009). During the 1980's other Dutch estuaries started to be colonized (Wolff and Reise, 2002) and since the 1990's Pacific oysters have colonized the entire Dutch coast (Dankers et al., 2004). Due to the predominant northeasterly water current in the area, oyster larvae dispersed and arrived at the western German Wadden Sea in 1996 (Wehrmann et al., 2000; Reise et al., 2006). In 1991, the first Pacific oysters were observed outside the commercial farm established in 1986 at the German island of Sylt (Reise et al., 1999). In the following years, the Pacific oyster population spread along the coastline (Diederich et al., 2005; Wehrmann and Schmidt, 2005; Nehring, 2006) and since 2004 the *M. gigas* distribution gap between the western and northern Wadden Sea has closed (Wehrmann et al., 2000; Reise et al., 2006). Based on molecular detection of sub-populations Moehler et al. (2011) suggested that the European Wadden Sea has been invaded from sub-populations besides other aquaculture related lineages. The southern region received input from British Columbia lineages whereas the northern region suggests a persistent influx from aquaculture hatchery production based upon numerous different lineages. In the mid-1990s the first specimens of feral *M. gigas* was observed in the Danish Wadden Sea, where Danish mussel fishermen caught them as a bycatch (Wrangle et al., 2010). In the Danish part of the Wadden Sea the biomass of Pacific oysters has recently been reported to be 70.000 tons (Nielsen et al., 2018) (see Fig. 3).

### 2.4. Distribution in Scandinavia and the Baltic

In the inner Danish waters, *M. gigas* was introduced around 1972 in the Limfjord (Dolmer et al., 2014; Laugen et al., 2015). In the following

years, several Pacific oyster farms were established, and aquaculture experiments conducted in the Limfjord, the Wadden Sea and at other locations all based upon imported seed (Kristensen, 1989; Jensen and Knudsen, 2005; Troost, 2010; Dolmer et al., 2014; Laugen et al., 2015). Some of the commercial farms continued production up through the 1980s and 1990s and the last farm in Denmark (in the Isefjord) closed their production in 1998 (Troost, 2010; Wrangle et al., 2010) leaving vast amounts of Pacific oyster on the estuarine bed sustaining an existing population. Today the only Danish waterbody without Pacific oysters is around Bornholm in the Baltic. However, an up-to-date presentation of distribution is not available in the scientific literature but is described here (Fig. 3). In the Baltic proper, Pacific oysters is reported in Kiel Bight (Ewers-Saucedo et al., 2020) and Flensburg Bight (pers. Comm. K. Reise, 2020). In Sweden, Pacific oyster spat was used in cultivations trials close to Strömstad, situated near to the Norwegian border (Eklund et al., 1977; Laugen et al., 2015). Feral Pacific oysters were observed in 2007 at the Swedish west coast and occur today from Falsterbo at the South of Øresund and northwards to the Norwegian border. The biomass is reported to be 100.000–500.000 tons (Laugen et al., 2015). In Norway, Pacific oysters spat were introduced into aquaculture in 1979 (Strand and Vøllstad, 1997) and during the last two decades imported Pacific oysters has been re-laid for growth to market size (Wrangle et al., 2010). The first feral Pacific oysters were observed at the Norwegian Skagerrak coast in 2005 and since then has dispersed from the Swedish border in east to about the 60° northern latitude north of Bergen. The Pacific oyster's recent expansion in Scandinavia is presumably a result of northwards larval drift. Anglès d'Auriac et al. (2016, 2017) investigated the genetic connectivity and possible spreading patterns between populations on the southern Norwegian coast in comparison to the Swedish and Danish populations by DNA microsatellite analysis of adult oysters besides computer simulated larvae drift. The reported pattern of genetic dissimilarity among the Norwegian populations suggests several different local introduction pathways rather than a unidirectional entry of larvae drifted from Denmark and Sweden.

### 2.5. Distribution at the British Islands, Ireland, and the Atlantic coast

Spencer et al. (1994) reported several spatfalls had taken place around 1990 in the United Kingdom. Although Spencer et al. (1994) anticipated the spat to die off, feral populations have later been reported both in the UK, Ireland, and North Ireland (Guy and Roberts, 2010; Herbert et al., 2012; Kochmann et al., 2012). At the Belgian coastline Pacific oyster is a dominant part of the marine fauna (Kerckhof et al., 2007). At the French Atlantic coast feral recruitment was low between 1970 and 1995 but have since been massive (Dutertre et al., 2010). At the north Atlantic coast of Spain, feral Pacific oysters are also present (Fabioux et al., 2020; Solaun et al., 2015). At the south Atlantic coast of Huelva, Spain no harvest of introduced Pacific oyster took place between 1987 and 2011 due to heavy metal concentrations of soft parts being exceeded, but production continued in the Cadiz region (López-Sanmartín et al., 2016). In the Huelva region feral Pacific oysters were present in 2011 (López-Sanmartín et al., 2016). At the west and south coast of Portugal feral population are likewise established (Fabioux et al., 2020) (Fig. 3).

### 2.6. Distribution in the Mediterranean and Black Sea

According to Zenetos et al. (2010) feral populations have established in the western, central and eastern part of the Mediterranean Sea including the Adriatic Sea. Although Zenetos et al. (2010) reported the Pacific oyster to be present in the Western Mediterranean Sea, both Cardoso et al. (2013) and Antonio and Camacho (2019) state that it is not known whether the species has established feral populations in the Mediterranean part of Spain. However, both authors conclude that the reproductive activity of the Pacific oysters in aquaculture in Mediterranean Spain and Portugal have the potential to allow feral populations

to establish. At the French Mediterranean coastline Pacific oysters was introduced in the 1970's and today 10% of the French production comes from this region (Robert et al., 2013). Contrary to the paradigm of "no Pacific oyster reproduction in Mediterranean lagoons" Lagarde (2017) and Ubertini et al. (2017) showed that spatfalls do occur. Although the Pacific oyster was introduced in Italy in the 1970's (Orban et al., 2004) it is only recently that small scale aquaculture of Pacific oysters has been initiated in Italy and especially at the Adriatic coastline, the Po delta, at Sardinia, at Sicily and the Liguria region (Burioli et al., 2018; Tamburini et al., 2019; Bordignon et al., 2020; Graham et al., 2020; Mikac et al., 2021; Mosca et al., 2021). Also farming of triploid Pacific oysters is reported from off the coast of the Puglia region (Mosca et al., 2021). Feral populations of Pacific oysters have established along the Italian coastline as stated by Elia et al. (2020): "*Crassostrea gigas* is a sentinel species along the Italian coast". In Slovenia feral populations of Pacific oyster are found along the whole coastline (Lipej et al., 2012; Mavrič et al., 2012). In Croatia feral populations were reported in the 1970s in Lim Bay, in the northern Adriatic Sea (Ezgeta-Balić et al., 2019; Ezgeta-Balić et al., 2020; Stagličić et al., 2020). Feral Pacific oyster populations has later been confirmed at the northern Croatian coastline but not the most southern part of the Croatian coastline (Ezgeta-Balić et al., 2019; Spagnolo et al., 2019). At the Montenegrin coast Pacific oyster aquaculture was initiated in the late 1970's, and feral populations were established (Petović et al., 2019). However, surveys at the Albanian and Montenegrin coasts show no presence of Pacific oysters (Katsanevakis et al., 2011; Petović et al., 2019). In accordance with this (except for Montenegro) Martínez-García et al. (2021) decided to rank Albania, Montenegro and Bosnia and Herzegovina as coastlines without any historical introduction of Pacific oysters. In Greece, the first observation of Pacific oyster was in 1989 in the Gulf of Corinth (Zenetos et al., 2004). In 2014 the only confirmed occurrence of Pacific oyster in Greece was still reported to be in the Gulf of Corinth (Elnais, 2014). Feral populations of Pacific oysters in the Marmara (and Levantine) Sea, Turkey, were reported in 1989 and 2001, respectively (Yüksek, 1989; Çevik et al., 2001; Gökçek et al., 2020). In the Black Sea, the first feral populations were reported in 1995 (Micu, 2004). At present Pacific oysters are reported from most of the Black Sea coastline (Skolka and Gomoiu, 2004; Krapal et al., 2019; Aydın and Gül, 2021). In the adjacent Sea of Azov, no presence of Pacific oysters has been found (Zaitsev and Öztürk, 2001). The Sea of Azov has a salinity of 13–14 (Paavola et al., 2005), which might be the reason behind the absence of the Pacific oyster. (Fig. 3).

At present, the effort of providing the distribution pattern has resulted in that Pacific oysters in European waters can be found along the coast of the Atlantic, North Sea, Mediterranean, Marmara Sea, Aegean Sea, Black Sea, around Ireland, North Ireland, the United Kingdom and in Scandinavian waters as depicted in Fig. 3 (Micu, 2004; Skolka and Gomoiu, 2004; Guy and Roberts, 2010; Crocetta, 2011a, 2011b; Nehring, 2011; Herbert et al., 2012; Kochmann et al., 2013; Dolmer et al., 2014; Lagarde, 2017; Krapal et al., 2019; Gökçek et al., 2020; Stagličić et al., 2020; Aydın and Gül, 2021). Also, offshore in the North Sea *M. gigas* is found at wind farm constructions (De Mesel et al., 2015). It is fair to state that *M. gigas* is present in all European waters except, or perhaps not yet, in Norwegian waters north of 60°, in the Baltic Sea at the east coast of Sweden, and the coast of Finland, Estonia, Latvia, Lithuania, Russia, Poland, and the Danish Baltic Sea Island Bornholm. In addition, Pacific oyster is not reported from Albania and the Sea of Azov.

## 2.7. Future predictions of Pacific oyster spreading if not regulated

To forecast future trajectories in the development of the European Pacific oyster populations and their expected distribution is not an easy task. Almost a decade ago Jones et al. published model predictions and suggested that "Pacific oyster will experience an opening of suitable habitats in northern UK waters, among other locations reaching the

Faroe Islands and the eastern Norwegian Sea by 2050" (Jones et al., 2013). Their predictions essentially hold true already today. Laugen et al. (2015) modelled large scale spread of larvae from donor populations by complex 3D oceanographic models and forecasted a distribution very similar to the presently observed distribution in Scandinavian waters. By including climate impact in relation to increased temperatures, the maximum distribution range can be identified. To forecast fine scale distribution patterns, habitat modelling in combination with known species requirements is a good starting point. A habitat model with high precision will require data on habitat level for hydrodynamic, hydrography, donor population of larvae and substrate conditions. Furthermore, if the habitat model must forecast distribution in a long-term perspective, data on climate change in relation to temperature is needed for predicting the northern distribution, and the effect of climate change on salinity is needed to forecast the distribution in brackish areas such as the Baltic Sea. A Scandinavian risk assessment based on an analysis of the scientific knowledge at that time of the distribution patterns of *M. gigas* including the change in density over time was reported by Dolmer et al. (2014) and Mortensen et al. (2017). It was suggested and quoted here that "at the habitat types 'Low energy rock, Littoral sand and mud and Sub-littoral sediment in low energy areas' there is a limited to moderate risk that a bio-invasion of *M. gigas* will develop." In contrast, "for 'Biogenic reefs and Sub-littoral sediment in high energy areas' there is a moderate to high risk for a bio-invasion". Mortensen et al. (2017) concluded that the information in the risk assessment may be used to develop site-specific strategies for conservation in areas with a present or an expected presence of *M. gigas* within the next decades. Mortensen et al. (2017) also suggests that different strategies can be implemented in concert. One strategy is simply to accept the presence of the species in the ecosystem (Reise et al., 2017a). Reise et al. (2017b) conclude that the Wadden Sea Pacific oyster population is ineradicable, and 'oyssel reefs' (reefs with coexisting Pacific oysters and blue mussels) should be accepted as a historical contingency (Eschweiler and Christensen, 2011). Obviously, the Pacific oyster will not only continue to expand its geographic range towards the poles, but it will also gradually adapt and thrive at the margins of its geographical range (Rinde et al., 2017b; King et al., 2021). An alternative strategy to Reise et al. (2017a) is immediate attempts to control density and dispersal of *M. gigas* in smaller or larger areas. Here the latter strategy is discussed.

## 3. Interactions with the ecosystem

In places where the Pacific oyster occurs sporadically no immediate ecosystem risk is observed. Hence, no need for urgent mitigation actions. In contrast, where Pacific oyster form dense reefs and fundamentally change marine habitats another and worse situation is often prevalent. To decide a management strategy there, it is crucial to understand the role of the species to evaluate the ecological and socioeconomical impact of the management. In a management scenario where the target is to reduce the density of the species, it may be at the cost of reduced ecosystem services provided by the species, and alternatively management with no density reduction can result in a large-scale change of the ecosystem. Knowledge of niche plasticity, species resilience, interactions with other species and goods and services from the species is key to decide a management strategy.

### 3.1. Natural regulating factors for Pacific oysters

The Pacific oyster is an important aquaculture species due to its biological capacity for a high somatic and propagule production. The same traits explain the species capacity to invade and modify marine habitats. When spawning, female Pacific oyster can produce up to 200 million eggs and the few that survive passed larval and juvenile phases, mature within a year. This reproduction potential combined with a high somatic growth rate support that the species, under favorable

conditions, can rapidly form dense populations. When a population has established itself in a habitat, the population is very resilient. According to CABI (2022) “*Magallana gigas* can resist freezing air temperatures (-17 °C)” (see Strand et al., 2011) “as well as a 20 °C difference between low and high tide in winter, and summer temperature on a muddy bottom up to 45 °C (a more than 25°C difference between low and high tide). Salinity and temperature tolerances are highly variable between varieties and depending on the location where they grow”. Hence, the Pacific oyster is considered a pronounced euryhaline and eurythermic species (Dutertre et al., 2010; Rohfritsch et al., 2013; Thomas et al., 2016; Rinde et al., 2017). Moreover, a combination of factors such as temperature and salinity are more representative of species tolerance than single factor values (Gouletquer, 1997; Hansen, 2022). Physiological status is a determining factor for environmental tolerances as well as differences among the life stages (Powell et al., 2000, 2002). Their thick shells protect against natural as well as anthropogenic stressors e.g., extreme temperature and/or salinity and from drying out, and against certain pollutants. However, as for numerous other organisms their gametes, eggs and larvae are far more vulnerable to environmental stressors than adults (His et al., 1989). The gametogenesis is controlled by day-degrees besides that a minimum temperature of 18–20 °C is a prerequisite for successful spawning (His et al., 1989). Egg survival and development rate depends on the salinity level. Apparently a certain inherit of salinity tolerance reflects the conditions where the spawning individuals reside. It is, however, noteworthy to be aware of that data on eggs and larvae tolerances are from a time where climate changes were not yet so profound and presumably before the organism was physiologically adapted to northern European habitats. Hence, it is reasonable to expect that also the propagules have adapted to the present abiotic conditions. This is evident by its spreading in Northern European waters (see Fig. 3) but remains to be thoroughly verified experimentally.

Winter mortality of *M. gigas* is an effective regulatory factor leading to occasionally significant population decline in Northern Europe (Strand et al., 2011, 2012). Büttger et al. (2011) reported very high mortality for oysters exposed for almost three months to seawater temperatures <2 °C and air temperatures from plus 2 to minus 13 °C in the North-Frisian Wadden Sea. Hence, severe winter conditions with ice cover could be a factor determining the species density and northern boundary.

Besides the limitations dictated by abiotic variables an organism operates within a set of biotic boundaries e.g., bottom-up as well as top-down regulatory processes in the food web controlling its population development. The Pacific oyster can feed within a wide spectrum of particulate food sizes and concentrations determining its growth and reproduction potential (e.g., Nielsen et al., 2017). Limitations in food availability is most pronounced in oligotrophic regions e.g., Mediterranean Sea (Lagarde, 2017; Ubertini et al., 2017) and in protected low tide shallow water habitats e.g., the Limfjord, Denmark, and presumably not in high tide habitats such as the Wadden Sea (Holm et al., 2016; Visman et al., 2016) and probably not along the Atlantic coast and the British Isles either, both characterized by substantial tidal amplitude. However, at present other natural regulatory mechanisms controlling the population development of *M. gigas* are absent or low due to lack of natural predators. The most common invertebrate shellfish predators in the Wadden Sea and Dutch estuaries are the brown shrimp *Crangon crangon*, the shore crab *Carcinus maenas* and the common starfish *Asterias rubens* (Troost, 2010). No doubt these invertebrates predate on spat and juvenile Pacific oyster specimens, but not so much in lower saline habitats where the Pacific oyster still thrives, but the predators face osmotic challenges. To our knowledge, thorough documentation on the significance of predation is still lacking. In the Wadden Sea herring gulls, *Larus argentatus*, and oyster catchers, *Haematopus ostralegus*, are the only reported bird species predated on *M. gigas* (Cadée, 2008a, 2008b). Moreover, the colonization by Pacific oysters certainly does not improve bird biodiversity but shows negative impacts mostly for three species:

Oystercatcher, Common Gull, and Knot (Waser et al., 2016). In the Wadden Sea ecosystem, the Pacific oyster is associated with five invasive and native macro parasite species thoroughly discussed by Goedknecht (2017). However, a more serious situation emerges concerning disease outbreaks among Pacific oysters. Recently an ostreid herpesvirus microvariant (OsHV-1  $\mu$  var. disease) was detected in culture installations as well as in wild populations in France, Sweden, Norway, USA, and Australia causing mass mortality among the oysters (e.g., Mortensen et al., 2016; King et al., 2019).

### 3.2. Pacific oysters providing ecosystem goods and services

It has been questioned whether Pacific oysters is a problem and if so, how big a threat it is for biodiversity? For tourism? For the employment and economy? Or is it of added ecological value by e.g., stimulating biodiversity as recent results indicate (e.g., Markert et al., 2010; Hollander et al., 2015; Zwerschke et al., 2020). At local scales, establishment of Pacific oysters can significantly alter diversity, community structure and ecosystem processes, with effects varying among habitats and locations and with the density of oysters (e.g., Herbert et al., 2016). However, seven years into the invasion in the Wadden Sea of Lower Saxony, southern German Bight, there was no suppression of indigenous invertebrate species (Markert et al., 2010). This even applied to *M. edulis*, which persisted at the site invaded by *M. gigas*. On the contrary the associated macro fauna community showed increased species richness, abundance, and biomass in the Pacific oyster reef (Markert et al., 2010). At three subtidal localities in Sweden there was reported no difference in associated fauna diversity between *M. edulis* and *M. gigas* populations (Hollander et al., 2015). However, the abundance of the associated fauna was significantly higher at the *M. gigas* populations as compared to *M. edulis* populations (Hollander et al., 2015). In the Limfjord, Denmark a sustainable co-existence between Pacific oyster and blue mussels has been prevailing for decades with numerous invertebrate species associated (Holm et al., 2016). Already Reise et al. (2006) stated that the Pacific oyster generally do not impair biodiversity and ecosystem functioning; invaders often expand ecosystem functioning by adding new ecological traits, intensifying existing ones and increasing functional redundancy. Moreover, Buschbaum et al. (2016) propose that presence of the species can cause beneficial effects for native organisms and should not be generally considered as a risk for the recipient ecosystems. Additionally, Christianen et al. (2018) stated that the return of native oysters (*Ostrea edulis*) may be facilitated by novel substrate provided by invasive oysters at sites where their distribution overlap. Gutow and Buschbaum (2019) go as far as stating that Pacific oyster reefs in the Wadden Sea represent biodiversity hotspots. Finally, Zwerschke et al. (2020) even suggest that *M. gigas* could compensate for the loss of ecosystem functions performed by the former but almost extinct native European oyster *Ostrea edulis*, i.e., a convincing example of functional redundancy in ecosystems.

Pacific oyster reefs provide numerous goods and services e.g., as food resource, pearl producers, nutrient capturing, water clarification, pollution removers and creators of important habitats for countless other marine species (see Beck et al., 2009 and chapters in Smaal et al., 2009). Species like mussels, barnacles, and sea anemones settle on the oyster shells and produce important prey items for predatory invertebrates and birds as well as commercially valuable fish species (NOAA Fisheries, 2022). In some locations, Pacific oyster reefs act as eco-engineers protecting underwater vegetation and waterfront communities from physical stress provided by waves, floods, and tides (e.g., Lebbe et al., 2021). Well established reefs and vegetation protect valuable habitats by reducing wave energy effects and erosion (e.g., Gonzalez et al., 2021; NOAA Fisheries, 2022). In the Netherlands, artificial reefs based on Pacific oyster shells are in fact constructed these days e.g., in the Eastern Scheldt for shore protection (see Ecoshape (2022) for details). Borsje et al. (2011) even formulated the term ‘Ecological engineering’ based on numerous species of both plants and invertebrates

including oysters operating alone or in concert with traditional man-made engineering initiatives as coastal protectors preventing flooding.

#### 4. Current and novel management strategies of the Pacific oyster in (northern) Europe

The goal is to implement a long-term perspective for the management practices of the invasive oyster. This is often not straight forward and requires thorough physiological, biological, and ecological knowledge of the species besides detailed information on source- and receiving environments. The literature does not mention any management strategies from southern Europe but merely from Northern France and northwards. Suggested prevention actions to avoid Pacific oysters becoming established in the wild should encompass education and public awareness raising in collaboration with a monitoring program to control the invasive species associated with relevant influx sources e.g., ballast water, marinas, and aquaculture (MedMIS, 2022). Thorough monitoring also helps in early detecting of oyster colonies and establishing eradication or containment before further spread occurs in e.g., Natura 2000 reserves. Modern molecular methods like eDNA might be a helpful tool to identify early presence of all life stages and is recently developed and implemented in monitoring (Andersen et al., 2021). In practice, actual control action is feasible only under conditions, such as when Pacific oyster is reaching high individual density in a very restricted area and, if possible, before spawning occurs. Prior to any control actions, it is recommendable to conduct an environmental impact assessment to scale an eventual effort. Complete eradication of established marine invasive species is difficult or even impossible (Cardigos et al., 2015; Shine, 2015). Therefore focus should be towards

regulation in specific vulnerable areas and targeting specific species of interest (Mortensen et al., 2017). Presented here is an attempt for conceptual managing models for the Pacific oyster *Magellana gigas* from aquaculture and from invasion perspectives (Fig. 4).

##### 4.1. Removing individual oysters for immediate destruction on-site

In Kent, United Kingdom, a trial was conducted by volunteers to combat Pacific oysters with the aim to return to former abundances. The trial lasted a whole year and was conducted simply by crushing the oyster shells one by one with ordinary handheld hammers (McKnight and Chudleigh, 2015). In the first-place whole oysters were removed but an unintended side effect appeared where the substrate was severely damaged. The substrate inhabited by the Pacific oysters were chalk reef structures declared as a fragile and protected habitat. To overcome that negative side effect the oysters were eradicated by crushing only the upper valve leaving the lower valve on the substrate. On non-protected chalk substrates entire individuals were crushed. The trial resulted in significant reduction of individuals' present leading to a habitat change from a dense oyster reef to a situation of less dense and mainly solitaire *M. gigas* on the location. The benefit was that the improved method was targeted on the alien oyster with minimal impact on the protected chalk formations and the naturally associated invertebrates but the disadvantage was the high cost of labor it required. McKnight and Chudleigh (2015) even did a cost benefit analysis of effectiveness and negative impacts from their oyster removal trial. They concluded this mitigation tool could effectively be used elsewhere if the goal sanctifies the means and the high cost is justified. In Northern Ireland, *M. gigas* individuals were crushed likewise. In the year after the eradication treatment

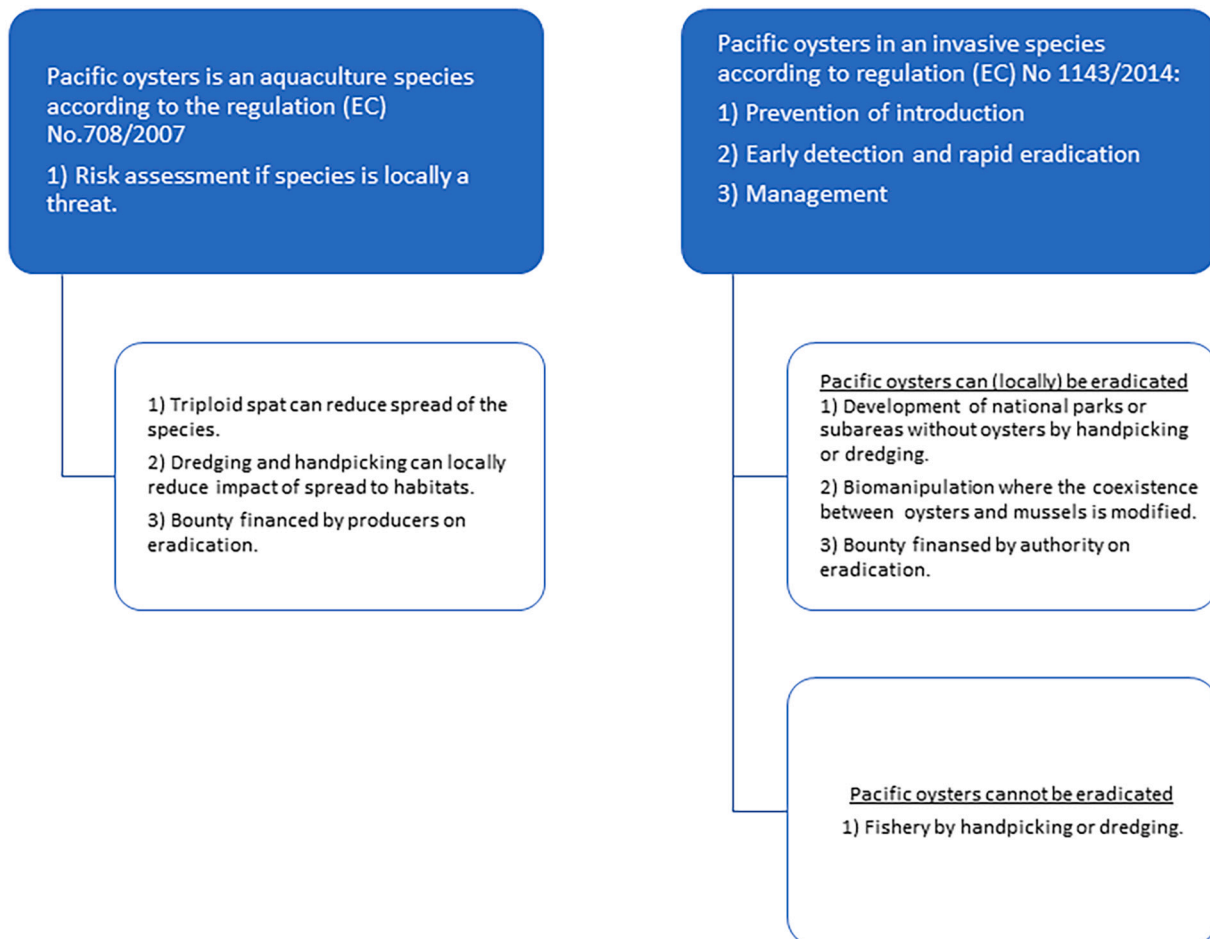


Fig. 4. Conceptual managing models in aquaculture for the Pacific oyster *Magellana gigas*, considered an invasive species.

oysters were almost 100% eradicated (Herbert et al., 2016). Hence, although labor-intensive and therefore relatively costly this simple mitigation strategy apparently works.

#### 4.2. Hand picking Pacific oysters for consumption by citizen and arranged tourist safaris

Handpicking was implemented 1976–1981 in The Netherlands to combat Pacific oysters, but these attempts proved to be unsuccessful. However, other studies have turned a problem into a resource by sustainable exploitation of minor sized Pacific oyster assemblages. In Denmark recreational handpicking is not regulated but permissions are given for hand brace. A survey shows that approximately 6% of the residents in areas where Pacific oyster reefs are present do hand pick oysters and mussels for personal use (Hjalager et al., 2019). As there is no supervision in the area, the number of individual visits and the harvested amounts of oysters are unknown (Hjalager et al., 2019). In the UK as well as the Danish Wadden Sea, guided walks to the oyster reefs are organized for tourists to collect wild oysters for food. If the demand from supermarkets and restaurants increase it will drive a market price further up leading towards a dual purpose of these collections: control of wild Pacific oysters and an income to the hand-collectors (Herbert et al., 2016). However, to our knowledge no quantitative data are yet available. Hjalager et al. (2018) reported that toxic algae or infectious microbial components on the collection site pose potential risks for humans when consuming the oysters and consider these as the two main barriers for expanding the private and organized collection.

#### 4.3. Dredging the Pacific oyster reefs for destruction purposes

In France a showcase of successful mechanical reduction by hand bracing of Pacific oyster is reported from the Marennes–Oléron Basin. The removal of wild *M. gigas* even had a positive side effect. An efficient removal of the slipper limpet (*Crepidula fornicata*) and the Japanese oyster drill (*Ocenebrellus inornatus*) from the area and thereby both a major food competitor and an invasive predator on Pacific oyster was brought down. The relatively large-scale dredging operation was conducted by powerful entrepreneur machinery modified for marine activities (Gouletquer et al., 2002). In the Netherlands a successful decimation trial where 50 ha of intertidal wild oysters and sub-littoral cultivated beds was dredged (Wijsman et al., 2008). However, the effort removing the oysters was substantial and with a relatively high expense of 20 boat hours per dredged hectare (Wijsman et al., 2008). Since oysters continued to settle on the areas where oysters were removed repetition of the action needs to be conducted every 5–7 years with a high risk of unintended habitat destruction (Herbert et al., 2018). By removing the target oyster a major nuisance emerge since the mechanical action also removes most of the associated macrofauna and flora. This is a high price to pay since it inevitably will translate into habitat destruction for other key organisms in the system e.g., predatory fish and birds (Reise et al., 2006). Hence, this mitigation strategy might not leave the ecosystem in a sustainable state, making it the easiest to reject. Dredging for oysters may be harmful to the ecosystem depending on the habitat type (Jennings and Kaiser, 1998). Dredging Pacific oysters to control the density might pose a reduced impact if conducted when the oysters are spread out as solitary individuals (Herbert et al., 2016). In contrast, removing oysters from a dense reef require more energy and often cause severe disturbances to the ecosystem. Alternative solutions can include various gentle fishing techniques which, to our knowledge, none are yet fully developed, e.g., where the Pacific oysters are collected by a robot controlled by a visual recognition system. Interestingly the Norwegian company Oyster Catch is working on such a solution with robot harvest of oysters, with no or little harm of the seabed (Karlsen et al., 2021).

#### 4.4. Regulated commercial fishing for resource utilization and thinning of Pacific oysters

Initiatives for gentle fishery of Pacific oyster has been proposed in e.g., Denmark in the Wadden Sea and the Limfjord. The philosophy is to transform a problem into a possibility by using the Pacific oyster as a high-quality human food resource and simultaneously thinning the oyster population. However, such an initiative is challenged by conservation regulations. These regulations are related to international obligations i.e., conventions in the Wadden Sea listed by UNESCO as World Heritage or in Natura 2000, a network of core breeding and resting sites for rare and threatened bird species, and some rare natural habitat types which are protected, stretching across all 27 EU countries, both on land and at sea. The aim of the Natura 2000 network is to ensure the long-term survival of Europe's most valuable and threatened species and habitats, listed under both the EU Birds Directive and the Habitats Directive. We envision fisheries by very light gear primarily upon individual smaller oysters since they have far greater commercial value than those in larger aggregates or with damaged shells caused by heavy fishing gears. Also, the larger individual oysters are to some degree used as ingredient at restaurants, although this market is much smaller. The increased focus on 'Nordic food' will inevitably increase the market for Pacific oysters the coming years.

### 5. Innovative biological regulatory methods suggested for future management of Pacific oyster

#### 5.1. Systematic large-scale hand picking of Pacific oyster

It is well known that hand picking has an impact on Pacific oyster populations but most likely just on individuals still not incorporated in biogenic reefs. Hence, this regulation method is only valid for *M. gigas* populations not yet in reef structures i.e., only a fraction of the individuals. However, in relatively pristine habitats where the oyster recently has established itself, the populations are in fact characterized by solitary individuals or small clumps of oysters relatively easy to hand pick. Therefore, a systematic and thorough effort might contribute to decreasing the populations at an early stage in the local invasion, expansion phase (sensu Reise et al. 2016), before reef formation. It requires a systematic approach and cannot rely on a few tourists harvesting for their own needs. An upscaling could be arranged by a larger group of licensed personnel either volunteers or (semi)professionals subsidized by the government. The daily harvest could be hand sorted into size/quality categories and the fractions subject to sale to restaurants, retailers and to the food processing industry. As an example, a Danish consultancy company did a trial in summer 2021 where three student workers for three working days were hand picking oysters at a location where they naturally were dispersed as individuals on sandy-clayed substrate in the Limfjord. They obtained a total harvest of a value of >130,000 DKr equal to >17,000 Euro (pers. Comm. J.W. Nielsen, Aquamind A/S). Besides the authorities' permission for commercial hand picking in an area, another barrier is again the food safety regulations. In various countries it is stated that the producers need to check the areas for algae toxins, microbiology and pollutants and the cost of these tests may be too expensive for individual hand pickers. So, if the authorities pay for food safety checks, handpicking can be expanded. The authorities could even go one step further by paying a bounty on eradication, as is the case for Pythons in Florida (State of Florida, 2022).

#### 5.2. Triploid breeding of Pacific oyster

An effective way of preventing spread from aquaculture facilities of a given invasive species already established is to prevent its reproduction. Hence, one of the only effective strategies for obtaining lack of reproduction from open water facilities like Pacific oyster beds is to provide

sterile individuals. This will, besides favorizing energy allocation to flesh production on the cost of gamete production (Herbert et al., 2012), prevent or at least significantly reduce spread of propagules. Hence, by breeding diploid and tetraploid conspecifics result in triploidity, which lead to a significantly lower reproduction ranging <2% of their diploid fellow species (Herbert et al., 2016). Triploidity can also be obtained by use of certain chemicals but will result in a lower efficiency and risk of toxic side effects. Therefore, crossbreeding between diploid and tetraploid individuals is the common practice to obtain sterility (Kochmann et al., 2012). It seems, however, that the triploid condition is not obtaining a complete sterility besides a certain fraction of triploid individuals being able to produce viable gametes and their offspring becoming fertile over time. This may get into conflict with aims of nature reserves, however it requires further methodological development (see Herbert et al., 2012 for a brief review on the subject).

### 5.3. Good husbandry

Temperature and food availability i.e., phytoplankton are the main limiting factors for growth and reproduction of farmed Pacific oysters. However, conditions for fast growth and reproduction at the same time promote the risk of Pacific oyster bio invasions. From a producer's viewpoint the oyster farmers select a site for their facility ensuring good growth and management conditions. The optimal productions may conflict an optimized somatic growth and production of Pacific oysters, and at the same time by not inducing propagules to the ecosystem. One solution is to keep the oyster production at a site or a water depth, where the temperature does not allow for reproduction i.e., low temperature with the inevitable tradeoff of slower growth (Herbert et al., 2016). However, achieving such a delicate balance poses serious practical challenges and is probably not manageable in open water oyster production facilities.

### 5.4. Choke or starve the Pacific oysters by covering the reefs with sand/gravel

Generally, many species of bivalves are adapted to survive periodic hypoxia frequently occurring in estuaries, bays, and lagoons. The Pacific oyster is an oxyregulator over a wide range of oxygen concentrations with a critical threshold of about  $3 \text{ mg O}_2 \text{ l}^{-1}$  below which the metabolic depression occurs quickly and particularly in the summer (Le Mouillac et al., 2007). In addition, the Pacific oyster has a relatively limited anaerobic capacity (Meng et al., 2018). Therefore, choking might be an instrument worth exploring. To choke (and starve) Pacific oyster reefs by preventing them access to oxygen and nutrient rich seawater a layer of sand and gravel might be a solution in shallow waters and low energy locations. One can envision that a layer of e.g., 0.2 m on top of the reef will do the job if tide or wind stress leave the material in place for months. Estimating a density of sand and gravel of 1.6-ton pr.  $\text{m}^3$  require approximately 300 kg of material per square meter reef. As an example, is a sheltered intertidal reef in the Limfjord, Denmark consisting of 12,000  $\text{m}^2$  (1.2 ha) large clusters of bivalve beds (Holm et al., 2015). To cover that reef with a 0.2 m layer would require >3500 tons of sand/gravel. In case a trial should be conducted the coverage material might be provided by dredging pumps on a barge anchored close by the oyster reef. The Bell Cutter Dredger 250 (Bell Dredging Pumps, Netherlands) is an example of a large commercially available dredging pump operating with a maximum capacity of 250  $\text{m}^3$  dredged solids in dry volume  $\text{h}^{-1}$ . With this pump it would require at least 14 h and most likely 24 h of pumping to finish the job on the exemplified reef. The initiative requires renting of the equipment besides several workers to operate it leaving the proposed regulation tool very expensive, comparable to the expense of 20 boat hours per hectare when eradicating oysters by dredging (Wijsman et al., 2008). Moreover, to get the authority's permission seems not so straight forward hence, quite unlikely to realize. The tradeoff is of course analogue to dredging oysters that removing vast

amounts of bottom material change the bottom topography and habitat which is potentially harmful for the benthic inhabitants living where the sediment is pumped from to where it is deposited (Reise et al., 2010). Moreover, oysters continue to settle on the treated areas, similarly to dredging beds would need to be treated regularly maybe every 5–7 years (sensu Herbert et al., 2018).

### 5.5. Starve the Pacific oyster out by using competing suspension feeding native bivalves as a tool

The effects of complete starvation on biochemical composition and gametogenesis were investigated in the Pacific oyster over 90 d by Liu et al. (2010). The oysters apparently did not exhibit excess mortality compared to the well-fed control group even after three months of treatment. The starved oysters also exhibited gonad development, but the progress was significantly delayed. Glycogen was the first storage substrate to be depleted. While glycogen was rapidly used, protein and lipid contents decreased only gradually. A decrease in the RNA/DNA ratio in all tissues was observed during starvation, suggesting that RNA/DNA ratio (i.e., protein synthesis) can be used as an indicator for instantaneous growth rate and a valid indicator of nutritional condition. Liu et al. (2010) observed a significant increase in water and ash contents of the visceral parts and a corresponding decrease in *M. gigas* condition index were observed in the starved groups. During starvation, energy reserves were mobilized for survival and gonad development, but spawning was arrested. We hypothesize that these biochemical and physiological responses could be provoked by deliberately complicating or even preventing the oysters to feed in situ. Therefore, we propose a large-scale eradication or merely decimation strategy by starving out the reef dwelling Pacific oyster individuals by applying a thick top layer of its major food competitor, the native blue mussel *Mytilus edulis*. The blue mussels will harvest the available food (phytoplankton) leaving the oysters below in an almost particle free environment and in low energy areas also lower the oxygen levels. In high tide environments the abundance of Pacific oysters can reach >2500 individuals per square meter where the individuals are positioned upright (e.g., Reise et al., 2017a). Such habitats cannot come into play with this regulation instrument. Holm et al. (2015) recorded on a sheltered intertidal mussel bed co-existing Pacific oysters and blue mussels with an abundance of 40–50 Pacific oysters  $\text{m}^{-2}$  equal to approx. 65 g shell-free dry weight and approx. 1200 blue mussels  $\text{m}^{-2}$  equal to 475 g shell-free dry weight. Hence, a factor of seven more blue mussels than Pacific oysters. It means that the relative biomass of blue mussels must be way higher, possibly a factor of 10–15 the biomass of oysters, to show an effect. Moreover, it can be anticipated that the treatment must be long-term, probably an entire season, before the Pacific oysters are beaten back and have given up leaving the scene to the blue mussels as the winners of the food competition. However, unless oyster larvae are decimated simultaneously with phytoplankton by the blue mussels the oysters will continue to settle on the treated areas and like for dredging beds or sand/gravel covered beds, the treatment would need to be repeated maybe every 5–7 years (sensu Herbert et al., 2018). The chosen habitats for this regulation tool must be accessible with barges or other flat-bottomed vessels equipped with pumping- or grab devices to apply the mussels onto the oyster reef. In the process the reef of invasive Pacific oysters is transformed to a mussel bed of native *Mytilus edulis* not only depleting the food source but presumably also conducting larviphagy on oyster propagules (Troost et al., 2008). It should be realized that the method only works in shallow water low tide habitats where food availability beforehand is a major challenge for the filtering bivalve assemblages (sensu Vismann et al., 2016). The method will most likely not work in e.g., the Wadden Sea or other high energy habitats. In such areas other regulatory tools must be implemented.

## 6. Design of a manageable biological regulation strategy for Pacific oysters

One must aim realistically since in most places a complete eradication of *M. gigas* is not possible at the present state of invasion. Only preventive measures may be effective (Reise et al., 1999). Hence, regulation actions should only be implemented where it is subject to work. To obtain an effective regulation one must differentiate among methodologies tailored to the actual habitat, substrate, tide amplitude etc. Overall, adaptive management must follow a dual or even multifaceted regulation strategy where e.g., starvation by coverage with sediment or competitive bivalves, systematic hand picking, and even more actions implemented simultaneously could lead to a more sustainable condition. This is an extremely expensive maneuver but presumably lead to a situation where the Pacific oyster becomes less dominant in some (not all) of the most vulnerable, protected coastal ecosystems covered by (inter)national conventions (see Fig. 3).

## 7. Conclusion

Our question is if it is ecological beneficial to implement measures that control the distribution of Pacific oysters? Moreover, if it at all is possible to effectively regulate the Pacific oyster? After reviewing a large amount of scientific literature and discussing pro and cons within several aspects here, it appears that the functional ecology of *Magellana gigas* is not that different from native filtering bivalves. They occupy similar trophic function, and a large element of ecosystem redundancy can be argued. Moreover, biogenic ref. structures based on *M. gigas* most likely do not reduce but instead add to already existing biodiversity and help establish a balanced co-existence with native bivalves (sensu Eschweiler and Christensen, 2011). Hence, maybe a reconsideration of eradication ambitions and even aquaculture permissions should be discussed and thoroughly analyzed. What is less obvious, however, is what effects on higher trophic levels a large influx of the alien species might have on the predators e.g., birds. Therefore, a significant research effort is required here and possibly also in the understudied pathogenicity and parasitology associated with the Pacific oyster. Eradication, or less ambitiously a reduction of the species seems quite laborious and expensive. However, when facing international obligations for protecting designated habitats, it is most realistic to keep a low oyster presence in local and restricted areas, especially low tide shallow habitats. This, however, only in the early phases of an oyster invasion (expansion phase) where the species appear individually on the seabed not forming large aggregates, long time before reefs are formed in the adjustment phase of the invasion (sensu Reise et al., 2016). Later in the invasion succession when reaching a tipping point in population size, eradication and even decimation at established biogenic reefs requires vast resources. Hence, it is too late, which is why we recommend against it. In conclusion, we tend to argue that combatting the Pacific oyster is more a socioeconomic and political ambition than an ecological one.

## Declaration of competing interest

The authors declare no competing financial interests or personal relationships that could appear to influence the work reported in this paper.

## Data availability

Data will be made available on request.

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## References

- Agius, C., Jaccarini, V., Ritz, D.A., 1978. Growth trials of *Crassostrea gigas* and *Ostrea edulis* in inshore waters of Malta (Central Mediterranean). *Aquaculture* 15, 195–218.
- Andersen, J.H., Knudsen, S.W., Murray, C., Carl, H., Møller, P.R., Hesselsoe, M., 2021. Ikke-hjemmehørende arter i marine områder. ISBN 978-82-577-7394-6 NIVA-rapport ISSN 1894-7948 RAPPORT L.NR. 7658-2021, 59 pp. (In Danish).
- Anglès d'Auriac, M.B., Norling, P., Rinde, E., 2016. A rapid and inexpensive DNA extraction protocol for oysters. *Anim. Genet.* 47 (3), 389–390.
- Anglès d'Auriac, M.B., Rinde, E., Norling, P., Lapègue, S., Staalstrøm, A., Hjermmann, D. Ø., Thaulow, J., 2017. Rapid expansion of the invasive oyster *Crassostrea gigas* at its northern distribution limit in Europe: naturally dispersed or introduced? *PLoS One* 12 (5), e0177481.
- Antonio, I.G., Camacho, A.P., 2019. Reproduction of the introduced oyster *Crassostrea gigas* (Bivalvia: Ostreidae) cultured on rafts in Spain. *Acta Zool.* 100, 257–267.
- Ashton, I., 2001. *Crassostrea gigas* invades marine reserves in San Juan Island. In: 2nd International Conference on Marine Bioinvasions, 9–11 April 2001, New Orleans, LA, Abstracts. MIT Sea Grant Center for Coastal Resources. Available online at: <http://massbay.mit.edu/exoticspecies/conferences/2001/abstracts01>.
- Aydin, M., Gül, M., 2021. Presence of the Pacific oyster (*Crassostrea gigas* Thunberg, 1793) in the Black Sea. *J. Anatolian Environm. Animal Sci.* 1, 14–17.
- Ayres, P., 1992. Introduced Pacific oyster in Australia. In: Leffler, M., Greer, J. (Eds.), *In the Ecology of Crassostrea gigas in Australia, New Zealand, France and Washington state*. University of Maryland Sea Grant publication UM-SG-TS-92.07, Maryland Sea Grant College, College Park, MD, pp. 3–7, 25 pp.
- Bayne, B.L., Ahrens, M., Allen, S.K., Anglès d'Auriac, M., Bäckeljau, T., Beninger, P., Bohn, R., Boudry, P., Davis, J., Green, T., Guo, X., Hedgecock, D., Ibarra, A., Kingsley-Smith, P., Krause, M., Langdon, C., Lapègue, S., Li, C., Manahan, D., Mann, R., Perez-Paralle, L., Powell, E.N., Rawson, P.D., Speiser, D., Sanchez, J.L., Shumway, S., Wang, H., 2017. The proposed dropping of the genus *Crassostrea* for all Pacific cupped oysters and its replacement by a new genus *Magallana*: a dissenting view. *J. Shellfish Res.* 36 (3), 545–547.
- Beck, M.W., Brumbaugh, R.D., Airoidi, L., Carranza, A., Coen, L.D., Crawford, C., Defeo, O., Edgar, G.J., Hancock, B., Kay, M., Lenihan, H., Luckenbach, M.W., Toropova, C.L., Zhang, G., 2009. Shellfish reefs at risk: a global analysis of problems and solutions. In: *The Nature Conservancy, Arlington VA*, 52 pp. <https://www.conservationgateway.org/ConservationPractices/Marine/Documents/Shellfish%20Reefs%20at%20Risk-06.18.09-Pages.pdf>.
- Blake, J.A., 2001. Shellfish culture as a vector for biological invasions. In: 2nd International Conference on Marine Bioinvasions, 9–11 April 2001, New Orleans, LA, Abstracts. MIT Sea Grant Center for Coastal Resources. Available online at: <http://massbay.mit.edu/exoticspecies/conferences/2001/abstracts01>.
- Boltovskoy, D., Sylvestre, F., Paolucci, E.M., 2018. Invasive species denialism: Sorting out facts, beliefs, and definitions. *Ecol. Evol.* 8, 11190–11198. <https://doi.org/10.1002/ece3.4588>.
- Bordignon, F., Zomeno, C., Xiccatoc, G., Biroloc, M., Pascuala, A., Trocinoa, A., 2020. Effect of emersion time on growth, mortality and quality of Pacific oysters (*Crassostrea gigas*, Thunberg 1793) reared in a suspended system in a lagoon in northern Italy. *Aquaculture* 528, 735481.
- Borsje, B.W., van Wesenbeeck, B.K., Dekker, F., Paalvast, P., Bouma, T.J., van Katwijk, M.M., de Vries, M.B., 2011. How ecological engineering can serve in coastal protection. *Ecol. Eng.* 37, 113–122.
- Burioli, A.V., Varello, K., Trancart, S., Bozzetta, E., Gorla, A., Preato, M., Houssin, M., 2018. First description of a mortality event in adult Pacific oysters in Italy associated with infection by a *Tenacibaculum soleae* strain. *J. Fish Dis.* 41, 215–221.
- Buschbaum, C., Cornelius, A., Goedknecht, M.A., 2016. Deeply hidden inside introduced biogenic structures – Pacific oyster reefs reduce detrimental barnacle overgrowth on native blue mussels. *J. Sea Res.* 117, 20–26.
- Büttger, H., Nehls, G., Witte, S., 2011. High mortality of Pacific oysters in a cold winter in the north-Frisian Wadden Sea. *Helgol. Mar. Res.* 65, 525–532.
- CABI, 2022. *Invasive Species Compendium*. <https://www.cabi.org/isc/>. Visited 08-03-2022.
- Cadee, G.C., 2008a. Oystercatchers *Haematopus ostralegus* cathing Pacific oysters *Crassostrea gigas*. *Basteria* 72, 25–31.
- Cadee, G.C., 2008b. Herring gulls feeding again on Pacific oysters *Crassostrea gigas* in the Dutch Wadden Sea near Texel. *Basteria* 72, 33–36.
- Cardigos, F., Monteiro, J., Fontes, J., Parretti, P., Santos, R.S., 2015. Ch 12 fighting invasions in the marine realm, a case study with *Caulerpa webbiana* in the Azores. In: Canning-Clode, João (Ed.), *Biological Invasions in Changing Ecosystems. Vectors, Ecological Impacts, Management and Predictions*, pp. 279–300. ISBN: 9783110438659.
- Cardoso, A.F.M.F., Peralta, N.R.E., Machado, J.P., van der Veer, H.W., 2013. Growth and reproductive investment of introduced Pacific oysters *Crassostrea gigas* in southern European waters. *Estuar. Coast. Shelf Sci.* 118, 24–30.
- Cassini, M.H., 2020. A review of the critics of invasion biology. *Biol. Rev.* 95, 1467–1478.
- Çevik, C., Öztürk, B., Buzzuro, G., 2001. The presence of *Crassostrea virginica* (Gmelin, 1791) and *Saccostrea commercialis* (Iredale and Roughley, 1933) in the eastern Mediterranean Sea. *La Conchiglia* 32 (298), 25–28.
- Christiansen, M.J.A., Lengkeek, W., Bergsma, J.H., Coolen, J.W.P., Didderen, K., Dorenbosch, M., Driessen, F.M.F., Kamermans, P., Reuchlin-Hugenholtz, E., Sas, H., Smaal, A., van den Wijngaard, K.A., van der Have, T.M., 2018. Return of the native facilitated by the invasive? Population composition, substrate preferences and

- epibenthic species richness of a recently discovered shellfish reef with native European flat oysters (*Ostrea edulis*) in the North Sea. *Mar. Biol. Res.* 14, 590–597.
- Council Regulation (EC) No 708/2007 of 11 June 2007 concerning use of alien and locally absent species in aquaculture, 2022. OJ L 168, 28.6.2007, p. 1–17 (BG, ES, CS, DA, DE, ET, EL, EN, FR, IT, LV, LT, HU, MT, NL, PL, PT, RO, SK, SL, FI, SV) Special edition in Croatian: Chapter 04 Volume 003 P. 112–128 In force: This act has been changed. Current consolidated version: 24/04/2011. ELL <http://data.europa.eu/eli/reg/2007/708/oj>.
- Coutteau, P., Coolsaet, N., Caers, M., Bogaert, P., De Clerck, R., 1997. Re-introduction of oyster cultivation in the sluice-dock in Ostend, Belgium. *J. Shellfish Res.* 16 (1), 262.
- Crocetta, F., 2011a. Marine alien Mollusca in Italy: a critical review and state of the knowledge. *J. Mar. Biol. Assoc. U. K.* 92 (6), 1357–1365.
- Crocetta, F., 2011b. Marine alien Mollusca in the Gulf of Trieste and neighbouring areas: a critical review and state of knowledge (updated in 2011). *Acta Adriat.* 52 (2), 247–260.
- Dankers, N.M.J.A., Dijkman, E.M., de Jong, M.L., de Kort, G., Meijboom, A., 2004. De verspreiding en uitbreiding van de Japanse Oester in de Nederlandse Waddenzee. - Alterra-rapport 909: 51 pp [in German].
- Davis, M.A., Chew, M.K., Hobbs, R.J., Lugo, A.E., Ewel, J.J., Vermeij, G.J., Brown, J.H., Rosenzweig, M.L., Gardener, M.R., Carroll, S.P., Thompson, K., Pickett, S.T.A., Stromberg, J.C., Tredici, P.D., Suding, K.N., Ehrenfeld, J.G., Grime, J.P., Mascaro, J., Briggs, J.C., 2011. Don't judge species on their origins. *Nature* 474, 153–154.
- De Mesel, I., Kerckhof, F., Norro, A., Rumes, B., Degraer, S., 2015. Succession and seasonal dynamics of the epifauna community on offshore wind farm foundations and their role as steppingstones for non-indigenous species. *Hydrobiologia* 756, 37–50.
- Diederich, S., Nehls, G., van Beusekom, J.E.E., Reise, K., 2005. Introduced Pacific oysters (*Crassostrea gigas*) in the northern Wadden Sea: invasion accelerated by warm summers? *Helgol. Mar. Res.* 59, 97–106.
- Dolmer, P., Holm, M.W., Strand, Å., Lindgarth, S., Bodvin, T., Norling, P., Mortensen, S., 2014. The Invasive Pacific Oyster, *Crassostrea gigas*, in Scandinavian Coastal Waters: A Risk Assessment on the Impact in Different Habitats and Climate Conditions. *Fisken og havet, Rapport*, pp. 2–2014, 67 pp. (ISSN 1894-5031).
- Drinkwaard, A.C., 1999. Introductions and developments of oysters in the North Sea area: a review. *Helgoländer Meeresun.* 52, 301–308.
- Dutertre, M., Beninger, P.G., Barillé, L., Papin, M., Haure, J., 2010. Rising water temperatures, reproduction, and recruitment of an invasive oyster, *Crassostrea gigas*, on the French Atlantic coast. *Mar. Environ. Res.* 69, 1–9.
- Ecoshape, 2022. Oyster reefs. <https://www.ecoshape.org/en/pilots/oyster-reefs/>. Visited 03-08-2022.
- Eklund, U., Håkansson, M., Haamer, J., 1977. En undersökning om förutsättningarna för ostron-odling vid svenska västkusten. In: Report B83. Department of Geology, Chalmers University of Technology and University of Gothenburg, 35 pp. [in Swedish].
- Elia, A.C., Burioli, E., Magara, G., Pastorino, P., Caldaroni, B., Menconi, V., Dörra, A.J.M., Colombo, G., Abete, M.C., Prearo, M., 2020. Oxidative stress ecology on Pacific oyster *Crassostrea gigas* from lagoon and offshore Italian sites. *Sci. Total Environ.* 739, 139886.
- Elnais, 2014. Hellenic Network for Aquatic Alien Species. <https://elnais.hcmr.gr/elnaidatabase/>. Visited 07-03-2022.
- Escapa, M., Isach, J.P., Daleo, P., Alberti, J., Iribarne, O., Borges, M., Dos Santos, E.P., Gagliardini, D.A., Lasta, M., 2004. The distribution and ecological effects of the introduced Pacific oyster *Crassostrea gigas* (Thunberg, 1793) in northern Patagonia. *J. Shellfish Res.* 23 (3), 765–772.
- Eschweiler, N., Christensen, H.T., 2011. Trade-off between increased survival and reduced growth for blue mussels living on Pacific oyster reefs. *J. Exp. Mar. Biol. Ecol.* 403, 90–95.
- Ewers-Saucedo, C., Heuer, N., Moesges, Z., Ovenbeck, K., Schröter, N., Brandis, D., 2020. First record of the Pacific oyster *Magallana gigas* (Thunberg, 1793) in the Baltic Sea proper. *Mar. Biodivers. Rec.* 13, 9. <https://doi.org/10.1186/s41200-020-00193-2>.
- Ezgeta-Balić, D., Segvić-Bubić, T., Stagličić, N., Lin, Y., Varezić, D.B., Grubišić, L., Briski, E., 2019. Distribution of non-native Pacific oyster *Magallana gigas* (Thunberg, 1793) along the eastern Adriatic coast. *Acta Adriat.* 60 (2), 137–146.
- Ezgeta-Balić, D., Radonić, I., Bojanić Varezić, D., Zorica, B., Arapov, J., Stagličić, N., Jozić, S., Peharda, M., Briski, E., Lin, Y., Segvić-Bubić, T., 2020. Reproductive cycle of a non-native oyster, *Crassostrea gigas*, in the Adriatic Sea. *Mediterr. Mar. Sci.* 21 (1), 146–156.
- Fabivoux, C., Huvet, A., Lapègue, S., Heurtebise, S., Boudry, P., 2020. Past and present geographical distribution of populations of Portuguese (*Crassostrea angulata*) and Pacific (*C. gigas*) oysters along the European and north African Atlantic coasts. *Haliotis* 31, 33–44.
- FAO, 2021. The State of World Fisheries and Aquaculture 2020. Sustainability in Action. Rome. <https://doi.org/10.4060/ca9229en>.
- Shellfish reef habitats: A synopsis to underpin the repair and conservation of Australia's environmentally, socially, and economically important bays and estuaries. In: Gillies, C.L., Creighton, C., McLeod, I.M. (Eds.), 2015. Report to the National Environmental Science Programme, Marine Biodiversity Hub. Centre for Tropical Water and Aquatic Ecosystem Research (TropWATER). Publication, James Cook University, Townsville, 68 pp.
- Goedknecht, M.A., 2017. Pacific Oysters and Parasites: Species Invasions and their Impact on Parasite-Host Interactions, 271 pp. PhD thesis. Vrije Universiteit Amsterdam, Holland.
- Gökçek, E.Ö., Acarlı, S., Karahan, B., Vural, P., Baştanlar, E.K., 2020. First molecular record of the alien species Pacific oyster (*Crassostrea gigas*, Thunberg 1793) in the Marmara Sea, Turkey. *Mar. Sci. Tech. Bull.* 9 (1), 23–31.
- Gonzalez, J.A., Coombes, M.A., Palomo, M.G., Isla, F.I., Soria, S.A., Gutiérrez, J.L., 2021. Enhanced weathering and Erosion of a cohesive shore platform following the experimental removal of mussels. *Front. Mar. Sci.* 8, 756016 <https://doi.org/10.3389/fmars.2021.756016>.
- Gouilletquer, P., 1997. Cycle de reproduction naturelle de l'huître creuse *Crassostrea gigas*. In: La reproduction naturelle et contrôlée des Bivalves cultivés en France, Nantes (France), 14–15 November 1995, pp. 7–19. Ifremer Rapport Interne DRV/RA/RST/97–11 RA /Brest. [in French].
- Gouilletquer, P., Bachelet, G., Sauriau, P.G., Noel, P., 2002. Open Atlantic coast of Europe: a century of introduced species into French waters. In: Leppäkoski, E., Gollasch, S., Olenin, S. (Eds.), *Invasive Aquatic Species in Europe: Distribution, Impacts and Management*. Kluwer Academic Publishers, Dordrecht, pp. 276–290, 583 pp.
- Graham, P., Brundu, G., Scolamacchia, M., Giglioli, A., Addis, P., Artioli, Y., Telfer, T., Carboni, S., 2020. Improving pacific oyster (*Crassostrea gigas*, Thunberg, 1793) production in Mediterranean coastal lagoons: validation of the growth model "ShellSIM" on traditional and novel farming methods. *Aquaculture* 516 article no. 734612. ISSN 0044-8486.
- Grizel, H., Héral, M., 1991. Introduction into France of the Japanese oyster (*Crassostrea gigas*). *J. Cons. Int. Explor. Mer* 47, 399–403.
- Gutow, L., Buschbaum, C., 2019. Invasion of the Wadden Sea by the Pacific oyster (*Magallana gigas*): a risk to ecosystem services? In: Schröter, et al. (Eds.), *Atlas of Ecosystem Services*. Chapter 36, 233–235. Eprint ID 49023. <https://hdl.handle.net/10013/epic.4c3c2784-1752-4fc0-924c-e35881f54fb0>.
- Guy, C., Roberts, D., 2010. Can the spread of non-native oysters (*Crassostrea gigas*) at the early stages of population expansion be managed? *Mar. Pollut. Bull.* 60, 1059–1064.
- Hansen, B.W., 2022. Two tropical marine copepods demonstrate physiological properties needed for mass production. *Revi. Fisheries Sci. Aquacult.* <https://doi.org/10.1080/23308249.2022.2095198> (In press).
- Herbert, R.J.H., Roberts, C., Humphreys, J., Fletcher, S., 2012. The Pacific Oyster (*Crassostrea gigas*) in the U.K.: Economic, Legal and Environmental Issues Associated with its Cultivation, Wild Establishment and Exploitation. Report for the Shellfish Association of Great Britain, 166 pp. [www.shellfish.org.uk](http://www.shellfish.org.uk).
- Herbert, R.J.H., Humphreys, J., Davies, C.J., Roberts, C., Fletcher, S., Crowe, T.P., 2016. Ecological impacts of non-native Pacific oysters (*Crassostrea gigas*) and management measures for protected areas in Europe. *Biodivers. Conserv.* 25, 2835–2865.
- Herbert, R.J.H., Davies, C.J., Bowgen, K.M., Hutton, J., Stillman, R.A., 2018. The importance of nonnative Pacific oyster reefs as supplementary feeding areas for coastal birds on estuary mudflats. *Aquatic Conserv. Mar. Freshw. Ecosyst.* 28, 1294–1307.
- His, E., Robert, R., Dinet, A., 1989. Combined effects of temperature and salinity on fed and starved larvae of the Mediterranean mussel *Mytilus galloprovincialis* and the Japanese oyster *Crassostrea gigas*. *Mar. Biol.* 100, 455–463.
- Hjalager, A.-M., Kwiatkowski, G., Larsen, M.O., 2018. Innovation gaps in Scandinavian rural tourism. 2018. *Scand. J. Hosp. Tour.* 18 (1), 1–17.
- Hjalager, A.M., Dolmer, P., Hansen, L.A., 2019. Tourists' foraging for oysters: a governance innovation perspective. *J. Gastronomy/Tourism* 3 (1), 67–80. ISSN: 2169-2971. <https://doi.org/10.3727/216929718X15193195617827>.
- Hollander, J., Blomfeldt, J., Carlsson, P., Strand, Å., 2015. Effects of the alien Pacific oyster (*Crassostrea gigas*) on subtidal macrozoobenthos communities. *Mar. Biol.* 162, 547–555.
- Holm, M.W., Davids, J.K., Dolmer, P., Vismann, B., Hansen, B.W., 2015. Moderate establishment success of Pacific oyster, *Crassostrea gigas*, on a sheltered intertidal mussel bed. *J. Sea Res.* 104, 1–8.
- Holm, M.W., Davids, J.K., Dolmer, P., Hansen, T.H.H., Vismann, B., Hansen, B.W., 2016. Coexistence of the invasive Pacific oyster, *Crassostrea gigas*, and the native blue mussel, *Mytilus edulis*, in a sheltered intertidal area in the Limfjord, Denmark, population structure. *Aquat. Inv.* 11, 155–165.
- Huvert, A., Fabivoux, C., McCombie, H., Lapègue, S., Boudry, P., 2004. Natural hybridization between genetically differentiated populations of *Crassostrea gigas* and *C. angulata* highlighted by sequence variation in flanking regions of a microsatellite locus. *Mar. Ecol. Prog. Ser.* 272, 141–152.
- Iceland review, 2018. Icelandic Oysters Coming to Reykjavík Restaurants. <https://www.icelandreview.com/culture/icelandic-oysters-coming-reykjavik-restaurants/>.
- Iglesias, D., Rodríguez, L., Gómez, L., Azevedo, C., Montes, J., 2012. Histological survey of Pacific oysters *Crassostrea gigas* (Thunberg) in Galicia (NW Spain). *J. Invertebr. Pathol.* 111, 244–251.
- Jennings, S., Kaiser, M.J., 1998. The effects of fishing on marine ecosystems. *Adv. Mar. Biol.* 34, 201–352.
- Jensen, K.R., Knudsen, J., 2005. A summary of alien marine benthic invertebrates in Danish waters. *Oceanological and Hydrobiological studies*, 34. Suppl. 1, 137–162.
- Jones, M.C., Dye, S.R., Pinnegar, J.K., Warren, R., Cheung, W.W.L., 2013. Applying distribution model projections for an uncertain future: the case of the Pacific oyster in UK waters. *Aquatic Conserv. Mar. Freshw. Ecosyst.* 23, 710–722.
- Karlsen, O.M., Mørland, K., Midtstøl, F., 2021. Oyster catch. <https://oystercatch.no>.
- Katsanevakis, S., Zenetos, A., Mačić, V., Beqiraj, S., Poursanidis, D., Kashta, L., 2011. Invading the Adriatic: spatial patterns of marine alien species across the Ionian-Adriatic boundary. *Aquat. Biol.* 13, 107–118.
- Kaufmann, M.J., Seamann, M.N.L., Andrade, C., Buchholtz, C., 1994. Survival, growth, and glycogen content of pacific oysters, *Crassostrea gigas* (Thunberg 1793) at Madeira Island (subtropical Atlantic). *J. Shellfish Res.* 13, 503–505.
- Kerckhof, F., Haelters, J., Gollasch, S., 2007. Alien species in the marine and brackish ecosystem: the situation in Belgian waters. *Aquat. Invasions* 2 (3), 243–257.
- King, W.L., Jenkins, C., Go, J., Siboni, N., Seymour, J.R., Labbate, M., 2019. Characterisation of the Pacific oyster microbiome during a summer mortality event. *Microb. Ecol.* 77, 502–512.

- King, N.G., Wilmes, S.B., Smyth, D., Tinker, J., Robins, P.E., Thorpe, J., Jones, L., Malham, S.K., 2021. Climate change accelerates range expansion of the invasive non-native species, the Pacific oyster, *Crassostrea gigas*. *ICES J. Mar. Sci.* 78 (1), 70–81.
- Kochmann, J., Carlsson, J., Crowe, T.P., Mariani, S., 2012. Genetic evidence for the uncoupling of local aquaculture activities and a population of an invasive species—a case study of Pacific oysters (*Crassostrea gigas*). *J. Heredity* 103 (5), 661–671.
- Kochmann, J., O'Beirn, F., Yearsley, J., Crowe, T.P., 2013. Environmental factors associated with invasion: modelling occurrence data from a coordinated sampling programme for Pacific oysters. *Biol. Invasions* 15, 2265–2279.
- Krapal, A.-M., Ioniță, M., Caplan, M., Buhaciu-Ioniță, E., 2019. Wild Pacific oyster *Magallana gigas* (Thunberg, 1793) populations in Romanian Black Sea waters – friend or foe? *Travaux du Muséum National d'Histoire Naturelle "Grigore Antipa"* 62 (2), 175–183. <https://doi.org/10.3897/travaux.62.e49074>.
- Kristensen, P.S., 1989. Mussel and oyster culture in Denmark. In: De Pauw, E., Jaspers, H., Ackerfors, N., Wilkins (Eds.), *Aquaculture—A Biotechnology in Progress*. European Aquaculture Society, Bredene, Belgium, pp. 342–350. ISBN 90-71625-03-6.
- Lagarde, F., Roque D'orbcastel, E., Ubertini, M., Mortreux, S., Bernard, I., Fiandrino, A., Chiantella, C., Bec, B., Roques, C., Bonnet, D., Miron, G., Richard, M., Pouvreau, S., Lett, C., 2017. Recruitment of the Pacific oyster *Crassostrea gigas* in a shellfish-exploited Mediterranean lagoon: discovery, driving factors and a favorable environmental window. *Mar. Ecol. Prog. Ser.* 578, 1–17.
- Lallias, D., Boudry, P., Batista, F.M., Beaumont, A., King, J.W., Turner, J.R., Lapègue, S., 2015. Invasion genetics of the Pacific oyster *Crassostrea gigas* in the British Isles inferred from microsatellite and mitochondrial markers. *Biol. Invasions* 17, 2581–2595.
- Laugen, A.T., Hollander, J., Obst, M., Strand, Å., 2015. The Pacific Oyster (*Crassostrea gigas*) Invasion in Scandinavian Coastal Waters: Impact on Local Ecosystem Services. In: *Biological Invasions in Changing Ecosystems. Vectors, Ecological Impacts, Management and Predictions* Edited by: João Canning-Clode, ISBN 9783110438659, pp. 230–252.
- Le Moullac, G., Quéau, I., Le Souchu, P., Pouvreau, S., Moal, J., Le Coz, J.R., Samain, J.F., 2007. Metabolic adjustments in the oyster *Crassostrea gigas* according to oxygen level and temperature. *Mar. Biol. Res.* 3, 357–366.
- Lebbe, T.B., Rey-Valette, H., Chaumillon, É., Camus, G., Almar, R., Cazenave, A., Claudet, J., Rocle, N., Meur-Férec, C., Viard, F., Mercier, D., Dupuy, C., Ménard, F., Rossel, B.A., Mullineux, L., Sicre, M.-A., Zivian, A., Gaill, F., Etuzen, A., 2021. Designing coastal adaptation strategies to Tackle Sea level rise. *Front. Mar. Sci.* 8, 740602 <https://doi.org/10.3389/fmars.2021.740602>.
- Leppäkoski, E., Gollasch, S., Gruszka, P., Ojaveer, H., Olenin, S., Panov, V., 2002. The Baltic—A Sea of invaders. *Can. J. Fish. Aquat. Sci.* 59, 1175–1188.
- Lipej, L., Mavrič, B., Orlando-Bonaca, M., Malej, A., 2012. State of the art of the marine non-indigenous flora and fauna in Slovenia. *Mediterr. Mar. Sci.* 13 (2), 243–249.
- Liu, W., Li, Q., Gao, F., Kong, L., 2010. Effect of starvation on biochemical composition and gametogenesis in the Pacific oyster *Crassostrea gigas*. *Fish. Sci.* 76, 737–745.
- López-Sanmartín, M., López-Fernández, J.R., Cunha, M.E., De la Herrán, R., Navas, J.I., 2016. Ostreid herpesvirus in wild oysters from the Huelva coast (SW Spain). *Dis. Aquat. Org.* 120, 231–240.
- Markert, A., Wehrmann, A., Kröncke, I., 2010. Recently established *Crassostrea*-reefs versus native *Mytilus*-beds: differences in ecosystem engineering affects the macrofaunal communities (Wadden Sea of Lower Saxony, southern German bight). *Biol. Invasions* 12, 15–32.
- Martínez-García, M.F., Ruesink, J.L., Grijalva-Chon, J.M., Lodeiros, C., Arreola-Lizárraga, J.A., de la Re-Vega, E., Varela-Romero, A., Chávez-Villalba, J., 2021. Socioecological factors related to aquaculture introductions and production of Pacific oysters (*Crassostrea gigas*) worldwide. *Rev. Aquac.* 00, 1–17. <https://doi.org/10.1111/raq.12615>.
- Mavrič, L.L.B., Orlando-Bonaca, M., Malej, A., 2012. State of the art of the marine non-indigenous Flora and Fauna in Slovenia. *Mediterr. Mar. Sci.* 13 (2), 243–249.
- MBLIS, 2019. The oyster farmers must stop cultivating. <https://www.mbl.is/200milur/fretir/2019/08/07/ostrebaendurnir-thurfa-ad-haetta-raekt/>.
- McAfee, D., Connell, S.D., 2021. The global fall and rise of oyster reefs. *Front. Ecol. Environ.* 19 (2), 118–125. <https://doi.org/10.1002/fee.2291>.
- McKenzie, C.L., Lopez, A., 1997. Molluscan fisheries of Nicaragua. In: McKenzie Jr., C.L., Burnell Jr., V.G., Rosenfield, A., Hobart, W.L. (Eds.), *The History, Present Condition, and Future of the Molluscan Fisheries of North, and Central America and Europe*, vol. 2, pp. 19–32.
- McKenzie, C.L., Burrell, V.G., Rosenfield, A., Hobart, W.L., 1997. *The History, Present Condition, and Future of the Molluscan Fisheries of North and Central America and Europe*, Volume 2, Pacific Coast and Supplemental Topics, 128. U.S. Dep. Commer., NOAA Tech. Rep. NMFS (217 p).
- McKnight, W., Chudleigh, J.J., 2015. Pacific oyster *Crassostrea gigas* control within the inter-tidal zone of the north East Kent marine protected areas, UK. *Conserv. Evid.* 12, 28–32.
- MedMIS, 2022. *Crassostrea gigas* - Invasive Alien Species Fact Sheet for Mediterranean Network of MPAs. From Online Database MedMIS (IUCN Center for Mediterranean Cooperation). Download date 11/02/2022.
- Meng, J., Wanga, T., Lia, L., Zhang, G., 2018. Inducible variation in anaerobic energy metabolism reflects hypoxia tolerance across the intertidal and subtidal distribution of the Pacific oyster (*Crassostrea gigas*). *Mar. Environ. Res.* 138, 135–148.
- Micu, D., 2004. Annotated checklist of the marine Mollusca from the Romanian Black Sea. In: Ozturk, B., Mokievsky, V.O., Topaloglu, B. (Eds.), *International Workshop on Black Sea Benthos*, 18–23 April 2004. Turkish Marine Research Foundation, Istanbul, pp. 84–149.
- Mikac, B., Tarullo, A., Colangelo, M.A., Abbiati, M., Costantini, F., 2021. Shell infestation of the farmed Pacific oyster *Magallana gigas* by the Endolith bivalve *Roccellaria dubia*. *Diversity* 13, 526.
- Miossec, L., Le Deuff, R.-M., Goulletquer, P., 2009. Alien species alert: *Crassostrea gigas* (Pacific oyster). In: *ICES Cooperative Research Report No. 299*, 42 pp. (ISBN 978-87-7482-069-7).
- Mitov, P., Uzunova, S., Kenderov, L., Dimov, S., Yanachkov, P., 2020. Pacific oyster invasion along Bulgarian Black Sea coast <https://www.uni-sofia.bg/bul/file> E&SD-15.
- Moehler, J., Wegner, K.M., Reise, K., Jacobsen, S., 2011. Invasion genetics of Pacific oyster *Crassostrea gigas* shaped by aquaculture stocking practices. *J. Sea Res.* 66, 256–262.
- Molares, J., Pascual, C., Quintana, R., 1986. Análisis de los factores determinantes de la producción de la ostra – *Crassostrea gigas* – cultivada en las rías gallegas. *Alimentaria* 172, 27–33 (in Spanish).
- Mortensen, S.H., 1993. Health survey of selected stocks of commercially exploited Norwegian bivalve molluscs. *Dis. Aquat. Org.* 16, 149–156.
- Mortensen, S., Strand, Å., Bodvin, T., Alfjorden, A., Skår, C.K., Jelmert, A., Aspán, A., Sælemyr, L., Naustvoll, L.-J., Albreten, J., 2016. Summer mortalities and detection of ostreid herpesvirus microvariant in Pacific oyster *Crassostrea gigas* in Sweden and Norway. *Dis. Aquat. Org.* 117, 171–176.
- Mortensen, S., Strand, Å., Holm, M.W., Dolmer, P., 2017. Effects of a bio-invasion of the Pacific oyster, *Crassostrea gigas* (Thunberg, 1793) in five shallow water habitats in Scandinavia. *Man. Biol. Inv.* 8, 543–552.
- Mortensen, S., Laugen, A.T., Strand, Å., Dolmer, P., Naustvoll, L.J., Jelmert, A., Albertsen, J., Broström, G., Gustafsson, M., Durkin, A., Khogyane, S.E., Partoft, H., Bøgwald, M., 2022. Stillehavstøsters i Norden: Bestandsutvikling, overvåking og forvaltning. Nordic Council of Ministers. <https://pub.norden.org/temaor/d2022-504> (in Norwegian).
- Mosca, F., Tiscar, P.G., Hattab, J., D'Antonuo, A.M., D'Onofrio, D., Arcangeli, G., Vetri, A., Bertolini, C., Pastres, R., 2021. *Crassostrea gigas* (Thunberg 1793) cultivation in southern Adriatic Sea (Italy): a one-year monitoring study of the oyster health. *Aquac. Res.* 52, 2879–2890.
- Nehls, G., Diederich, S., Thielgtes, D.W., Strasser, M., 2006. Wadden Sea mussel beds invaded by oysters and slipper limpets: competition or climate control? *Helgol. Mar. Res.* 60, 135–143.
- Nehring, S., 2006. Four arguments why so many alien species settle into estuaries, with special reference to the German river Elbe. *Helgol. Mar. Res.* 60, 127–134.
- Nehring, S., 2011. NOBANIS – Invasive Alien Species Fact Sheet – *Crassostrea gigas*. – From: Online Database of the European Network on Invasive Alien Species - NOBANIS. [www.nobanis.org](http://www.nobanis.org). Date of access 22/02/2022.
- Nielsen, M., Hansen, B.W., Vismann, B., 2017. Feeding traits of the European flat oyster, *Ostrea edulis*, and the invasive Pacific oyster, *Crassostrea gigas*. *Mar. Biol.* 164, 1–10.
- Nielsen, P., Geitner, K., Jakobsen, J., Köppl, C.J., Petersen, J.K., 2018. Fagligt grundlag for forvaltningsplan for udvikling af bæredygtige fiskerier af muslinger og østers i Vadehavet. DTU Aqua-rapport nr. 334. Institut for Akvatisk Ressourcer, Danmarks Tekniske Universitet (33 pp. + bilag. in Danish).
- NOAA Fisheries, 2022. Oyster reef habitat. <https://www.fisheries.noaa.gov/national/habitat-conservation/oyster-reef-habitat>.
- Orban, E., Di Lena, G., Masci, M., Navigato, T., Casini, I., Caproni, R., Gambelli, L., Pellizzato, M., 2004. Growth, nutritional quality and safety of oysters (*Crassostrea gigas*) cultured in the lagoon of Venice (Italy). *J. Sci. Food Agric.* 84, 1929–1938.
- Orensanz, J.M., Schwindt, E., Pastorino, G., Bortolus, A., Casas, G., Darrigran, G., Elias, R., et al., 2002. No longer the pristine confines of the world ocean: a survey of exotic marine species in the southwestern Atlantic. *Biol. Invasions* 4, 115–143.
- Paavola, M., Olenin, S., Leppäkoski, E., 2005. Are invasive species most successful in habitats of low native species richness across European brackish water seas? *Estuar. Coast. Shelf Sci.* 64, 738–750.
- Petović, S., Marković, O., Durović, M., 2019. Inventory of non-indigenous and cryptogenic marine benthic species of the south-East Adriatic Sea, Montenegro. *Acta Zool. Bulgaria* 71 (1), 47–52.
- Powell, E., Klinck, J., Hofmann, E., Bochenek, E., 2000. Food quality and feeding strategies in hatchery rearing of Pacific oyster *Crassostrea gigas* larvae: a modelling approach. *J. Shellfish Res.* 1, 604.
- Powell, E.N., Bochenek, E.A., Klinck, J.M., Hofmann, E.E., 2002. Influence of food quality and quantity on the growth and development of *Crassostrea gigas* larvae: a modeling approach. *Aquaculture* 210, 89–117.
- Regulation (EU) No 1143/2014 Of The European Parliament And Of The Council of 22 October 2014 on the prevention and management of the introduction and spread of invasive alien species The European Parliament And The Council Of The European Union. <https://eur-lex.europa.eu/legal-content/EN/TXT/PDF/?uri=CELEX:32014R1143&rid=5>.
- Reise, K., 1998. Pacific oysters invade mussel beds in the European Wadden Sea. *Senckenberg. Marit.* 28, 167–175.
- Reise, K., Gollasch, S., Wolff, W.J., 1999. Introduced marine species of the North Sea coasts. *Helgoländer Meeresun.* 52, 219–234.
- Reise, K., Olenin, S., Thielgtes, D.W., 2006. Are aliens threatening European aquatic coastal ecosystems? *Helgol. Mar. Res.* 60, 77–83.
- Reise, K., Wegener, A., Sea, W., List, S., 2010. How to deal with alien species in the Wadden Sea? In: Marencic, H., Eskildsen, K., Farke, H., Hedtkamp, S. (Eds.), *Science for Nature Conservation and Management: The Wadden Sea Ecosystem and EU Directives Wadden Sea Ecosystem*, No. 26. Common Wadden Sea Secretariat, Wilhelmshaven, Germany, pp. 69–74.
- Reise, K., Buschbaum, C., Büttger, H., Rick, J., Wegner, K.M., 2017a. Invasion trajectory of Pacific oysters in the northern Wadden Sea. *Mar. Biol.* 164, 68.

- Reise, K., Buschbaum, C., Buttger, H., Wegner, M.K., 2017b. Invading oysters and native mussels: from hostile takeover to compatible bedfellows. *Ecosphere* 8 (9). <https://doi.org/10.1002/ecs2.1949> e 01949.
- Ricciardi, A., Ryan, R., 2018. The exponential growth of invasive species denialism. *Biol. Invasions* 20, 549–553.
- Rinde, E., Tjomsland, T., Hjermand, D.Ø., Kempa, M., Norling, P., Kolluru, V.S., 2017. Increased spreading potential of the invasive Pacific oyster (*Crassostrea gigas*) at its northern distribution limit in Europe due to warmer climate. *Mar. Freshw. Res.* 68, 252–262.
- Robert, R., Sanchez, J.L., Perez-Pareille, L., Ponis, E., Kamermans, P., O'Mahoney, M., 2013. A glimpse on the mollusc industry in Europe. *Aquac. Eur.* 38, 5–11.
- Rohlfritsch, A., Bierre, N., Boudry, P., Heurtebise, S., Cornette, F., Lapegue, S., 2013. Population genomics shed light on the demographic and adaptive histories of European invasion in the Pacific oyster, *Crassostrea gigas*. *Evol. Appl.* 6, 1064–1078.
- Sagof, M., 2018. What is invasion biology? *Ecol. Econ.* 154, 2–30.
- Savini, D., Occhipinti-Ambrogi, A., Marchini, A., Tricarico, E., Gherardi, F., Olenin, S., Gollasch, S., 2010. The top 27 animal alien species introduced into Europe for aquaculture and related activities. *J. Appl. Ichthyol.* 26 (Suppl. 2), 1–7.
- Shelmerdine, R.L., Mouat, B., Shucksmith, R.J., 2017. The most northerly record of feral Pacific oyster *Crassostrea gigas* (Thunberg, 1793) in the British Isles. *Bioinv Records.* 6 (1), 57–60.
- Shine, R., 2015. Ch 13 reducing the ecological impact of invasive cane toads. In: *Biological invasions in changing ecosystems*. In: Canning-Clode, João (Ed.), *Vectors, Ecological Impacts, Management and Predictions*, pp. 301–317. ISBN: 9783110438659.
- Skolka, M., Gomoiu, M.T., 2004. Specii invazive în Marea Neagră. Impactul ecologic al pătrunderii de noi specii în ecosistemele acvatice [Invasive species in the Black Sea. Ecological impact of new species entering aquatic ecosystems]. Ovidius University Press, Constanța, 185 pp. (in Romanian).
- Smaal, A.C., Kater, B.J., Wijsman, J., 2009. Introduction, establishment and expansion of the Pacific oyster *Crassostrea gigas* in the Oosterschelde (SW Netherlands). *Helgol. Mar. Res.* 63, 75–83.
- Smith, I.P., Guy, C., Donnan, D., 2015. Pacific oysters, *Crassostrea gigas*, established in Scotland. *Aquatic Conserv. Mar. Freshw. Ecosyst.* 25, 733–742.
- Solaun, O., Rodríguez, J.G., Borja, A., Larreta, J., Legorburu, I., Valencia, V., 2015. Source characterisation and mid-term spatial and temporal distribution of polycyclic aromatic hydrocarbons in molluscs along the Basque coast (northern Spain). *Chem. Ecol.* 31 (5), 416–431.
- Son, M.O., 2010. Alien mollusks within the territory of Ukraine: sources and directions of invasions. *Russian J. Biol. Inv.* 1 (1), 37–44.
- Spagnolo, A., Auriemma, R., Bacci, T., Balković, I., Bertasi, F., Bolognini, L., Cabrini, M., Cilenti, L., Cuicchi, C., Cvitković, I., Despalatović, M., Grati, F., Grossi, L., Jaklin, A., Lipej, L., Marković, O., Mavrić, B., Mikac, B., Nasi, F., Nerlović, V., Pelosi, S., Penna, M., Petović, S., Punzo, E., Santucci, A., Scirocco, T., Straffella, P., Trabucco, B., Travizi, A., Žuljević, 2019. Non-indigenous macrozoobenthic species on hard substrata of selected harbours in the Adriatic Sea. *Mar. Pollut. Bull.* 147, 150–158.
- Spencer, B.E., Edwards, D.B., Kaiser, M.J., Richardson, C.A., 1994. Spatfalls of the nonnative Pacific oyster, *Crassostrea gigas*, in British waters. *Aquatic Conserv. Mar. Freshw. Ecosyst.* 4 (3), 203–217. <https://doi.org/10.1002/aqc.3270040303>.
- Stagličić, N., Segvić-Bubić, T., Ezgeta-Balić, D., Bojanić Varezić, D., Grubišić, L., Žuvić, L., Lin, Y., Briski, E., 2020. Distribution patterns of two co-existing oyster species in the northern Adriatic Sea: the native European flat oyster *Ostrea edulis* and the nonnative Pacific oyster *Magallana gigas*. *Ecol. Indic.* 113, 106233.
- State of Florida, 2022. Florida Python Challenge. <https://flpythonchallenge.org/>. Visited 08-03-2022.
- Steele, S., Mulcahy, M.F., 1999. Gametogenesis of the oyster *Crassostrea gigas* in southern Ireland. *J. Mar. Biol. Assoc. UK* 79, 673–686.
- Strand, Å., Lindegarth, S., 2014. Japanska ostron i svenska vatten. Rapport nummer 2 från Vattenbrukscentrum Väst. Göteborgs universitet (62 pp. ISBN 978-91-637-6174-4. in Swedish).
- Strand, Ø., Vøllstad, J.H., 1997. The molluscan fisheries and culture of Norway. In: MacKenzie Jr., C.L., Burrell, V., Rosenfield, A., Hobart, W.L. (Eds.), *The history, present condition, and future of the Molluscan fisheries of North America and Europe*, 129. U.S. Dep. Commer., NOAA Tech. Rep. NMFS, pp. 7–24, 240pp.
- Strand, Å., Waenerlund, A., Lindegarth, S., 2011. High tolerance of the Pacific oyster (*Crassostrea gigas*, Thunberg) to low temperatures. *J. Shellfish Res.* 30 (3), 733–735.
- Strand, Å., Blanda, E., Bodvin, T., Davids, J.K., Jensen, L.F., Holm-Hansen, T.H., Jelmert, A., Lindegarth, S., Mortensen, S., Moy, F.E., Nielsen, P., Norling, P., Nyberg, C., Christensen, H.T., Vis-mann, B., Holm, M.W., Hansen, B.W., Dolmer, P., 2012. Impact of an icy winter on the *C. gigas* (*Crassostrea gigas* Tunberg, 1793) populations in Scandinavia. *Short Communicat. Aquat. Inv.* 7, 433–440.
- Tamburini, E., Fano, E.A., Castaldelli, G., Turolla, E., 2019. Life cycle assessment of oyster farming in the Po Delta, Northern Italy. *Resources* 8, 170.
- Thomas, Y., Pouvreau, S., Alunno-Bruscia, M., Barillé, L., Gohin, F., Brye' re, P., Gernez, P., 2016. Global change and climate-driven invasion of the Pacific oyster (*Crassostrea gigas*) along European coasts: a bioenergetics modelling approach. *J. Biogeogr.* 43, 568–579.
- Troost, K., 2010. Causes and effects of a highly successful marine invasion: case-study of the introduced Pacific oyster *Crassostrea gigas* in continental NW European estuaries. *J. Sea Res.* 64, 145–165.
- Troost, K., Kamermans, P., Wolff, W.J., 2008. Larviphagy in native bivalves and an introduced oyster 2008. *J. Sea Res.* 60, 157–163.
- Ubertini, M., Lagarde, F., Mortreux, S., Le Gall, P., Chiantella, C., Fiandrino, A., Bernard, I., Pouvreau, S., Roque d'Orbcastel, E., 2017. Gametogenesis, spawning behavior and larval abundance of the Pacific oyster *Crassostrea gigas* in the Thai lagoon: evidence of an environment-dependent strategy. *Aquaculture* 473, 51–61.
- Viðskiptablaðið, 2014. 100 tons Icelandic oysters. <https://www.vb.is/frettit/100-tonn-f-islenskum-ostrum/>.
- Vismann, B., Holm, M.W., Davids, J.K., Dolmer, P., Pedersen, M.F., Blanda, E., Christensen, H.T., Nielsen, P., Hansen, B.W., 2016. Field clearance of an intertidal bivalve bed: relative significance of the co-occurring blue mussel *Mytilus edulis* and Pacific oyster *Crassostrea gigas*. *Aquat. Biol.* 25, 107–119.
- Walne, P.R., Spencer, B.E., 1971. The introduction of the Pacific oyster (*Crassostrea gigas*) into the United Kingdom. *Shellfish Information Leaflet No. 2*, 14 pp.
- Waser, A.M., Zeuzeman, S., Kangeri, A.K., van Winden, E., Postma, J., et al., 2016. Impact on bird fauna of a non-native oyster expanding into blue mussel beds in the Dutch Wadden Sea. *Biol. Conserv.* 202, 39–49. <https://doi.org/10.1016/j.biocon.2016.08.007>.
- Wehrmann, A., Schmidt, A., 2005. Die Einwanderung der Pazifischen Auster in das Niedersächsische Wattenmeer. - Report WWF Frankfurt/M. Meiners Druck OHG, Bremen, 26 pp. (in German).
- Wehrmann, A., Herlyn, M., Bungenstock, F., Hertweck, G., Millat, G., 2000. The distribution gap is closed—first record of naturally settled Pacific oysters (*Crassostrea gigas*) in the east Frisian Wadden Sea, North Sea. *Senckenberg. Marit.* 30, 153–160.
- Wijsman, J.W.M., Dubbeldam, M., De Kluijver, M., Van Zanten, E., Van Stralen, M.R., Smaal, A.C., 2008. Wegvisproef Japanse oesters in de Oosterschelde. Eindrapportage Rapport C063/08 Institute for Marine Resources and Ecosystem Studies, Yerseke, The Netherlands, p. 95 (BTW nr. NL 811383696B04. [in Dutch]).
- Wolff, W.J., Reise, K., 2002. Oyster imports as a vector for the introduction of alien species into northern and Western European coastal waters. In: Leppäkoski, E., Gollasch, S., Olenin, S. (Eds.), *Invasive Aquatic Species of Europe*. Distribution, Impacts and Management. Springer, Dordrecht. [https://doi.org/10.1007/978-94-015-9956-6\\_21](https://doi.org/10.1007/978-94-015-9956-6_21) (ISBN 978-90-481-6111-9).
- Wood, L.E., Silva, T.A.M., Heal, R., Kennerley, A., Stebbing, P., Fernand, L., Tidbury, H. J., 2021. Unaided dispersal risk of *Magallana gigas* into and around the UK: combining particle tracking modelling and environmental suitability scoring. *Biol. Invasions* 23, 1719–1738.
- Wrange, A.-L., Valero, J., Harkestad, L.S., Strand, Ø., Lindegarth, S., Christensen, H.T., Dolmer, P., Kristensen, P.S., Mortensen, S., 2010. Massive settlements of the Pacific oyster, *Crassostrea gigas*, in Scandinavia. *Biol. Invasions* 12, 1453–1458.
- Yüksek, A., 1989. The investigation of littoral biota of southern coast of Marmara Island. *Bulletin of Institute of Marine Sciences and Geography, Istanbul University* 6 (6), 203–216.
- Zaitsev, Y., Öztürk, B., 2001. Exotic species in the Aegean, Marmara, Black, Azov and Caspian Sea. Turkish Marine Research Foundation, Istanbul, Turkey, 267pp.
- Zenetos, A., Koutsoubas, D., Vardala-Theorou, E., 2004. Origin and vectors of introduction of exotic molluscs in greek waters. *Belgian J. Zool.* 134 (sup. 1), 161–168.
- Zenetos, A., Gofas, S., Verlaque, M., Çinar, M.E., García Raso, J.E., Bianchi, C.N., Morri, C., Azzurro, E., Bilecenoglu, M., Frogli, C., Siokou, I., Violanti, D., Sfriso, A., San Martín, G., Giangrande, A., Katagan, T., Ballesteros, E., Ramos-Esplá, A., Mastrototaro, F., Ocaña, O., Zingone, A., Gambi, M.C., Streftaris, N., 2010. Alien species in the Mediterranean Sea by 2010. A contribution to the application of European Union's marine strategy framework directive (MSFD). Part I. Spatial distribution. *Mediterr. Mar. Sci.* 11 (2), 381–493.
- Zibrowius, H., 1991. Ongoing modification of the Mediterranean marine fauna and flora by the establishment of exotic species. *Mesogee* 51, 83–107.
- Zolotarev, V., 1996. The Black Sea ecosystem changes related to the introduction of new Mollusc species. *Mar. Ecol.* 17 (1–3), 227–236.
- Zwerschke, N., Eagling, L., Roberts, D., O'Connor, N., 2020. Can an invasive species compensate for the loss of a declining native species? Functional similarity of native and introduced oysters. *Mar. Environ. Res.* 153, 104793 <https://doi.org/10.1016/j.marenvres.2019.104793>.