Spatial Distributions and Temporal Changes of Coastal Bivalve Populations

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Doctoral thesis

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“Shellfish are the prime cause of the decline of morals and the adaptation of an extravagant lifestyle.” – Pliny the Elder, Natural History, Book IX, Chapter 53.

ABSTRACT

Bivalves are common animals in coastal ecosystems that alter energy flows and the characteristics of their surroundings, which contributes to ecosystem functions and services. Most bivalve species are suspension-feeders, clearing the water from organic particles and phytoplankton and thereby lowering water turbidity and exert top-down control on phytoplankton communities. Faeces are deposited on the sea floor, coupling the pelagic and benthic ecosystem components and enhancing the long-term storage and remineralization of nutrients which is important for mitigating negative effects of eutrophication. The infaunal species' burrowing behaviour reworks the sediment which increases the flux of oxygen and other solutes between sediments and water, while epifaunal species create complex reef structures that can be utilized by other species promoting biodiversity. Globally, much of the epifaunal bivalve reefs have been greatly diminished, resulting in a loss of function and services, while invasive species have been introduced in many areas causing shifts in ecosystems.

The aim of this thesis was to describe the coastal bivalve communities on the Skagerrak coast in terms of species composition, distribution, abundances and biomass. This was done in order to identify key species, functional groups and habitat types that contribute to ecosystem functions and services. Recently collected data was contrasted against older records to access temporal changes in the structure of the bivalve populations. The possible underlying mechanisms to these changed and the potential consequences for ecosystem functioning was also explored.

The results showed that populations are shaped by a combination of environmental factors, species habitat preference and the availability of those habitats. While epifaunal species are overall more ecologically relevant than infaunal species, the later can be locally more impactful. Since the invasive Pacific oyster arrived it has become the dominant species in terms of biomass which has, together with a general decline of infaunal bivalves, likely caused shifts in bivalve ecosystem functions and services. The methods and analyses described provide an important current baseline for the bivalve populations in this area and to compare further changes to in the future.

Keywords: *mussels, oysters, species distribution models, niche, invasive species, predation, filamentous algae, ecosystem functions, ecosystem services*

Sammanfattning

Musslor är vanliga djur i kustnära ekosystem som förändrar energiflöden och olika egenskaper i sin omgivning, vilket bidrar till ekosystemfunktioner och ekosystemtjänster. De flesta musselarterna är suspensionsätare som rensar vattnet från organiska partiklar och växtplankton och därigenom minskar vattnets grumlighet och utövar top-down-kontroll på växtplankton. Fekalier deponeras på havsbotten, vilket kopplar samman de pelagiska och bentiska ekosystemkomponenterna och förbättrar den långsiktiga lagringen och remineraliseringen av näringsämnen, vilket är viktigt för att mildra de negativa effekterna av eutrofiering. Infauna arternas grävbeteende omarbetar sedimentet vilket ökar flödet av syre och andra lösta ämnen mellan sediment och vatten, medan epibentiska arter skapar komplexa revstrukturer som kan utnyttjas av andra arter och främjar den biologiska mångfalden. Globalt sett har en stor del av de epibentiska musselreven minskat kraftigt, vilket har lett till en förlust av funktioner och tjänster, samtidigt som invasiva arter har introducerats i många områden och orsakat förändringar i ekosystemen.

Syftet med denna avhandling var att beskriva kustnära musselsamhällen längs Skagerrakkusten med avseende på artsammansättning, utbredning, abundans och biomassa. Detta gjordes för att kunna identifiera nyckelarter, funktionella grupper och livsmiljötyper som bidrar till ekosystemets funktioner och tjänster. Nyligen insamlade data jämfördes med äldre uppgifter för att utvärdera tidsmässiga förändringar i strukturen hos musselpopulationerna. De möjliga bakomliggande mekanismerna till dessa förändringar och de potentiella konsekvenserna för ekosystemets funktion undersöktes också.

Resultaten visade på att populationerna formas av en kombination av miljöfaktorer, arternas habitatpreferenser och tillgången till dessa habitat. Även om epibentiska arter generellt sett är mer ekologiskt relevanta än infauna arter, så kan de senare ha större påverkan lokalt. Sedan introduktionen av det invasiva stillahavsostronet så har det blivit den dominerande arten i fråga om biomassa och tillsammans med en allmän minskning av infauna musslor, har det sannolikt orsakat förändringar i musslornas ekosystemfunktioner och ekosystemtjänster. De resultat beskrivs ger en viktig aktuell baslinje för musselpopulationerna i detta område och är viktiga för att kunna utvärdera ytterligare förändringar i framtiden.

LIST OF PAPERS

Paper I **Greeve Y**, Bergström P, Strand Å and Lindegarth M (2023) Estimating and scaling-up biomass and abundance of epi- and infaunal bivalves in a Swedish archipelago region: Implications for ecological functions and ecosystem services. *Frontiers in Marine Science*. 10:1105999.

Paper II **Greeve Y**, Reamon MC, Bergström P, Strand Å, Laugen AT, Lindegarth M (in review) Improving large-scale population estimates and assessments of ecological importance of three epifaunal bivalve species by combining distribution and abundance models. *Ecology and Evolution.*

Paper III Reamon MC, **Greeve Y**, Korslund LM, Laugen AT, Lindegarth M, Strand Å, Bergström P (manuscript) Niche expansion in an invasive bivalve leads to greater overlap with native species without evidence of displacement.

Paper IV **Greeve Y**, Bergström P, Strand Å, Lindegarth M (manuscript) Decline in abundance and size of infaunal bivalves have more than halved biomass and filtration capacity in shallow, Swedish coastal habitats since the 1990's.

Paper V **Greeve Y**, Speck C, Bergström P, Strand Å, Lindegarth M, Moksnes P (manuscript) Cage experiment reveals the effect of predation and filamentous algae on the recruitment success of bivalves in western Sweden.

TABLE OF CONTENTS

BACKGROUND

BIVALVES

Bivalves form a diverse class of species of aquatic molluscs that are best recognized by an external calcified shell that is made up of two halves which are connected at a single hinge. There exist a wide variety in feeding strategies within the bivalve class ranging from detrivory (Ward & Shumway, 2004), predatory (Morton & Machado 2019) and symbiosis with chemotrophic (Duperron et al., 2013) and photosynthetic (McCoy et al., 2024) single celled organisms, though most species feed through what is called suspension-feeding (Rosa et al., 2018). Suspension feeding bivalves use their highly modified gills to pump water and capture particles using specialized hair-like cilia (Ward et al., 1998). Both organic and inorganic particles of a variety of sizes are captured this way, though the majority of what is ingested are phytoplankton (Both et al., 2020) and less valuable or indigestible particles (e.g. silt) may be sorted out and rejected as pseudofaeces (Ward & Shumway, 2004).

Reproduction in bivalves typically happens externally in what is known as broadcast spawning where both eggs and sperm are released in the water (Gosling 2003). In some species, fertilization of the eggs happens internally, where they are kept for some time while the larvae develop and are later released (Ó Foighil & Taylor 2000). The larvae spend several weeks in the water column feeding on suspended particles until they settle on soft (i.e. sedimentary) or hard (e.g. stones and shells) substrates and metamorphize into adults.

Most bivalves broadly fall into two categories based on their morphology and overall lifestyle; infaunal or epifaunal. Infaunal bivalves, generally referred to as clams, live partially or completely burrowed into soft sediments. They are able to move freely by the use of their foot to reposition themselves and migrate short distances. Epifaunal bivalves live above the sea floor often attached to hard substrate using byssal threads or by cementing themselves permanently into place. Well known examples of epifaunal bivalves are mussels and oysters. They are mostly sessile, either never or hardly moving after settlement.

Humans have used bivalves throughout history as a food source, with early forms of aquaculture even dating back millennia (Rogers 2024). Nowadays, bivalves comprise about 16% of yearly food production from the growing aquaculture sector globally (FAO, 2024), and both commercial and recreational bivalve fishery are also widely practiced (Smaal et al., 2019).

ECOSYSTEM ENGINEERS

Ecosystem engineering species are organisms which have a disproportionally large effect on ecosystems through changing the availability of resources to other species and physically altering and creating habitat (Jones et al., 1997). Ecosystem engineering effects are separated into two categories: autogenic and allogenic. Autogenic engineering effects are changes brought on by the physical presence of a species (e.g. trees in a forest), while allogenic engineering effects impose changes beyond a species physical presence (e.g. a beaver’s dam). Ecosystem engineering typically has a large effect on ecosystem functions (i.e. process that drive fluxes of nutrients and energy in ecosystems) while some of these functions contribute to ecosystem services (i.e. aspects of natural systems that are to the benefit of humans) and are thus of importance to the welfare, stability and cultural identity of societies (Costanza et al., 1997, Millennium Ecosystem Assessment 2005, Rönnbäck et al., 2007).

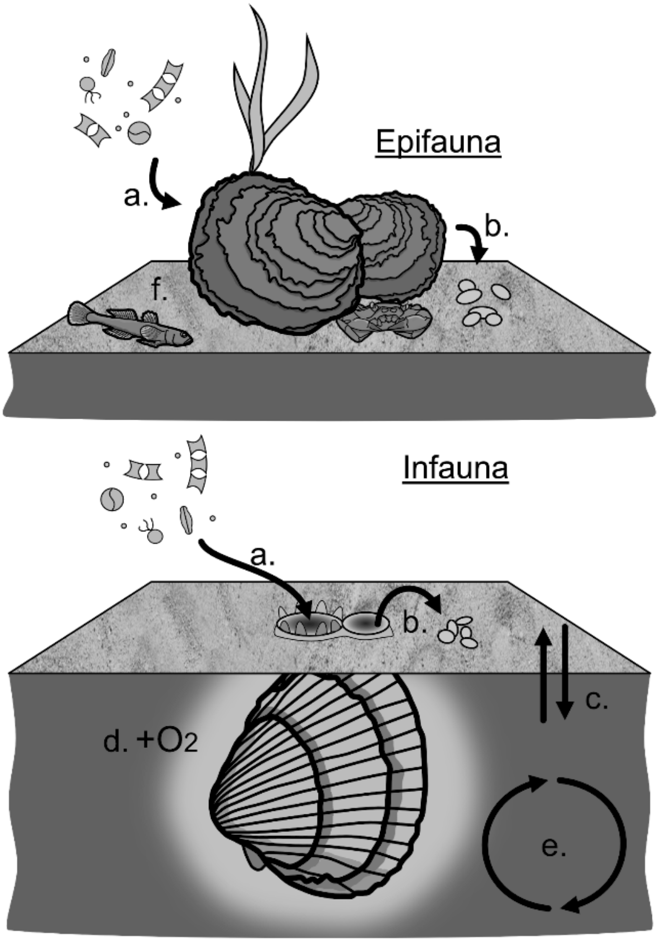

Figure 1: *Ecosystem functions related to (suspension-feeding) epifaunal and infaunal bivalves.* ***a****) Removing suspended particles through feeding.* ***b****) Deposition of (pseudo-)faeces pellets to the benthos.* ***c****) Increasing fluxes of solutes between sediments and overlaying water.* ***d****) Oxygenating sediments.* ***e****) Mixing and redistribution of sediments through burrowing.* ***f****) Provide habitat to other species.*

One of the most well-known impacts of bivalves is the allogenic effect that suspension-feeding has on the surrounding water and nutrient cycles. The grazing of bivalves, when present in high numbers, can exert significant top-down pressures on phytoplankton communities, lowering the overall abundance and altering species composition (Prins et al., 1997) (**Fig. 1a**). The resulting faeces and pseudofaeces are deposited (i.e. biodeposition) to the seabed, transporting nutrients from pelagic to benthic ecosystems, where the organic matter mater is broken down by detrivores and microbes mineralizing it back into bioavailable forms, after which it is released back to the pelagic in a process called benthic-pelagic coupling (Norkko et al., 2001) (**Fig. 1b**). The combined effect of lowered turbidity from grazing and remineralization of nutrients can improve growth rates of other important primary producing and habitat forming species such as seagrasses (Peterson & Heck 2001, Newell & Koch 2004). The process of removing nutrients from the pelagic and bringing them to the benthos where they can be recycled can also contribute in mitigating harmful effects of eutrophication (Carmichael et al., 2012). The aquaculture of bivalves is for these reasons seen as a viable way to improve water quality and mitigate eutrophication in coastal areas (Petersen et al., 2016) with the added benefit of providing a very sustainable source of proteins (Gephart et al., 2021).

In a process called bioturbation, bivalves further impact sediment by reworking it, which is an allogenic effect mostly restricted to infaunal species. By burrowing in and pumping water through the sediment, the exchanges rates of solutes between the sediment pore-water and the overlaying water increases (Norkko & Shumway, 2011) (**Fig. 1c**). This allows for oxygen to penetrate deeper into the sediment and enriches it with organic matter, which can positively affect other benthic animals and microbial activity, further enhancing the benthic-pelagic coupling process (Jones et al., 2011; Newell et al., 2002) (**Fig. 1d**). Additionally, the burrows and sediment reworking of infaunal bivalves introduce heterogeneities that contribute to habitat complexity and diversity (Reise, 2002; **Fig. 1e**). Bioturbation, sediment composition changes and nutrient enrichment can affect the photosynthesizing microbial community as well, enhancing the primary production of organisms on the sediment, which fixes the greenhouse gas carbon dioxide through photosynthesis (Thomas et al., 2021).

The physical presence of bivalves also has substantial autogenic impacts on their surroundings. Most notably, epifaunal bivalves such as mussels and oysters are able to create biogenic reefs by accumulating in high numbers. These reefs grow through successive generations of settlement, deposition of dead shells and trapping of sediment (Rodriguez et al., 2014), and historically covered multiple hectares (Thurstan et al., 2024). Bivalve reefs function much in the same way as forests or coral reefs in the sense that they provide complex structural habitat for a plethora of other species and thereby increase local biodiversity (**Fig. 1f**). As biological hotspots, epifaunal bivalves support small animals hiding within the reef structure (Longmire et al., 2021), the larger predators that forage on them (Macreadie et al., 2012) and sessile animals and algae that use them as substrate (Mascorda-Cabre et al., 2024), supporting overall richer and more complex ecosystems (Norling & Kautsky 2007, Humphries et al., 2011, Norling et al., 2015). Oyster reefs are also used by commercially interesting fish species as foraging and nursery grounds, contributing to and thus the provisioning services of these habitats (Grabowski et al., 2012, Gilby et al., 2018). Additionally, the presence of bivalve reefs stabilizes sediments by reducing sheer stress from currents and waves, which reduces shoreline erosion (Morris et al., 2019).

UNDER THREAT

Though only covering 7% of the earth’s surface, coastal seas contribute the most economic value through ecosystem services than any other biome (Costanza et al., 1997). Through a combination human-related overexploitation, habitat destruction and pollution many coastal ecosystems and habitats have, however, been severely damaged in recent history (Lotze et al., 2006). A situation being exacerbated by the pressures of a rapidly changing climate, which are expected to be especially impactful in coastal regions (IPCC 2023). Bivalve reefs are among the most degraded marine ecosystems worldwide, with estimated losses of about 85% globally (Beck et al., 2011). Most of this decline has happened relatively recently in the late nineteenth century due to increasing demands and more efficient fishing gear (Berghahn & Ruth 2005). In Europe, overfishing quickly resulted in the almost complete disappearance of large reefs of the European flat oyster *Ostrea edulis*, which was further worsened by poor water quality and disease outbreaks (Thurstan et al., 2024, Zu Ermgassen et al., 2024). Reefs of various mussel species have also seen similarly large declines in some areas in the world (Sorte et al., 2017, Baden et al., 2021, Toone et al., 2023). The decline of bivalve reefs is worrisome, as once removed recovery is notoriously difficult, and as the loss of these habitats is associated with a loss of associated ecosystem services (Beck et al., 2011, Grabowski et al., 2012). To facilitate bivalve reef recovery and sustain ecosystem services, efforts have been initiated to restore some of these vital habitats, although with various degrees of success (Hemraj et al., 2022). These restoration projects are examples of a shift in perspective from seeing bivalves as an exploitable resource to a more holistic understanding of the importance of protecting and restoring bivalve habitats for the good of society.

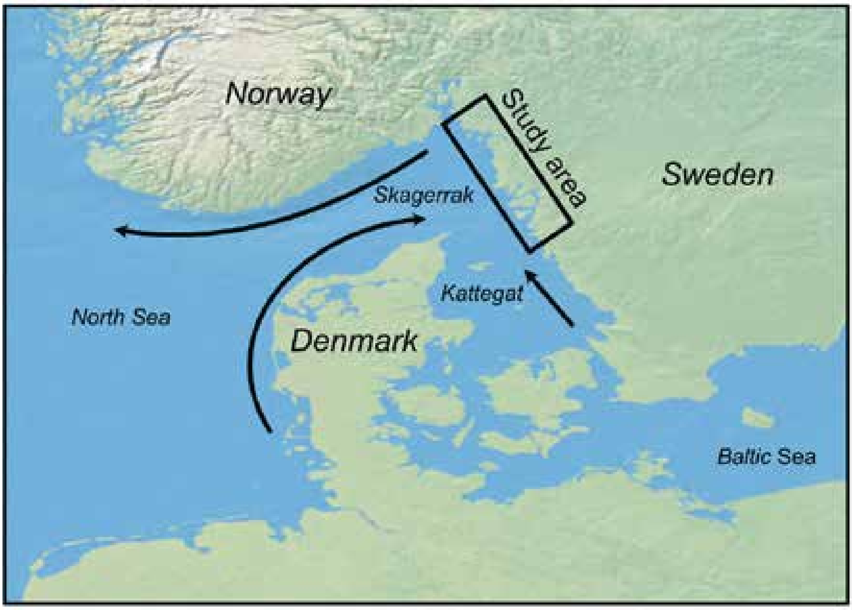

Figure 2. *Overview of the waters and countries surrounding the study area for this thesis. Arrows represent prevailing water currents.*

BIVALVES OF THE SKAGERRAK COAST

This thesis centres on the shallow-living bivalve communities on the coastline of the Skagerrak strait in western Sweden (**Fig. 2**). The Skagerrak is part of the North Sea and, together with the Kattegat, forms the connection to the Baltic Sea. Currents bring water from the brackish Baltic Sea, creating a surface layer of low saline water, which meets the saltier North Sea in the Skagerrak (Rodhe 1996). Surface salinity is, however, variable through the effects of winds and seasonal freshwater input from riverine systems. The tidal range is small (± 30 cm), but is occasionally amplified by wind and atmospheric pressure to exceed ± 1 m (Johannesson 1989). The Skagerrak coastline is archipelagic, with a great number of islands and rocky islets in a variety of sizes. There are also several fjord systems. This complex coastline creates steep gradients in varying wave exposure conditions resulting in a wide variety of habitat types with sediments ranging from exposed rocky shores to sheltered silty bays.

In terms of species composition, the bivalve communities in the intertidal and shallow subtidal zones of the Skagerrak can be described as typical for temperate north-east Atlantic coasts, including infaunal species of the genus *Cerastoderma* (the common cockle *C. edule* and the lagoon cockle *C. glaucum*) and the soft-shell clam *Mya arenaria*. The population structure of these species varies across spatial scales (Lindegarth et al., 1995) which is in part driven by variation in local sediment type and depth (Evans & Tallmark 1976, Möller 1986). Communities are typically dominated by strong cohorts that originate from years of high recruitment and that survived into adulthood (Möller & Rosenberg 1983, Lindegarth et al., 1995). This survival of these recruits is impacted by both the abundance of predators (mobile epifaunal crustaceans, starfish, and fish [Flach, 2003; Möller et al., 1985]) and the intensity of competition with adults from previous years (Möller 1986). Cold winters are characterized by high mortalities of both juveniles and adults, which affects intra- and interspecific interactions in the following year (Möller & Rosenberg 1983, Möller 1986). Thus, both fixed variation in habitats and the annual variation in abiotic conditions, settlement and survival compound into both spatial and temporal patterns and variation in infaunal bivalve communities.

The most common epifaunal species in shallow waters in the Skagerrak are the blue mussel *Mytilus spp.*, the European flat oyster *O. edulis* and the Pacific oyster *Magallana gigas*. The *Mytilus* genus in Sweden is made up of a species complex with a Baltic (*M. trossulus*) and North Sea (*M. edulis*) population that form a hybrid zone in the Kattegat (Riginos & Cunningham 2005). Using byssal threads as a way of attachment, semi-sessile *Mytilus spp.* can organise its self into complex heterogeneous reef structures to optimize growth and survival (Koppel et al., 2005), and also create refuges for other species and juveniles mussels that rejuvenate the reef (Bertolini et al., 2018, Van Der Ouderaa et al., 2021). Reports of shrinking or disappearing reefs of *Mytilus* on the Swedish west coast have been made recently (Baden et al., 2021, Laugen et al., 2023), which resembles changes in other populations in the North Atlantic ocean. The evidence for the decline in Sweden has for the most part been anecdotal, as documented historic extents of *Mytilus* reefs are limited to a few locations and time periods, and a multitude of possible causes is suggested without consensus on which are the most impactful (Baden et al., 2021).

Recent efforts have been made to map the distribution of *O. edulis* in Sweden (Thorngren et al., 2017, 2019), which is of particular importance considering its dramatic collapse across its entire native distribution in Europe (Zu Ermgassen et al., 2024). These studies have shown that the population in Sweden is still of a considerable size and densities that can be considered as reefs still occur sporadically (Thorngren et al., 2019, Bergström et al., 2021). The oysters are partially protected from exploitation through the fishing rights which belong to the landowner. Despite this encouraging situation, the historical extent *O. edulis* reefs in Sweden are mainly unknown, and as historical records reveal significant commercial harvests in the 19th century (Zu Ermgassen et al., 2024) there are causes to believe that the oyster population is, as in the rest of Europe, probably much reduced in their current state.

M. gigas, which is native in parts of the Pacific Ocean, was imported to Europe for aquaculture in the 1960s as an alternative to the cultivation of native oysters (Troost 2010). Though first believed to be unable to reproduce in the colder waters of Europe, *M. gigas* progressively spread around the continent and established itself as an invasive species. Despite earlier trials of *M. gigas* cultivation in Norway, Denmark and Sweden, a large-scale invasion on the west coast of Sweden only occurred as late as 2006 (Wrange et al., 2010) originating from feral populations in Denmark (Laugen et al., 2015, Faust et al., 2017). Ever since, the population of *M. gigas* in Sweden has expanded and the species now occurs ubiquitously along the west coast. Though no extinctions of native bivalves due to the invasion of *M. gigas* have been recorded, there has been wide-spread concern about it outcompeting native epibenthic bivalves, especially *Mytilus spp.* with which it overlaps highly in terms of habitat preference (Laugen et al., 2015, Bergström et al., 2021). In areas where *M. gigas* has established itself less recently, it has brought about mixed reefs with *Mytilus spp.* (Reise et al., 2017) and *O. edulis* (Zwerschke et al., 2016, Christianen et al., 2018). The reefs made up of *M. edulis* and *M. gigas* appear stable with no indication that one species is outcompeting the other (Reise et al., 2017), while the competitive outcome with *O. edulis* is still uncertain. Further, the effect of *M. gigas* on ecosystem functions and services has been debated and the impacts seem to vary among habitats and locations (Ruesink et al., 2005, Herbert et al., 2016).

KNOWLEDGE GAPS

Although the various ecological functions and services associated with bivalves are relatively well understood, much less is known about the overall impact that these animals have on ecosystems at larger scales. To assess this quantitatively, population-level data on ecologically relevant estimates, such as abundances and biomass, are needed of different components of the overall community. This would also require an understanding of how various habitat-types are utilized by bivalves, as the total population is ultimately shaped to some degree by the extent of suitable habitat. As coastal areas are under increasing pressure and continuously degrading, the importance of setting current baselines becomes ever more pressing. It is therefore important to evaluate the current status and, if possible, temporal changes of ecosystems in recent history to prevent shifting baseline syndrome (Soga & Gaston 2018) and ecosystem functions and services disappearing unnoticed. Finally, as bivalve populations have already seen major shift due to declines and introductions of invasive species, it is also crucial to understand the implications of these events and their causes for improving the management of functions and services.

AIMS

This thesis aimed to describe the coastal bivalve communities in terms of species composition and the distribution patterns of abundances and biomass, with the Skagerrak coast as the study area. This was done to identify key species and functional groups (epi- or infaunal) in terms of contribution towards ecosystem functions and services. These findings would serve as a current baseline of bivalve populations in this area, as well as further the understanding how spatial distributions and relative importances across various habitat-types shape these processes. Additionally, comparisons were made between past and present situations to assess temporal changes while some of the mechanisms that could underly these changes were also explored. The methods and analyses described serve as a case study for future work on both marine and other ecosystems to understand and preserve functions and services in the future.

To address these aims, the research objectives of the individual papers were as follows:

Paper I *Explorative survey:* The objective of this study was to describe the distribution, abundance and biomass of in- and epifaunal bivalve species in various habitat types to estimate overall and relative contribution of each component to ecosystem functions.

Paper II *Population estimates through modelling:* The objective of this study was to use computational modelling to produce estimates of population sizes of epifaunal bivalves at a large spatial scale, as well as describe patterns in distribution and habitat use in high resolution to evaluate the relative contribution of each species towards ecosystem functions.

Paper III *Modelling temporal changes in habitat use and niche-overlap:* The objective of this study was to investigate changes in habitat use and niche-overlap between an invasive and two native epifaunal bivalve species to assess recent changes in species interactions.

Paper IV *Infaunal bivalve decline:* The objective of this study was to investigate whether observed low abundances of infaunal bivalves where due to consistent declines across large spatial scales and to estimate the potential change in ecosystem functioning.

Paper V *Cage experiment:* The objective of this study was to experimentally investigate whether increased abundance of meso-predators and cover of filamentous algae mats are plausible causes for observed declines of bivalve populations.

METHODS

In **Paper I** the bivalve communities of a section of the Swedish west coast were described with the main goal of identifying which species and functional groups (epi- and infaunal) of bivalves are most important for ecosystem functions and services. The sampling design combined quadrates and core samples to allow for direct comparison between epi- and infaunal species. Twenty sites were randomly selected from all suitable (<2 m depth for a >100 m stretch) sites in the area, which were equally divided among a combination of offshore ("Koster") vs inshore ("Tjärnö") and exposed vs sheltered habitats (**Fig. 3**). Within each site, ten core (0.068 – 0.07 m^2, **Fig. 4a**) and ten quadrate (1 m^2, **Fig. 4b**) samples were taken in both the intertidal (0 – 0.5 m, "Shallow") and shallow subtidal (0.5 – 2 m, "Deep") zone. Both the abundance (individuals m^{-2}) and biomass (ash free dry weight m^{-2}) were recorded for all species of bivalves. The overall contribution of each species toward ecosystem-wide abundance and biomass was calculated by combining the estimates of average densities with the areal extent of each habitat type (in – offshore, exposed – sheltered and shallow – deep).

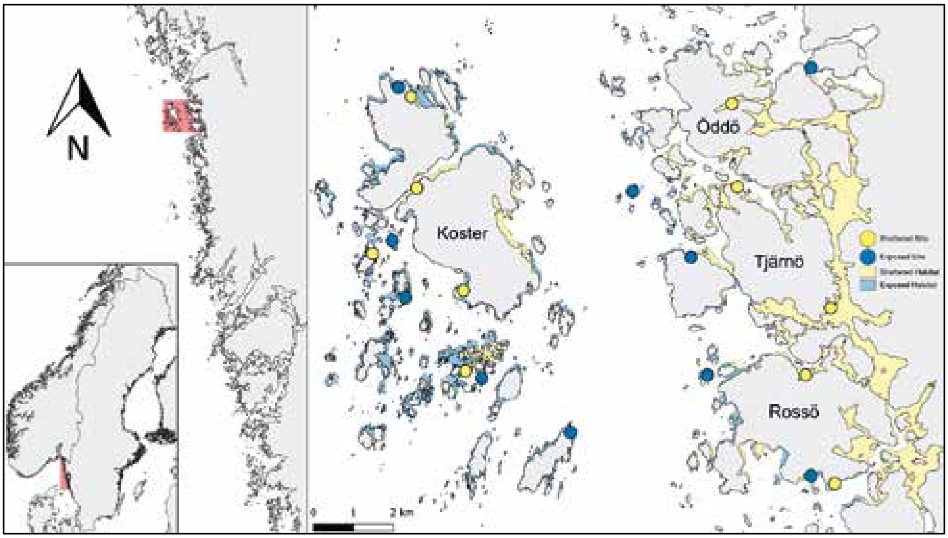

Figure 3. *A map of study area and sampling sites on the Swedish west coast for* ***Paper I****. Shallow habitat (<2 m depth) is shown in blue for exposed, and yellow for sheltered. Sampled sites are shown as circles in blue for exposed and yellow for sheltered. Note that small differences in exposure can be obscured by the symbols for sample locations.*

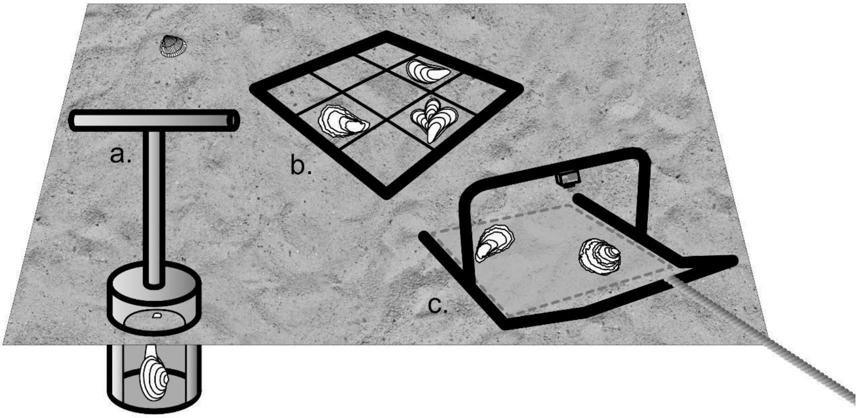

Figure 4. *A graphical representation of the three main sampling methods used to record bivalve presence, abundance and biomass in this thesis:* ***a****) Sampling core for infaunal bivalves (***Paper I, IV*** *and* ***V****).* ***b****) Quadrate for epifaunal bivalves (***Paper I*** *and* ***II****).* ***c****) Towed camera sled for epifaunal bivalves (***Paper II*** *and* ***III****).*

Paper II also had the goal of comparing the relative contribution of bivalves to ecosystem functions and services but with different methods, larger extent and focusing on the three most common epifaunal species. Computational models were trained using a large collection of sampling locations surveyed using a combination of quadrate (**Fig. 4b**) and video transects (**Fig. 4c**) across a large section of the Swedish west coast between 2018 and 2023 (**Fig. 5**). Gradient boosted models (GBMs, a machine learning based modelling technique) were used to construct species distribution models (**Box 1**) to predict the distribution and occurrences of *Mytilus spp.*, *M. gigas* and *O. edulis* using field observations and linking those to a collection of environmental variable raster layers at a resolution of 10x10 m. Additionally, similar models were constructed to predict local abundances. The environmental variables included physical (e.g. depth, slope and wave exposure), water-related (e.g. turbidity, salinity and temperature) and substrate characteristics (e.i. soft and hard substrates) which are known to be limiting factors for bivalve distribution. There was a special emphasis on estimating model uncertainty, which was assessed with a bootstrap method to evaluate model performance and uncertainty of the final predictions.

The models were used to predict the most likely patterns in occurrences and abundances of the three target species at high resolution. These were then used to investigate which kind of habitats, stratified on the two important environmental variables (depth and wave exposure), were most occupied by each species and to what extent they overlapped with each other. Additionally, predictions of abundances were used to identify how many individuals were predicted to occupy different habitats and geographic areas and estimate total population sizes. The population size estimates were compared to estimates using methods with less or no modelling involved to access whether distribution and abundance models resulted different estimates. In the end these predictions were then translated to estimates of total biomass and used to evaluate the overall importance of each species towards ecosystem functions and services across the study area.

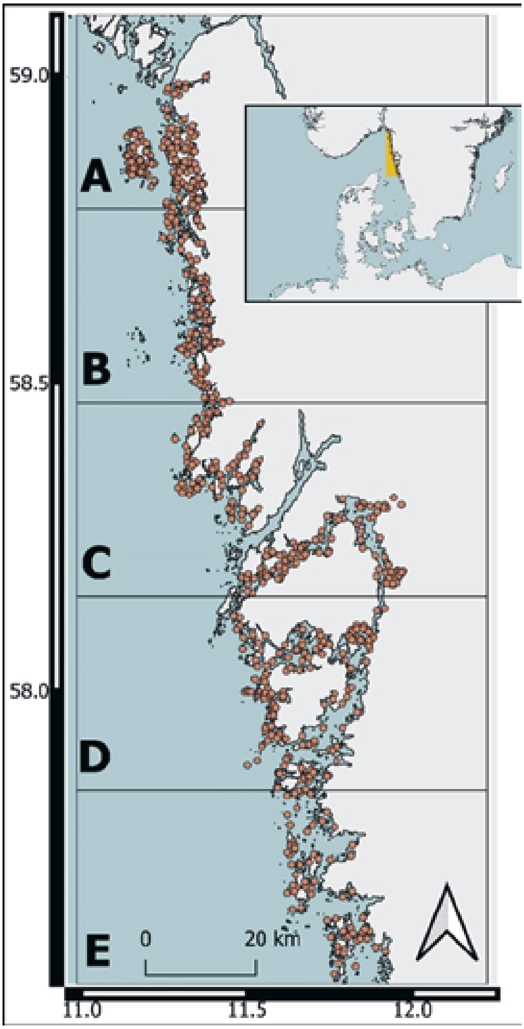

Figure 5. *A map of the study area with sampled locations marked (red dots) used in **Paper II**. 796 sites were sampled using a towed camera sled and the resulting videos were used to record epifaunal bivalve abundance.*

Box 1. Species distribution models (SDMs) are computational models that are used to predict the distribution patterns of species (Guisan & Zimmermann, 2000). Observations of the presence or absence of a species are linked to environmental variables using GPS coordinates, which are then used to train models that can predict the likelihood that species occurs in areas where no observations have been made. SDMs have become widely used in recent decades, and the maps they produce are applied in variety of contexts. One of the advantages of SMDs is that it is feasible to predict distribution patterns under new conditions with altered environmental variables, such as future climate scenarios. The low mobility of bivalves is ideal for SDMs, since records of presence almost guaranties that the conditions are suitable for them, which is not always the case for mobile animals with more unpredictable occupation of different habitats.

In **Paper III**, temporal changes in realized niche, areal extent of habitat use and overlap between the invasive *M. gigas* and the native *Mytilus spp.* and *O. edulis* were investigated in the northern parts of the Swedish west coast (**Fig. 6**). This was done using observational data from two periods (2013 – 2014 and 2018 – 2020) gathered with towed camera transects (**Fig. 4c**). Changes in the realized niches and the overlap among species between the two periods were quantified and deconstructed using the Centroid shift, Overlap, Unfilling, and Expansion (COUE) framework. Additionally, species distribution models (**Box 1**) using an ensemble modelling technique (combining weighted predictions of multiple model algorithms) were fitted to predict the distribution of all three species in both periods. The predicted distributions of these models were compared to quantify changes in the spatial occupation and overlap between species as well as infer changes in realized niches.

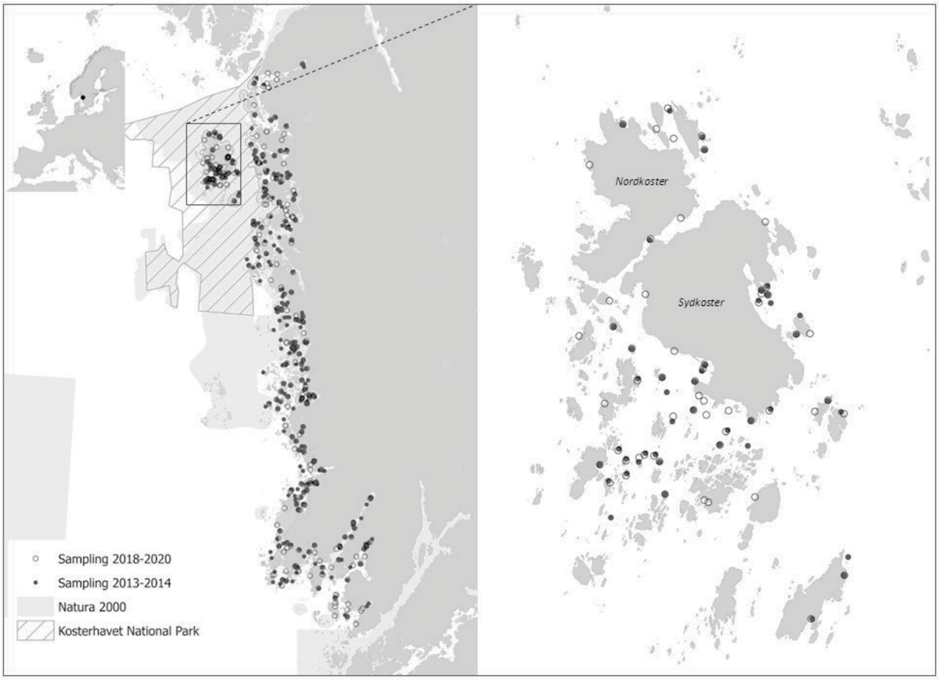

***Figure 6.** Study area and sample distribution of the sites sampled in **Paper III** for the first survey (2013 – 2014, **black**) and the second survey (2018 – 2020, **white**).*

In **Paper IV** the potential decline of infaunal bivalves on the Swedish and Norwegian Skagerrak coast in terms of abundance and biomass was investigated following observations of lower-than-expected abundances made in **Paper I**. Data from several field studies recording infaunal bivalve abundances performed between 1992 and 2004 along the Skagerrak coast from the eastern parts of the Oslo fjord to south of Gothenburg were compiled (**Fig. 7**). Out of the 96 original sites, 72 were resampled using comparable methods in 2022 and 2023 (**Fig. 7**). The historical data (1992 – 2004) was grouped into two periods (1990's and 2000's) based on the year of sampling and compared to recent sampling (2020's). In addition to the abundance, size (shell length, L) and dry weight (DW) biomass were also measured in the recent sampling.

Changes in abundances were tested between periods and between historic and recent samples for individual species and total infaunal bivalve abundance in the entire region, as well as four sections of the coastline (Region 1 – 4, **Fig. 7**). Additionally, the frequencies of positive and negative changes within sites were also statistically compared across the entire study area.

In part of the historic data shell length measurements were made, which were compared to the recent records to test whether average sizes of individual species had changed over time. Though no biomass measurements were made prior to the recent sampling, one study from the 1990's provided measurements of shell length of all encountered species in eight randomly selected sites. The relationship between shell length and dry weight biomass of individual species derived from recent measurements was then used to estimate historic biomass (DW m^{-2}) in these eight sites, which were then compared to current estimates. These biomass estimates were roughly translated in filtration rates (FR) using a generic equation for the relationship between DW and FR to represent changes in average FR m^{-2} of infaunal bivalves.

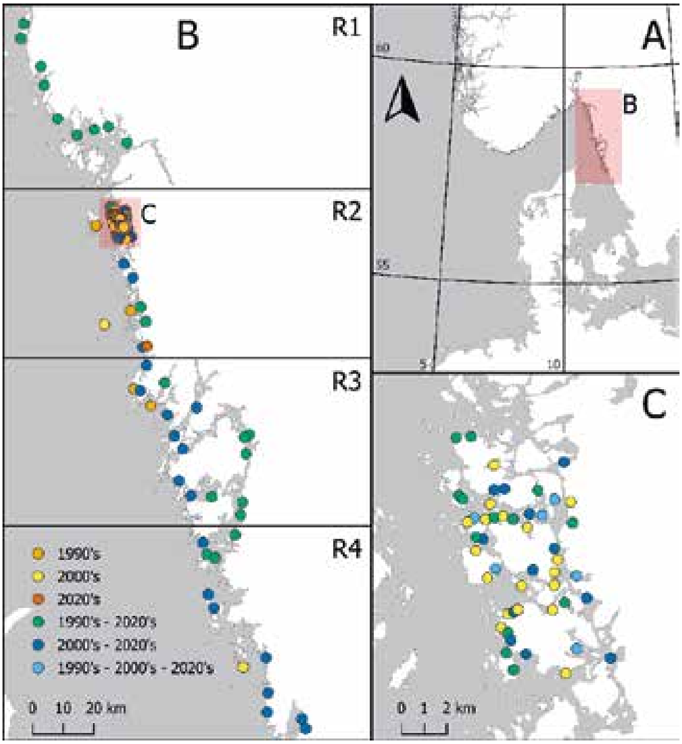

Figure 7. *Map of the geographic area (**A**), sampling regions (R1 – 4, **B**) and sites (coloured points) of **Paper IV**. Different colours represent in which decade certain sites were sampled and resampled.*

In **Paper V** the effect of meso-predators (e.g. shrimps, crabs and small fish) on the recruitment success of bivalves (epifaunal mussels and infaunal species) was experimentally quantified using predator exclusion cages. Additionally, the effect of filamentous algae on recruitment success was also assessed by adding an equal amount of algae to half of the plots. Experimental sites were established at four locations before seasonal peaks of bivalve settlement with six replicates of fully caged, partially caged and uncaged plots (**Fig. 8**). The fully caged plots were used to keep out potential predators, while the uncaged plots served as a control that represents full access from predators. The partially caged plots, which did allow predators to enter, served as a control to separate artifacts whereby the presence of cages affects the recruitment in ways other than restricting predation. The experiment was ended 76 to 81 days after the sites were established and sediment core samples (**Fig. 4a**) were taken to quantify the number of new recruits on the sediment of all plots. The recruits that had settled on algae and the caging structures were also collected and counted.

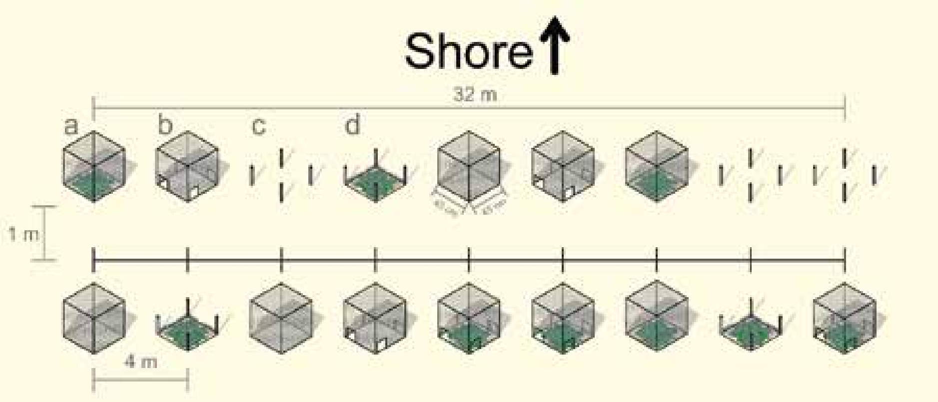

Figure 8. *Layout of the experimental design for* ***Paper V****. With fully- (****a****), partially- (****b****) and uncaged plots with (****c****) and without algae (****d****). The green shapes inside the plots represent the added filamentous algae.*

MAIN RESULTS

The survey of bivalve communities done in **Paper I** found that samples from pre-defined habitat levels (in – offshore, exposed – sheltered and shallow – deep) resulted in different bivalve biomass and abundances (**Fig. 9**). In general, both abundances and biomasses were higher in the deeper strata for epi- and infaunal bivalves, though this pattern was only fully consistent and significant for the infauna, which can be attributed to the high variability in bivalve communities between sites within habitat classifications. The difference between exposed and sheltered sites were contrasting among areas, with higher abundances and biomasses of both fauna in exposed sites in “Tjärnö” and sheltered sites in “Koster”. The collective average biomass of epifaunal species was greater than that of the infauna (≈7 times), though the reverse was true for abundances where infaunal species had higher averages (≈3 times).

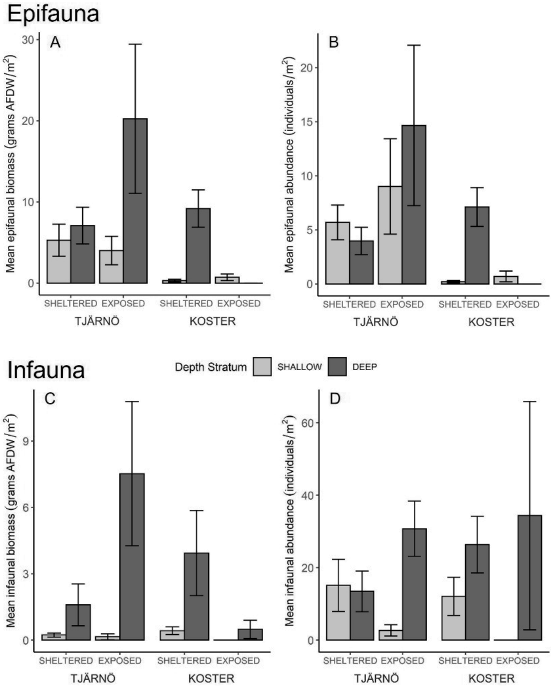

Figure 9. *Average biomass (AFDW g•m-2,* ***A****,* ***C****) and abundance (#•m-2,* ***B****,* ***D****) of epifauna (top) and infauna (lower)(mean ± SE). Note the different scales on the response axes between epi- and infauna.*

When extrapolated to ecosystem-wide patterns using the areal extent of each habitat type, the total estimated biomass and abundance of epi- and infaunal bivalves shifted to a larger importance of the sheltered habitats of “Tjärnö” (**Fig. 10**). This was due to the relatively large areal extent of this habitat, though “Tjärnö exposed” and “Koster sheltered” contributed considerable despite their small areal extent (both ≈9%), which was due to the higher averages in these habitats. Overall, epifaunal species contribute approximately 80 – 90% of all the bivalve biomass in this region and infaunal species 75% of the abundance. For both faunal groups, invasive species (epifauna: *M. gigas*, infauna: *Ensis leei*) contributed the largest proportion of the total biomass (65 and 60% for *M. gigas* and *E. leei* respectively), even though they weren't the most abundant.

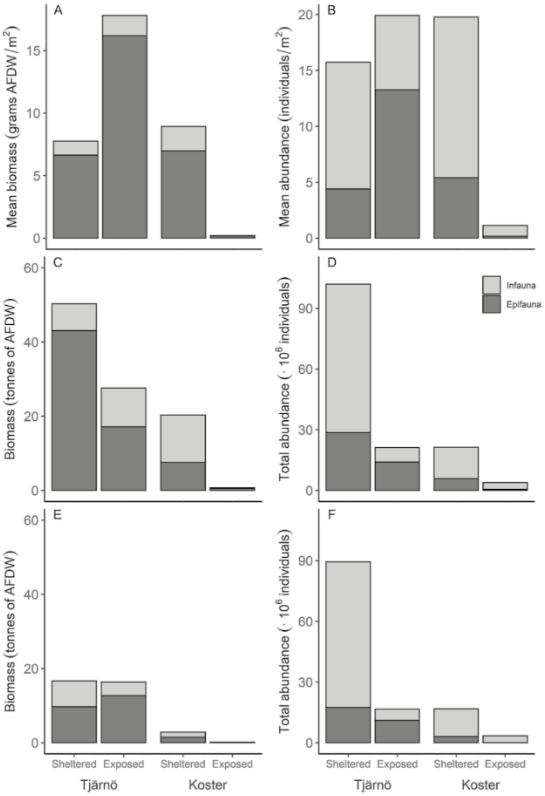

Figure 10. *Total biomass (AFDW) and total abundance of epi- and infauna in sheltered and exposed parts of Tjärnö and Koster areas. The first row shows biomass (**A**) and abundance (**B**) per m^2 accounting for habitat availability, and the second row show the totals accounting also for areal extent (**C**, **D**). The third row shows total biomass (**E**) and abundance (**F**) for each area excluding the two invasive species, M. gigas and E. leei.*

The use of models in **Paper II** to predict distribution and abundance of epifaunal bivalve species *M. edulis*, *M. gigas* and *O. edulis* resulted in both overlapping and contrasting patterns of habitat use. *M. edulis* was predicted to occupy 92 km^2 (or 13.2%) of the available habitat between 0 and 10 m depth, sharing 86% of that with *M. gigas* and 11% with *O. edulis*. *M. gigas* occupied 109 km^2 (or 15.6%) of the same habitat, sharing 72% of that with *M. edulis* and 8% with *O. edulis*. *O. edulis* was predicted to occupy 84 km^2 (or 12%) and shared 13% with *M. edulis* and 11% with *M. gigas*. In 1.1% of the total area all three species were predicted simultaneously. Both

M. edulis and *M. gigas* mostly occupied the shallowest depth strata (0 – 1 m), reaching almost full occupation of these habitats while it was slightly lower in exposed habitats. *O. edulis* was on the other hand almost completely absent from the shallowest habitat (0 – 0.5 m) and instead occupied deep areas, especially in sheltered habitats.

The patterns of abundances were similarly distributed across depth strata in exposed and sheltered habitats as the occupancy rates, but they were more pronounced (**Fig. 11**). The largest part of *M. edulis* and *M. gigas* individuals were predicted to occur in the shallowest habitats (0 – 0.5 m), for the most part in sheltered habitat. Of the total abundance of these species, 86 and 80% of *M. edulis* and *M. gigas* were predicted to occur in sheltered habitats respectively. Highest abundances of *O. edulis* were predicted between 0.5 and 2.5 m, after which it sharply declined towards deeper habitat. The majority of *O. edulis* individuals were predicted to reside in depths between 0.6 and 6 m, 61% of which were in sheltered habitats.

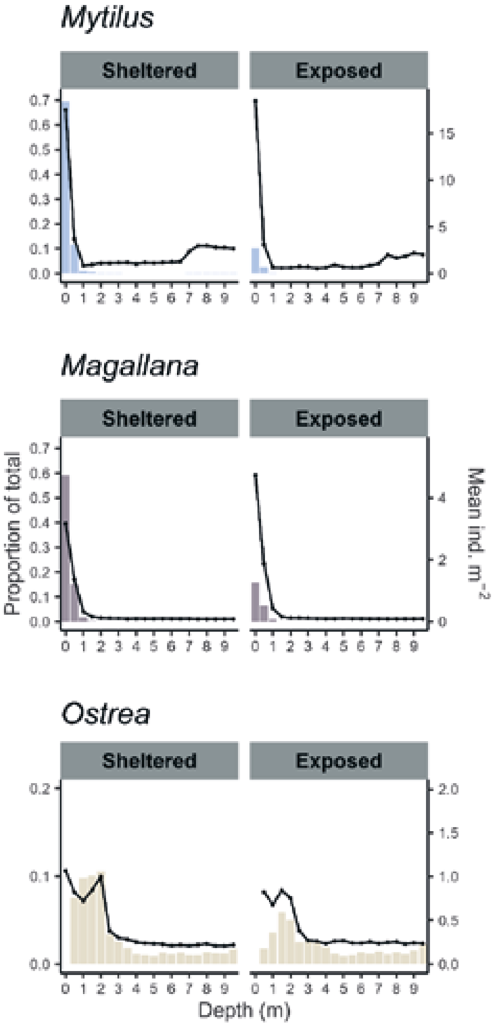

***Figure 11.** The proportion of total abundance (left axes, **coloured bars**) and mean abundance (ind. m^{-2}) (right axes, **lines**) of the modelled population for each species within each 0.5 m interval between 0 and 10 m depth for sheltered (**left**) and exposed (**right**) habitats.*

The combination of distribution and abundance models (Method 3) resulted in different estimates of total population sizes for *M. edulis* and *M. gigas*, compared to methods using no modelling (Method 1) or only distribution models (Method 2) (**Table 1**). The population size estimates for *O. edulis*, however, were consistent across the different methods. The total population size estimates for *M. edulis* were the largest (620 million), followed by *M. gigas* (214 million) and *O. edulis* (45 million). When converted to biomass (dry weight) the largest total was achieved by *M. gigas* (560 tonnes), followed by *M. edulis* (490 tonnes) and *O. edulis* (67 tonnes).

Table 1. *Populations size estimates (millions of individuals) (± SE) of three methods using no modelling (Method 1), presence-absence modelling (Method 2) and presence-absence combined with abundance modelling (Method 3). Dry weight and live wet weight biomass estimates (metric tonnes) (± SE) are based on Method 3 and average weights for each species.*

Species	Method 1	Method 2	Method 3	Dry weight	Live wet weight
Mytilus	2000 ± 290	2080 ± 78	620 ±30	490 ± 33	12 700 ± 860
Magallana	420 ± 43	550 ± 51	214 ± 6	560 ± 30	31 000 ± 1800
Ostrea	47 ± 8	43 ± 3	45 ± 2	67 ± 9	2 600 ± 320

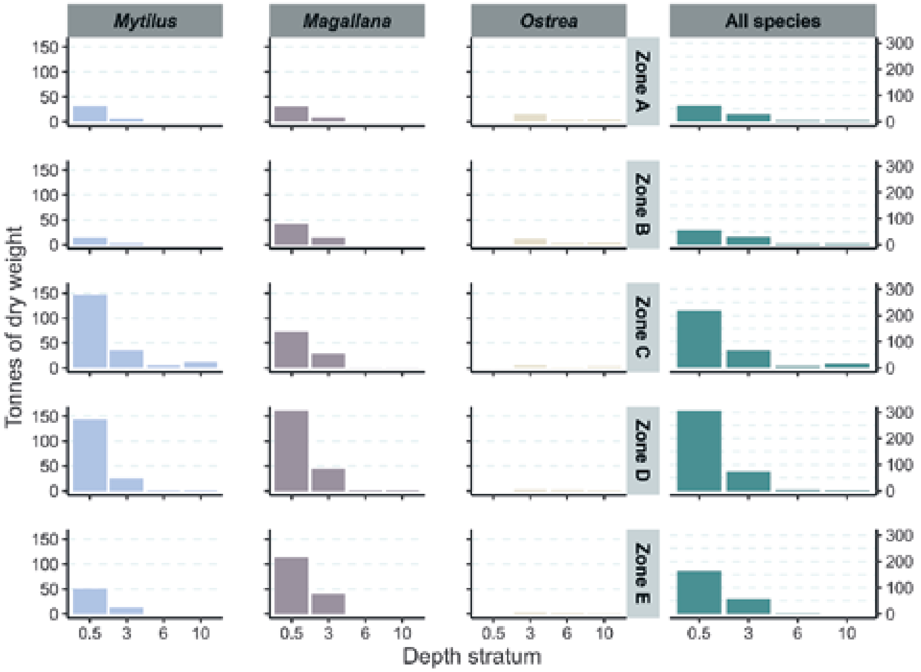

Figure 12. *The estimated tonnes of dry weight (DW, from Method 3) of each species and all species combined (columns) across four depth strata (0 – 0.5, 0.5 – 3, 3 – 6 and 6 – 10) within each zone (rows, A – E).*

In terms of distribution across the geographic range of the study area, each species showed distinct patterns (**Fig. 12**). Zone C and D were predicted to hold the largest part of the estimated biomass of *M. edulis*, while *M. gigas* biomass was predicted to be slightly more evenly distributed. The north of the study area (zone A and B) were predicted to contain most of the population of *O. edulis*.

When comparing the observational data of the occurrences of epifaunal bivalve *Mytilus spp.*, *M. gigas* and *O. edulis* in depths from 0.5 to 10 m and during the periods 2013 – 2014 (survey 1) and 2018 – 2020 (survey 2) in **Paper III**, it was found that the niche overlap had increased between all combinations of these species (**Fig. 13**). For each species the realized niche increased, with *M. gigas* showing the most expansion, and in accordance the prevalence increased for each species (8 – 10%) as well as their abundance.

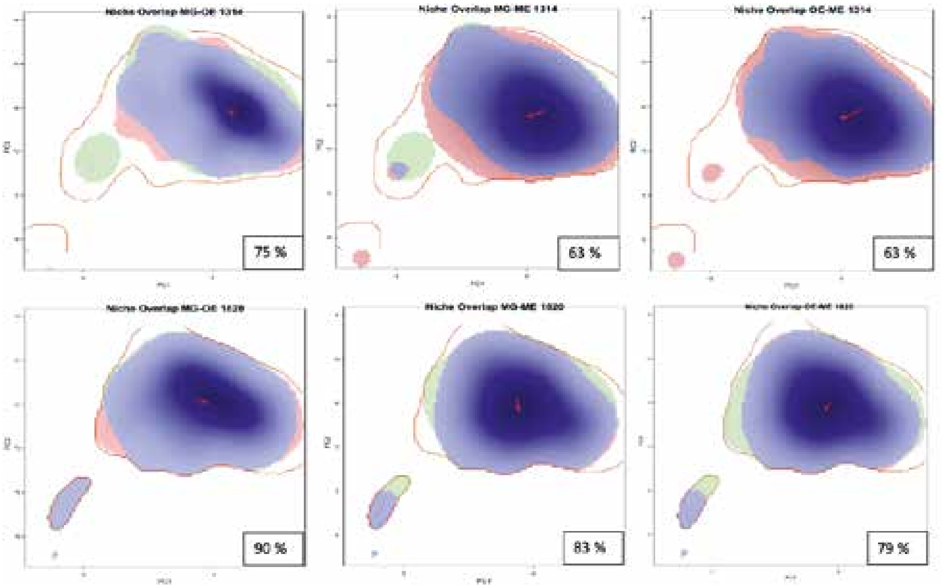

***Figure 13.** Interspecies niche comparisons between Magallana and Ostrea (**left**), Magallana and Mytilus (**centre**), and Ostrea and Mytilus (**right**) in the first survey (**upper row**) and the second survey (**bottom row**) as depicted by the biplot of the first two PCs. Blue areas represent overlap of the niches (% overlap shown in lower right). The solid line represents the available environments in each of the surveys. The arrow points in the direction of the difference in centroids between species within each survey. The correlation circle shows the distribution of twelve environmental variables along with the PC biplot.*

The distribution models for each individual species within each period performed well (AUC between 0.78 – 0.95), but the environmental variables that were most important for predicting distributions varied between species and periods. Depth was the most important variable for *M. gigas* in the first period, but wave exposure in second. For *O. edulis* the most important variable shifted from gravel substrate to wave exposure, while for *Mytilus spp.* depth was the most important in both periods. The realized niches of *M. gigas* and *O. edulis* inferred from partial dependence curves shifted between surveys, indicating that both species occurred in less exposed and shallower habitats during the second survey, compared to the first, while the niche of *Mytilus spp.* appeared to be stable.

The proportion of area predicted to be occupied by *M. gigas* decreased from 19 to 13% between the first to the second survey, while there was an increase for *Mytilus spp.* (from 17 to 30%) and *O. edulis* (from 6 to 14%) (**Fig. 14**). In terms of overlapping occupancy rates, the largest changes occurred in habitats predicted to be shared by *Mytilus spp.* and *M. gigas*, which dropped 11% and those where are all three species were predicted to occur which increased by 8%. The area where *M. gigas* and *O. edulis* were predicted to co-occur, however, remained stable.

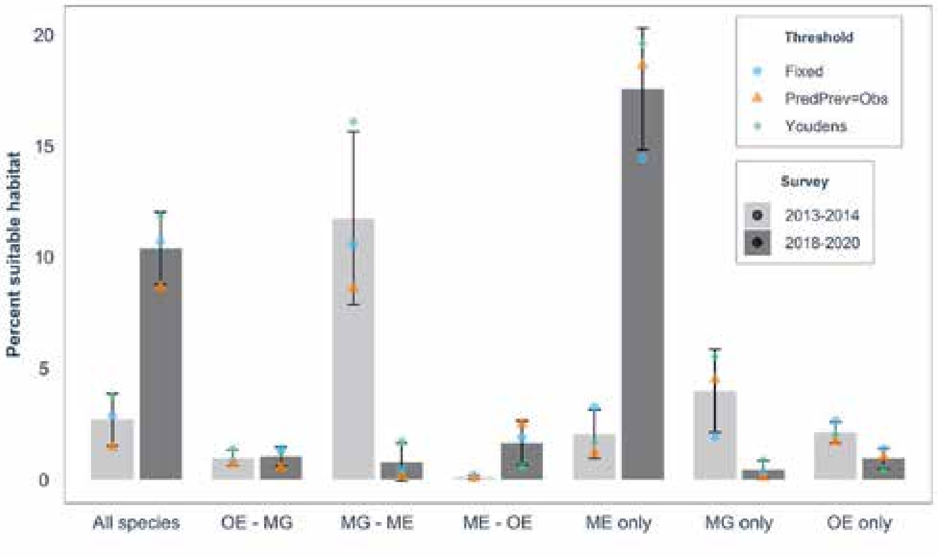

Figure 14. Predicted area suitable for all species, for Ostrea edulis (OE) and Magallana gigas (MG), for MG and Mytilus spp. (ME), for ME and OE, and for each of the three species alone (OE only, MG only, and ME only) during the first survey (2013-2014) and the second survey (2018-2020). Percent of suitable area is estimated by transforming predicted probability of occurrence into binary presence-absence predictions using three different threshold setting methods. Solid bars represent the mean and error bars represent the standard deviation.

By revisiting sites that were sampled between 1992 and 2004, it was revealed in **Paper IV** that there has evidently been a decline in abundances and/or sizes of several infaunal bivalve species on the Swedish and Norwegian Skagerrak coast, which together resulted into a decline of biomass and filtration rates. Mean abundances of both species in the genus *Cerastoderma* (*C. edule* and *C. glaucum*) showed a general trend of decline from the historic (1990's – 2000's) to the recent (2020's) data (**Fig. 15**). Declines in *C. edule* were larger and significantly collectively and in two separate regions (R2 and R4). The trends for *C. glaucum* were mixed, with declines in R1 – 3 (R1 significantly) and an increase in R4 though the overall trend was negative (**Fig. 15**).

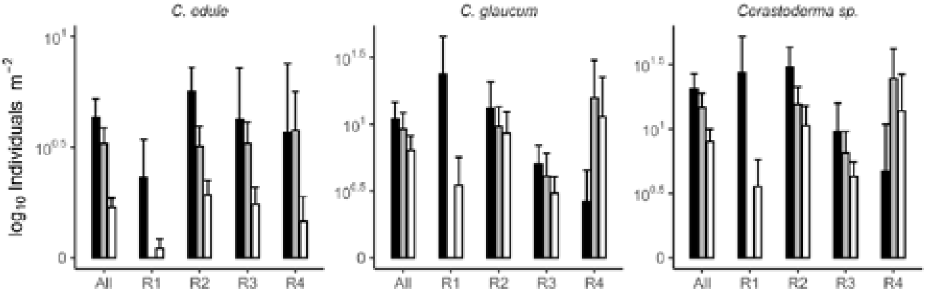

__Figure 15.__ Mean densities of C. edule, C. glaucum and Cerastoderma sp. for different regions (mean±SE). __Black__ = 1990's, __Grey__ = 2000's, __White__ = 2020's. Y axis on log10 scale.

Mean abundances of other species did not reveal any significant differences between historical and recent data, though the direction of change was consistently negative among regions for the species *Mya arenaria*, *Macoma balthica* and *Macomangulus tenuis* (**Fig. 16**). The trends for *Scrobicularia plana* were mixed, but with an overall increase, and *Polititapes aureus* had increased in all regions (**Fig. 16**).

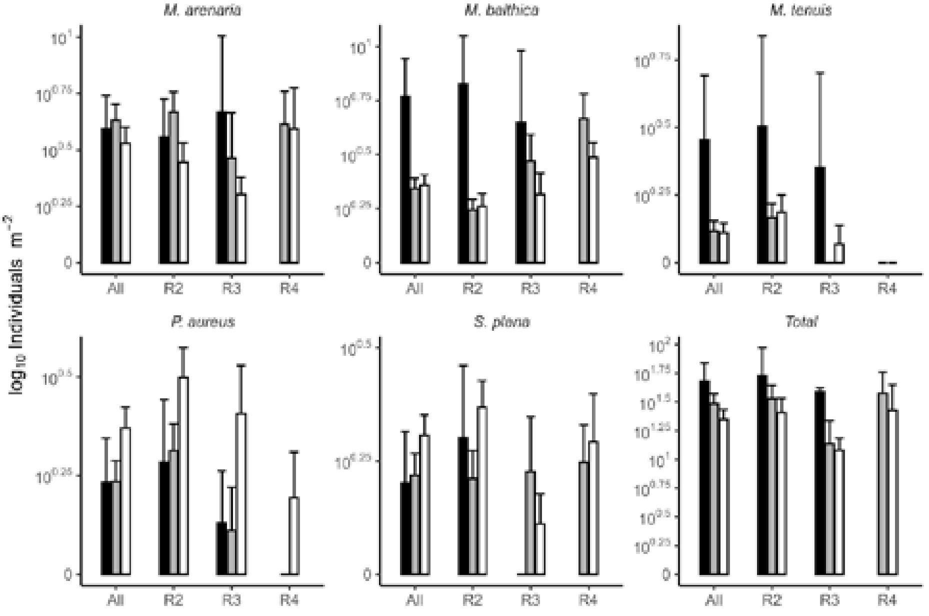

__Figure 16.__ Mean densities of individual species and total number of infaunal bivalves for all and separate regions (mean±SE). __Black__ = 1990's, __Grey__ = 2000's, __White__ = 2020's. Y axis on log10 scale.

Analysis on size distribution revealed there was a general trend towards smaller sizes in recent samples, specifically in the species *C. edule*, *C. glaucum*, *M. arenaria*. After these sizes were converted to biomass dry weight (DW m^{-2}), estimates showed a decline, both collectively (62% less) and for individual species (**Fig. 17C**). Interestingly, the estimates for filtration rates (l h^{-1} m^{-2}) showed an even more drastic decline (75%, **Fig. 17D**). This was even though historical average abundances for two important species (*C. glaucum* and *M. arenaria*) were higher than the recent averages in these particular sites, which was contrary to the general trend but highlights the effect size on filtration rates.

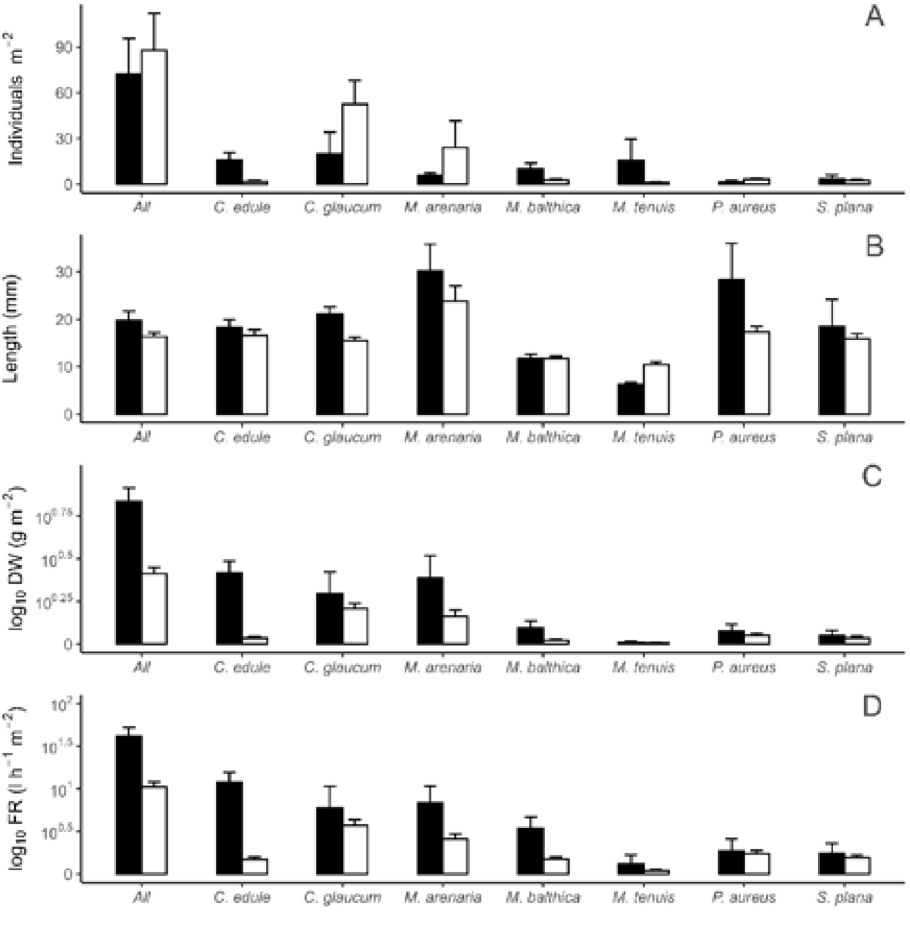

Figure 17. *Estimated mean abundances (**A**), length (**B**), biomass (**C**) and filtration rate (**D**) of seven infaunal bivalve species individually, and summed, at eight sites along the Swedish Skagerrak coast. Data from 1990's ($N_{1990's}$=8) black columns) and 2020's (white columns, $N_{2020's}$=72) (mean±SE).*

The caging experiment done in **Paper V** revealed that meso-predation is an important factor in regulating the recruitment success of juvenile bivalves. Across all sites, most juvenile bivalves were observed in sediment samples taken from fully closed cages, though there was a high degree of variability in these patterns and of recruitment intensity between sites. Statistical analysis confirmed that recruitment of *M. edulis* was on average highest in the plots where meso-predators were excluded (**Fig. 18**). Elevated recruitment in the partial cages where meso-predators still had access was indicative of caging artifacts, though this effect only present for *M. edulis* and was not large enough to obscure the effect of predation. After adjusting for the artifacts, recruitment of *M. edulis* in plots in the absence of meso-predators was 5.1 times higher than that in uncaged plots. There was also a significant effect of the addition of filamentous algae to the recruitment of *M. edulis,* which increased 2.4 times compared to plots without algae. Because there was no interactive effect between the filamentous algae and caging treatments this is indicative of a positive effect of settlement by the algae and not of any effects on the predation rates.

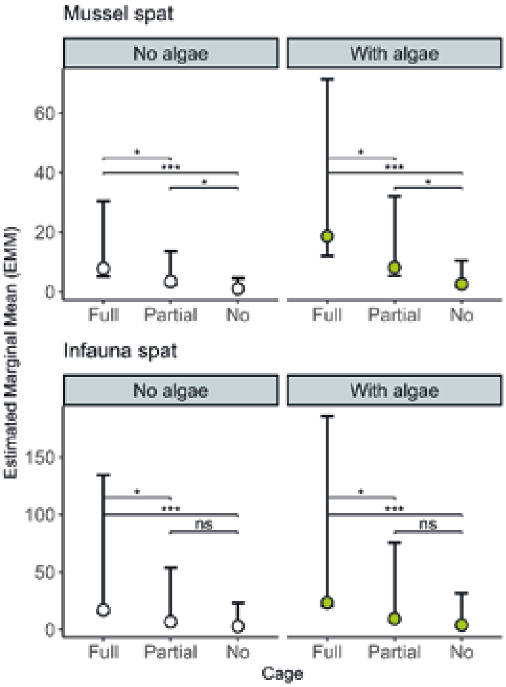

Figure 18. *The Estimated Marginal Means (EMMs) of the number of mussels (M. edulis) and infauna spat (for each combination of cage and algae treatment) standardized to ind. 0.1* m^{-2}*. Error bars represent the 95% confidence intervals. T-test p values are given in: **>0.01, ***>0.001 or ns (not significant).*

There was a similar significant effect found by meso-predator exclusion on the recruitment of infaunal bivalves, but there was no indication of caging artifacts (**Fig. 18**). The recruitment in the absence of meso-predators was 4.8 times higher for infaunal species, but there was no significant effect of filamentous algae on recruitment.

DISCUSSION

SPATIAL DISTRIBUTION AND RELATIVE IMPORTANCE

One of the aims of this thesis was to describe the current bivalve community structures on the Skagerrak coast to identify important species and overall contribution of functional groups (epi- or infaunal) towards ecosystem functions and services. In **Paper I**, a sampling design structured to address this aim revealed complex patterns between the environmental factors depth and wave exposure, substrate characteristics and bivalve communities. The importance of wave exposure is often linked to substrate characteristics and sedimentation rates, which in turn impact habitat suitability for epi- and infaunal bivalves (Emerson & Grant 1991, Westerbom & Jattu 2006, Compton et al., 2009). Indeed, the results in **Paper I** showed that the availability of sedimentary habitat (i.e. other than rock) and composition was linked to wave exposure but also depended on coastal location (i.e. in or offshore). There was also a strong pattern of bivalve abundances and biomass in relation to depth, with higher averages below the intertidal zone (> 0.5 m). This pattern was possibly due to an interactive effect between depth and exposure because shallow habitats experience higher levels of shear stress from waves (Bekkby et al., 2008). The combination of low tides and cold winter temperatures has, however, also been shown to cause high mortalities of bivalves in shallow water (Möller & Rosenberg 1983, Möller 1986, Strand et al., 2012).

Although there were strong differentiations in community structures between habitat-types, it was the areal extent of these habitats that ultimately shaped the overall regional total for abundances and biomass. Of the total bivalve biomass, it was found that ≈80 to 90% constituted of epifaunal species (i.e. mussels and oysters), thereby making this group more important for providing ecosystem functions and services than infaunal species in a general perspective. This percentage was, however, not equal across all habitat types and infaunal bivalves were sometimes observed to be locally more important than epibenthic bivalves for biomass especially in deeper (0.5 – 2 m) habitats with moderate levels of wave exposure.

The variability in abundance and biomass within habitat-types indicated that there remained more complexity to be accounted for in regards the environment and associated bivalve communities. To address this, the application of successive modelling of distribution and abundances of three of the most common epifaunal species (*M. edulis*, *M. gigas* and *O. edulis*) in **Paper II** allowed for simultaneous evaluation of many variables at finer scales, thereby capturing more of the habitat-population structure complexity and theoretically resulting in better estimates of population sizes. Although species distribution models have become a mainstream tool to study species geographical ranges, the use of abundance models is much less commonplace despite the benefits they could provide for ecological research questions (Waldock et al., 2022 and references therein).

It was found that modelling distribution and abundances resulted in not only realistic estimates of population size, but also provided detailed information on habitat use and geographic distribution of all three species. The two most abundant species, *M. edulis* and *M. gigas*, locally occupied very similar habitats in a narrow, shallow depth range (0 – 1 m) though they differed in large scale distribution with *M. gigas* being more common throughout and *M. edulis* being more concentrated in certain parts of the coast. In contrast, *O. edulis* was predicted to be more abundant in deeper habitats which corresponds to differences found between *M. gigas* and *O. edulis* depth preferences in the Adriatic Sea (Stagličić et al., 2020) and mostly in the northern parts of the study area which is possible due to larval transport towards this region (Gustafsson et al., 2023).

These results represent the first fully comprehensive population size estimates for *M. edulis* and *O. edulis* in this area, and an updated and extended assessment of the population size of *M. gigas*. This is especially relevant for the native species as the reefs formed by these species are designated as critical habitats for protection and restoration (OSPAR 2009, OSPAR 2015, EU 2024). *M. edulis* is currently believed to have declined in this area in recent decades (Baden et al., 2021), and *O. edulis* was recently assessed as functionally extinct in all of Europe (zu Ermgassen et al., 2024). Importantly, it was found that population size estimates of *O. edulis* were similar to those made earlier by Thorngren et al., (2019), despite originating from different data sets and methods, which suggests this threatened species has remained stable, and underpins the validity of the modelling approach. These populations size estimates and distribution patterns provide current baselines for future monitoring of these important habitat forming species.

TEMPORAL CHANGES

The second aim of this thesis was to describe temporal changes in the bivalve population structure on the Skagerrak coast. Perhaps the most striking is the extent to which the invasive oyster *M. gigas* dominates total epifaunal biomass estimates currently (50 – 60%, **Paper I** and **II**), after arriving in this area in 2006 (Wrange et al., 2010). Results from **Paper III** indicate that between 2013 and 2020 *M. gigas* was still in the process of expanding its range and now occurs in a wide range of habitats and overlaps with native species, especially with *M. edulis*. There was, however, no indication that this invasion event resulted in the displacement and decline of native epifaunal species, which is concurrence with other studies that found persisting cohabitation with *M. edulis* (Kochmann et al., 2008, Holm et al., 2016, Reise et al., 2017) and *O. edulis* (Christianen et al., 2018). Still, complex interactive processes (both positive and negative) between *M. gigas* and *M. edulis* have been found (Eschweiler & Christensen 2011, Buschbaum et al., 2016, Joyce et al., 2021), which suggests that also in this area the native species are affected by this invasion event. The outcome of these interactions will likely become more apparent as time passes and if *M. gigas* continues to expand its range and become more abundant, which will require further monitoring in the future to evaluate. Although the complete eradication of *M. gigas* is not feasible, management action can be taken depending on the desired outcomes which must be weighed against both environmental and socioeconomic costs (Hansen et al., 2023).

The abundances of infaunal bivalves found in **Paper I** were lower than expected, based on previous research (e.g. Lindegarth et al., 1995). Whether this observation was indicative of a long-term decline across a larger geographic area was tested in **Paper IV** using available historic data. Negative trends in abundances were found for most common species in all regions on the investigated Skagerrak coast, but most pronounced in the cockles *C. edule* and *C. glaucum*. Additionally, average sizes for *C. edule*, *C. glaucum* and *M. arenaria* were lower in recent samples with a general lack of larger individuals, which could be due to higher mortalities. These observations match those made on cockles in the UK (Callaway 2022) and other bivalves in Denmark (Riemann et al., 2016) where the declines were attributed to reduced nutrient input and thus lower food availability. Populations of infaunal bivalves are, however, known to fluctuate significantly due to events of mass mortality and recruitment (Beukema et al., 2001, Burdon et al., 2014), which means long-term monitoring with consistent effort is needed to interpret temporal trends (Zettler et al., 2017). Nonetheless, the data spanned a large geographic area, with multiple years of observation within each period which indicate that consistent declines in infaunal bivalve abundances, size and biomass have occurred in the last 30 years.

Mussels (*Mytilus spp.*) have been perceived to have declined in several locations in the north Atlantic region in a similar time span (Sorte et al., 2017, Baden et al., 2021). Because individuals living away from the sea bed on floating artificial substrates seem less affected (Christie et al., 2020, Baden et al., 2021) it is hypothesized that predation by benthic meso-predators (e.g. shrimps, crabs and starfish) could be an underlying mechanism for these observed patterns. The abundance of these predators have also been observed to have increased in recent decades due to the overfishing of top-predators (Eriksson et al., 2011, Baden et al., 2012), which has caused so-called trophic cascades in other habitats in the area such as seagrass meadows (Moksnes et al., 2008). In **Paper V**, it was concluded that predation on recruits of mussels and infaunal bivalves was high and in theory could be causing the observed declines in both, though not all recruits were removed by predators during the timespan of the experiment and the effect of predation was variable among sites. Thus, further studies are required to understand the interplay between recruitment intensity and the distribution and abundance of predators in determining the long-term effects on bivalve populations. Filamentous algal mats have been increasingly observed to cover shallow bays in Sweden (Pihl et al., 1995), and are also thought to impact mussels negatively (Baden et al., 2021). These mats can impact benthic faunal communities by reducing flow and causing episodes of hypoxia (Norkko et al., 2000, Arroyo et al., 2012). Results in **Paper V**, however, showed that filamentous algae was positive for mussel recruitment which was likely due to increased settlement of plantigrade spat on the algae (Dobretsov & Wahl 2008). The negative effects likely occur at larger spatial and temporal scales which could not be addressed in this experiment due methodological limitations and requires additional research to evaluate in their effect on bivalve populations on the Skagerrak coast.

IMPLICATIONS FOR ECOSYSTEM FUNCTIONS AND SERVICES

In bivalves, the rate of most processes performed by an individual is to a large extent related to its biomass, e.g. filtration rate, secondary production, oxygen consumption and reproductive output (Honkoop et al., 1999, Riisgård 2001, Beukema & Dekker 2013, Sanders et al., 2018). Thus, in this thesis biomass is used as a measurement to draw conclusions on the relative ecological importance of separate species or functional groups (**Paper I**, **II**). The relationship between biomass and filtration rate was utilized in **Paper IV** to changes in estimates of average filtration capacity of infaunal bivalves. It must be noted, however, that the nature of some of these relationships are also influenced by other external factors. For instance, for filtration rates, the species, food density and quality, temperature, water flow speeds and conditioning prior to measurements all affect the rates of filtration for each unit of biomass (Riisgård 2001). The efficiency of suspension feeding is also reduced when bivalves are in proximity to other suspension feeders (Jones et al., 2011) or when they are only partially inundated within a tidal cycle (Vismann et al., 2016). It is therefore logical that the relation of biomass to ecological functions such as water filtration is highly dependent on the context of each individual and its environment. Total ecosystem function provision is therefore more complicated than the straightforward addition of abundances and biomass (Sanders et al., 2024). Nonetheless, the use of biomass was assumed to be at least representable of ecological significance regardless of these limitations.

It was shown that biomass related ecosystem functions, such as filtration, is chiefly performed by epifaunal species in general. In smaller spatial context, the infaunal biomass at times still exceeds that of the epifauna, meaning that in some habitats they are still ecologically more impactful. Also, among the epifaunal species, *O. edulis* is more important in deeper habitats than other species along the Swedish Skagerrak coast and especially so in the northern parts of its distribution range.

The temporal changes described (i.e. *M. gigas* expansion and infaunal decline) in bivalve populations are likely to have had implications for ecosystem functions and services on the Skagerrak coast, but to evaluate this quantitatively, knowledge about habitat-use and extent, biomass density and temporal trends need to be combined. As an example of this, biomasses measured in **Paper I** were transformed into individual estimates of filtration rates (FR), using the same generic formula used in **Paper IV** ($FR = 5 \times DW^{0.7}$) and transformed to average FR m^{-2} in each habitat-type. Applying the same methods with the known areal extent of those habitats, the current total filtration capacity of both epi- and infaunal bivalves in this area could be estimated (2020's, **Fig. 19**).

Next, these estimates were used to back-cast the state in the 1990's using knowledge about recent events and observation gathered in this thesis (from 1990's to 2020's, **Fig. 19**). First, we used the observed decline in overall infaunal filtration capacity (75%) observed in **Paper IV**, assuming also that it extended to sediment habitats down to 2 m depth. Second, the filtration capacity of *M. gigas* was set to zero in the 1990's, as they were not present before 2007. The last remaining important component in this area is *M. edulis*, which is believed to have declined as well, but the magnitude of this is unknown (Baden et al., 2021). To address this, three different alternative scenarios for back-casting were compared, assuming that **1**) *M. edulis* filtration capacity was the same as current (i.e. no decline in *M. edulis* biomass m^{-2}); **2**) a 50% decline in *M. edulis* biomass has occurred; and **3**) a 75% decline of *M.* edulis biomass has occurred (1990's, **Fig. 19**). Interestingly, the results of these calculations indicate that the total filtration capacity of bivalves has declined (30 – 55%) in recent decades under all scenarios. Furthermore, it is suggested that the relative importance of epi- and infaunal bivalves has undergone a major functional shift, from a more infaunal to an epifaunal dominated system. Therefore, the findings from this thesis suggest that, potentially, some losses of ecosystem functions related to filtration and those related to infaunal species (e.g. bioturbation and irrigation) have occurred. The potential implications of these changes include altered states of pelagic communities, reduced efficiency in nutrient cycling and benthic-pelagic coupling and less-oxygenated sediments.

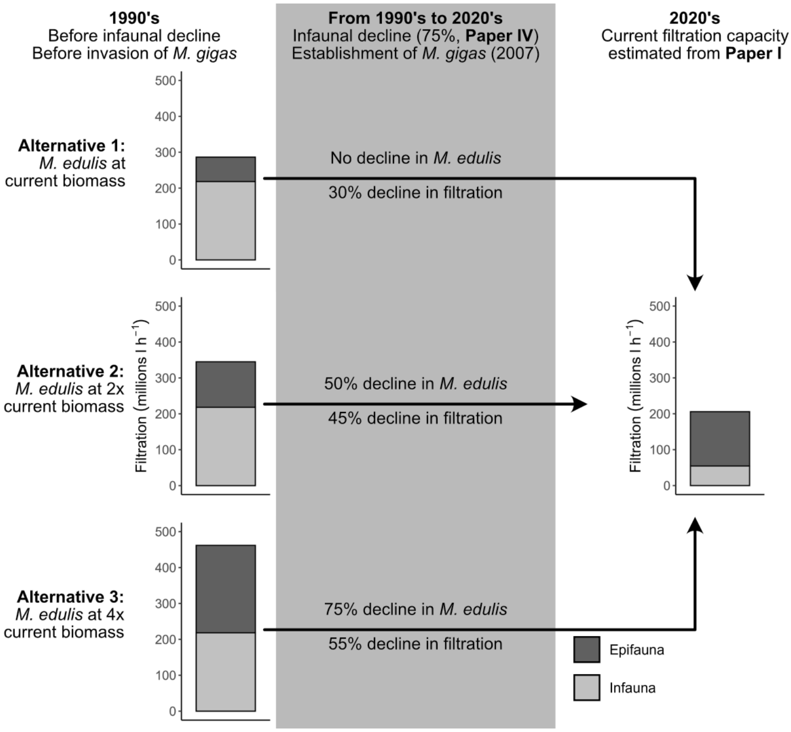

Figure 19. *Comparing estimated total filtration capacity (millions l h^{-1}) of bivalves in the Koster – Tjärnö area from* ***Paper I*** *(0 – 2 m depth) in current (2020's) and past (1990's) using 3 alternative scenarios of change in the M. edulis biomass.*

CONCLUSION

This thesis provides a contribution towards a more comprehensive understanding of the population structure of shallow-living bivalves on the Skagerrak coast and some of the environmental factors and biotic interactions that shape them. The modelling of distributions and abundances was shown to be an effective method for evaluating this in more detail and on larger scales, which resulted in new estimates of population size for some of the most important species. These estimates can serve as current baselines for the future as it was shown that some extensive changes have occurred in the bivalve populations in this area in the recent future. The relative contribution of species and functional groups towards ecosystem functions were discussed, which can be seen as a first step into this endeavor. More sophisticated methods should be developed to address the actual realized ecological functions, and ultimately services.

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REFERENCES

Arroyo NL, Aarnio K, Mäensivu M, Bonsdorff E (2012) Drifting filamentous algal mats disturb sediment fauna: Impacts on macro–meiofaunal interactions. *Journal of Experimental Marine Biology and Ecology* 420–421:77–90.

Baden S, Emanuelsson A, Pihl L, Svensson C, Åberg P (2012) Shift in seagrass food web structure over decades is linked to overfishing. *Marine Ecology Progress Series* 451:61–73.

Baden S, Hernroth B, Lindahl O (2021) Declining Populations of Mytilus spp. in North Atlantic Coastal Waters—A Swedish Perspective. *Journal of Shellfish Research* 40.

Beck MW, Brumbaugh RD, Airoldi L, Carranza A, Coen LD, Crawford C, Defeo O, Edgar GJ, Hancock B, Kay MC, Lenihan HS, Luckenbach MW, Toropova CL, Zhang G, Guo X (2011) Oyster Reefs at Risk and Recommendations for Conservation, Restoration, and Management. *BioScience* 61:107–116.

Bekkby T, Isachsen PE, Isæus M, Bakkestuen V (2008) GIS Modeling of Wave Exposure at the Seabed: A Depth-attenuated Wave Exposure Model. *Marine Geodesy* 31:117–127.

Berghahn R, Ruth M (2005) The disappearance of oysters from the Wadden Sea: a cautionary tale for no-take zones. *Aquatic Conservation: Marine and Freshwater Ecosystems* 15:91–104.

Bergström P, Thorngren L, Strand Å, Lindegarth M (2021) Identifying high-density areas of oysters using species distribution modeling: Lessons for conservation of the native *Ostrea edulis* and management of the invasive *Magallana* (*Crassostrea*) *gigas* in Sweden. *Ecology and Evolution* 11:5522–5532.

Bertolini C, Montgomery WI, O'Connor NE (2018) Habitat with small inter-structural spaces promotes mussel survival and reef generation. *Marine Biology* 165:163.

Beukema J, Dekker R (2013) Evaluation of Brey's production/biomass model on the basis of a long-term data set on a clam population. *Marine Ecology Progress Series* 489:163–175.

Beukema J, Dekker R, Essink K, Michaelis H (2001) Synchronized reproductive success in the main bivalve species in the Wadden Sea: causes and consequences. *Marine Ecology Progress Series* 211:143–155.

Both A, Byron CJ, Costa-Pierce B, Parrish CC, Brady DC (2020) Detrital Subsidies in the Diet of Mytilus edulis; Macroalgal Detritus Likely Supplements Essential Fatty Acids. *Frontiers in Marine Science* 7:561073.

Burdon D, Callaway R, Elliott M, Smith T, Wither A (2014) Mass mortalities in bivalve populations: A review of the edible cockle Cerastoderma edule (L.). *Estuarine, Coastal and Shelf Science* 150:271–280.

Buschbaum C, Cornelius A, Goedknegt MA (2016) Deeply hidden inside introduced biogenic structures – Pacific oyster reefs reduce detrimental barnacle overgrowth on native blue mussels. *Journal of Sea Research* 117:20–26.

Callaway R (2022) 50 years of estuarine cockles (Cerastoderma edule L.): Shifting cohorts, dwindling sizes and the impact of improved wastewater treatment. *Estuarine, Coastal and Shelf Science* 270:107834.

Carmichael RH, Shriver AC, Valiela I (2012) Bivalve Response to Estuarine Eutrophication: The Balance between Enhanced Food Supply and Habitat Alterations. *Journal of Shellfish Research* 31:1–11.

Christianen MJA, Lengkeek W, Bergsma JH, Coolen JWP, Didderen K, Dorenbosch M, Driessen FMF, Kamermans P, Reuchlin-Hugenholtz E, Sas H, Smaal A, Van

Den Wijngaard KA, Van Der Have TM (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. *Marine Biology Research* 14:590–597.

Christie H, Kraufvelin P, Kraufvelin L, Niemi N, Rinde E (2020) Disappearing Blue Mussels – Can Mesopredators Be Blamed? *Frontiers in Marine Science* 7:550.

Compton T, Troost T, Drent J, Kraan C, Bocher P, Leyrer J, Dekinga A, Piersma T (2009) Repeatable sediment associations of burrowing bivalves across six European tidal flat systems. *Marine Ecology Progress Series* 382:87–98.

Costanza R, d'Arge R, De Groot R, Farber S, Grasso M, Hannon B, Limburg K, Naeem S, O'Neill RV, Paruelo J, Raskin RG, Sutton P, Van Den Belt M (1997) The value of the world's ecosystem services and natural capital. *Nature* 387:253–260.

Dobretsov S, Wahl M (2008) Larval recruitment of the blue mussel Mytilus edulis: The effect of flow and algae. *Journal of Experimental Marine Biology and Ecology* 355:137–144.

Duperron S, Gaudron SM, Rodrigues CF, Cunha MR, Decker C, Olu K (2013) An overview of chemosynthetic symbioses in bivalves from the North Atlantic and Mediterranean Sea. *Biogeosciences* 10:3241–3267.

Emerson CW, Grant J (1991) The control of soft-shell clam (Mya arenaria) recruitment on intertidal sandflats by bedload sediment transport. *Limnology & Oceanography* 36:1288–1300.

Eriksson BK, Sieben K, Eklöf J, Ljunggren L, Olsson J, Casini M, Bergström U (2011) Effects of Altered Offshore Food Webs on Coastal Ecosystems Emphasize the Need for Cross-Ecosystem Management. *AMBIO* 40:786–797.

Eschweiler N, Christensen HT (2011) Trade-off between increased survival and reduced growth for blue mussels living on Pacific oyster reefs. *Journal of Experimental Marine Biology and Ecology* 403:90–95.

EU (2024) Regulation (EU) 2024/1991 of the European Parliament and of the Council of 24 June 2024 on nature restoration and amending Regulation (EU) 2022/869.

Evan Ward J, Shumway SE (2004) Separating the grain from the chaff: particle selection in suspension- and deposit-feeding bivalves. *Journal of Experimental Marine Biology and Ecology* 300:83–130.

Evans S, Tallmark B (1976) Distribution and Size Frequency of Bivalve Molluscs on a Shallow, Sandy Bottom in Gullmar Fjord (Sweden). *ZOON* 4:49–52.

FAO (2024) The State of World Fisheries and Aquaculture 2024 – Blue Transformation in action. *FAO, Rome*.

Faust E, André C, Meurling S, Kochmann J, Christiansen H, Jensen L, Charrier G, Laugen A, Strand Å (2017) Origin and route of establishment of the invasive Pacific oyster Crassostrea gigas in Scandinavia. *Marine Ecology Progress Series* 575:95–105.

Flach EC (2003) The separate and combined effects of epibenthic predation and presence of macro-infauna on the recruitment success of bivalves in shallow soft-bottom areas on the Swedish west coast. *Journal of Sea Research* 49:59–67.

Gephart JA, Henriksson PJG, Parker RWR, Shepon A, Gorospe KD, Bergman K, Eshel G, Golden CD, Halpern BS, Hornborg S, Jonell M, Metian M, Mifflin K, Newton R, Tyedmers P, Zhang W, Ziegler F, Troell M (2021) Environmental performance of blue foods. *Nature* 597:360–365.

Gilby BL, Olds AD, Peterson CH, Connolly RM, Voss CM, Bishop MJ, Elliott M, Grabowski JH, Ortodossi NL, Schlacher TA (2018) Maximizing the benefits of oyster reef restoration for finfish and their fisheries. *Fish and Fisheries* 19:931–947.

Gosling E (2003) Bivalve Molluscs: Biology, Ecology and Culture, 1st ed. Wiley.

Grabowski JH, Brumbaugh RD, Conrad RF, Keeler AG, Opaluch JJ, Peterson CH, Piehler MF, Powers SP, Smyth AR (2012) Economic Valuation of Ecosystem Services Provided by Oyster Reefs. *BioScience* 62:900–909.

Gustafsson M, De Wit P, Robert C, Wrange A-L, Laugen AT, Strand Å (2023) Kunskapsunderlag för en enhetlig förvaltning av OSPAR-listade Mytilus- och Ostrea-bankar Del 3 – Underlag för bedömning av bevarandevärde av Mytilus- och Ostrea-bankar. *IVL Svenska Miljöinstitutet*, Stockholm.

Hansen BW, Dolmer P, Vismann B (2023) Too late for regulatory management on Pacific oysters in European coastal waters? *Journal of Sea Research* 191:102331.

Hemraj DA, Bishop MJ, Hancock B, Minuti JJ, Thurstan RH, Zu Ermgassen PSE, Russell BD (2022) Oyster reef restoration fails to recoup global historic ecosystem losses despite substantial biodiversity gain. *Science Advances* 8:eabp8747.

Herbert RJH, Humphreys J, Davies ClareJ, Roberts C, Fletcher S, Crowe TasmanP (2016) Ecological impacts of non-native Pacific oysters (Crassostrea gigas) and management measures for protected areas in Europe. *Biodiversity and Conservation* 25:2835–2865.

Holm MW, Davids JK, Dolmer P, Holmes E, Nielsen T (2016) Coexistence of Pacific oyster Crassostrea gigas (Thunberg, 1793) and blue mussels Mytilus edulis Linnaeus, 1758 on a sheltered intertidal bivalve bed? *Aquatic Invasions* 11:155–165.

Honkoop PJC, Van Der Meer J, Beukema JJ, Kwast D (1999) Reproductive investment in the intertidal bivalve Macoma balthica. *Journal of Sea Research* 41:203–212.

Humphries AT, La Peyre MK, Kimball ME, Rozas LP (2011) Testing the effect of habitat structure and complexity on nekton assemblages using experimental oyster reefs. J*ournal of Experimental Marine Biology and Ecology* 409:172–179.

IPCC (2023) Oceans and Coastal Ecosystems and Their Services. In: *Climate Change 2022 – Impacts, Adaptation and Vulnerability: Working Group II Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*, 1st ed. Cambridge University Press

Johannesson K (1989) The Bare Zone of Swedish Rocky Shores: Why Is It There? *Oikos* 54:77.

Jones CG, Lawton JH, Shachak M (1997) Positive and Negative Effects of Organisms as Physical Ecosystem Engineers. *Ecology* 78:1946–1957.

Jones HFE, Pilditch CA, Bruesewitz DA, Lohrer AM (2011a) Sedimentary Environment Influences the Effect of an Infaunal Suspension Feeding Bivalve on Estuarine Ecosystem Function. *PLoS ONE* 6:e27065.

Jones HFE, Pilditch CA, Bryan KR, Hamilton DP (2011b) Effects of infaunal bivalve density and flow speed on clearance rates and near-bed hydrodynamics. *Journal of Experimental Marine Biology and Ecology* 401:20–28.

Joyce PWS, Smyth DM, Dick JTA, Kregting LT (2021) Coexistence of the native mussel, Mytilus edulis, and the invasive Pacific oyster, Crassostrea (Magallana) gigas, does not affect their growth or mortality, but reduces condition of both species. *Hydrobiologia* 848:1859–1871.

Kochmann J, Buschbaum C, Volkenborn N, Reise K (2008) Shift from native mussels to alien oysters: Differential effects of ecosystem engineers. *Journal of Experimental Marine Biology and Ecology* 364:1–10.

Koppel J van de, Rietkerk M, Dankers N, Herman PMJ (2005) Scale-Dependent Feedback and Regular Spatial Patterns in Young Mussel Beds. T*he American Naturalist* 165:E66–E77.

Laugen AT, 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*, p 230–252

Laugen AT, Wrange A-L, Krång A-S, Reamon MC, Svedberg K, Waldetoft H, Strand Å (2023) Kunskapsunderlag för en enhetlig förvaltning av OSPAR-listade Mytilus- och Ostrea-bankar: Del 1 Nulägesanalys av Mytilus- och Ostrea-bankar i Sverige. *IVL Svenska Miljöinstitutet*, Stockholm.

Lindegarth M, Andre M, Jonsson P (1995) Analysis of the spatial variability in abundance and age structure of two infaunal bivalves, Cerasto-derma edule and C. lamarcki, using hierarchical sampling programs. *Marine Ecology Progress Series* 116:85–97.

Longmire K, Seitz R, Smith A, Lipcius R (2021) Saved by the shell: Oyster reefs can shield juvenile blue crabs Callinectes sapidus. *Marine Ecology Progress Series* 672:163–173.

Lotze HK, Lenihan HS, Bourque BJ, Bradbury RH, Cooke RG, Kay MC, Kidwell SM, Kirby MX, Peterson CH, Jackson JBC (2006) Depletion, Degradation, and Recovery Potential of Estuaries and Coastal Seas. *Science* 312:1806–1809.

Macreadie P, Geraldi N, Peterson C (2012) Preference for feeding at habitat edges declines among juvenile blue crabs as oyster reef patchiness increases and predation risk grows. *Marine Ecology Progress Series* 466:145–153.

Mascorda-Cabre L, Hosegood P, Attrill MJ, Sheehan EV (2024) Biogenic reef creation and biodiversity enhancement by an offshore longline mussel farm. *Ecological Indicators* 167:112708.

McCoy DE, Burns DH, Klopfer E, Herndon LK, Ogunlade B, Dionne JA, Johnsen S (2024) Heart cockle shells transmit sunlight to photosymbiotic algae using bundled fiber optic cables and condensing lenses. *Nature Communications* 15:9445.

Millennium Ecosystem Assessment (2005) *Ecosystems and human well-being: synthesis.* Island Press, Washington, DC.

Moksnes P, Gullström M, Tryman K, Baden S (2008) Trophic cascades in a temperate seagrass community. *Oikos* 117:763–777.

Möller P (1986) Physical factors and biological interactions regulating infauna in shallow boreal areas. *Marine Ecology Progress Series* 30:33–47.

Möller P, Pihl L, Rosenberg R (1985) Benthic faunal energy flow and biological interaction in some shallow marine soft bottom habitats. *Marine Ecology Progress Series* 27:109–121.

Möller P, Rosenberg R (1983) Recruitment, abundance and production of Mya arenaria and Cardium edule in marine shallow waters, Western Sweden. *Ophelia* 22:33–55.

Morris RL, Bilkovic DM, Boswell MK, Bushek D, Cebrian J, Goff J, Kibler KM, La Peyre MK, McClenachan G, Moody J, Sacks P, Shinn JP, Sparks EL, Temple NA, Walters LJ, Webb BM, Swearer SE (2019) The application of oyster reefs in shoreline protection: Are we over-engineering for an ecosystem engineer? *Journal of Applied Ecology* 56:1703–1711.

Morton B, Machado FM (2019) Predatory marine bivalves: A review. In: *Advances in Marine Biology*. Elsevier, p 1–98

Newell RIE, Cornwell JC, Owens MS (2002) Influence of simulated bivalve biodeposition and microphytobenthos on sediment nitrogen dynamics: A laboratory study. *Limnology & Oceanography* 47:1367–1379.

Newell RIE, Koch EW (2004) Modeling seagrass density and distribution in response to changes in turbidity stemming from bivalve filtration and seagrass sediment stabilization. *Estuaries* 27:793–806.

Norkko A, Hewitt JE, Thrush SF, Funnell T (2001) Benthic-pelagic coupling and suspension-feeding bivalves: Linking site-specific sediment flux and biodeposition to benthic community structure. *Limnology & Oceanography* 46:2067–2072.

Norkko J, Bonsdorff E, Norkko A (2000) Drifting algal mats as an alternative habitat for benthic invertebrates: Species specific responses to a transient resource. *Journal of Experimental Marine Biology and Ecology* 248:79–104.

Norkko J, Shumway SE (2011) Bivalves as Bioturbators and Bioirrigators. In: *Shellfish Aquaculture and the Environment*, 1st ed. Shumway SE (ed) Wiley, p 297–317

Norling P, Kautsky N (2007) Structural and functional effects of Mytilus edulis on diversity of associated species and ecosystem functioning. *Marine Ecology Progress Series* 351:163–175.

Norling P, Lindegarth M, Lindegarth S, Strand Å (2015) Effects of live and post-mortem shell structures of invasive Pacific oysters and native blue mussels on macrofauna and fish. *Marine Ecology Progress Series* 518:123–138.

Ó Foighil D, Taylor DJ (2000) Evolution of Parental Care and Ovulation Behavior in Oysters. *Molecular Phylogenetics and Evolution* 15:301–313.

OSPAR (2009) Background Document for *Ostrea edulis* and *Ostrea edulis* Beds. *OSPAR Biodiversity Series publication.*

OSPAR (2015) Background Document on Intertidal *Mytilus edulis* Beds on Mixed and Sandy Sediments. *OSPAR Biodiversity Series publication.*

Petersen JK, Saurel C, Nielsen P, Timmermann K (2016) The use of shellfish for eutrophication control. *Aquaculture International* 24:857–878.

Peterson B, Heck K (2001) An experimental test of the mechanism by which suspension feeding bivalves elevate seagrass productivity. *Marine Ecology Progress Series* 218:115–125.

Pihl L, Isaksson I, Wennhage H, Moksnes P-O (1995) Recent increase of filamentous algae in shallow Swedish bays: Effects on the community structure of epibenthic fauna and fish. *Netherlands Journal of Aquatic Ecology* 29:349–358.

Prins TC, Smaal AC, Dame RF (1997) A review of the feedbacks between bivalve grazing and ecosystem processes. *Aquatic Ecology* 31:349–359.

Reise K (2002) Sediment mediated species interactions in coastal waters. *Journal of Sea Research* 48:127–141.

Reise K, Buschbaum C, Büttger H, Wegner KM (2017) Invading oysters and native mussels: from hostile takeover to compatible bedfellows. *Ecosphere* 8:e01949.

Riemann B, Carstensen J, Dahl K, Fossing H, Hansen JW, Jakobsen HH, Josefson AB, Krause-Jensen D, Markager S, Stæhr PA, Timmermann K, Windolf J, Andersen JH (2016) Recovery of Danish Coastal Ecosystems After Reductions in Nutrient Loading: A Holistic Ecosystem Approach. *Estuaries and Coasts* 39:82–97.

Riginos C, Cunningham CW (2005) INVITED REVIEW: Local adaptation and species segregation in two mussel (Mytilus edulis × Mytilus trossulus) hybrid zones. *Molecular Ecology* 14:381–400.

Riisgård HU (2001) On measurement of filtration rates in bivalves—the stony road to reliable data. *Marine Ecology Progress Series* 211: 275–291.

Rodhe J (1996) On the dynamics of the large-scale circulation of the skagerrak. *Journal of Sea Research* 35:9–21.

Rodriguez AB, Fodrie FJ, Ridge JT, Lindquist NL, Theuerkauf EJ, Coleman SE, Grabowski JH, Brodeur MC, Gittman RK, Keller DA, Kenworthy MD (2014) Oyster reefs can outpace sea-level rise. *Nature Climate Change* 4:493–497.

Rogers AJ (2024) Aquaculture in the Ancient World: Ecosystem Engineering, Domesticated Landscapes, and the First Blue Revolution. *Journal of Archaeological Research* 32:427–491.

Rönnbäck P, Kautsky N, Pihl L, Troell M, Söderqvist T, Wennhage H (2007) Ecosystem Goods and Services from Swedish Coastal Habitats: Identification, Valuation, and Implications of Ecosystem Shifts. *AMBIO* 36:534–544.

Rosa M, Ward JE, Shumway SE (2018) Selective Capture and Ingestion of Particles by Suspension-Feeding Bivalve Molluscs: A Review. J*ournal of Shellfish Research* 37:727–746.

Ruesink JL, Lenihan HS, Trimble AC, Heiman KW, Micheli F, Byers JE, Kay MC (2005) Introduction of Non-Native Oysters: Ecosystem Effects and Restoration Implications. *Annual Review Ecology, Evolution and* Systematics 36:643–689.

Sanders T, Schmittmann L, Nascimento-Schulze JC, Melzner F (2018) High Calcification Costs Limit Mussel Growth at Low Salinity. Frontiers in Marine Science 5:352.

Sanders T, Solan M, Godbold JA (2024) Trait-mediated processes and per capita contributions to ecosystem functioning depend on conspecific density and climate conditions. *Communications Earth & Environment* 5:79.

Smaal AC, Ferreira JG, Grant J, Petersen JK, Strand Ø (eds) (2019) In: *Goods and Services of Marine Bivalves*. Springer International Publishing, Cham

Soga M, Gaston KJ (2018) Shifting baseline syndrome: causes, consequences, and implications. *Frontiers in Ecology & the Environment* 16:222–230.

Sorte CJB, Davidson VE, Franklin MC, Benes KM, Doellman MM, Etter RJ, Hannigan RE, Lubchenco J, Menge BA (2017) Long-term declines in an intertidal foundation species parallel shifts in community composition. *Global Change Biology* 23:341–352.

Stagličić N, Šegvić-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 non-native Pacific oyster Magallana gigas. *Ecological Indicators* 113:106233.

Strand Å, Blanda E, Bodvin T, Davids JK, Fast Jensen L, Holm-Hansen TH, Hjelmert A, Lindegarth S, Mortensen S, Moy FE (2012) Impact of an icy winter on the Pacific oyster (Crassostrea gigas Thunberg, 1793) populations in Scandinavia. *Aquatic Invasions* 7:433–440.

Thomas S, Pilditch CA, Thrush SF, Baltar F, Crawshaw JA, Thomson B, Savage C (2021) Does the Size Structure of Venerid Clam Populations Affect Ecosystem Functions on Intertidal Sandflats? *Estuaries and Coasts* 44:242–252.

Thorngren L, Bergström P, Dunér Holthuis T, Lindegarth M (2019) Assessment of the population of *Ostrea edulis* in Sweden: A marginal population of significance? *Ecology and Evolution* 9:13877–13888.

Thorngren L, Dunér Holthuis T, Lindegarth S, Lindegarth M (2017) Developing methods for assessing abundance and distribution of European oysters (Ostrea edulis) using towed video. *PLoS ONE* 12:e0187870.

Thurstan RH, McCormick H, Preston J, Ashton EC, Bennema FP, Cetinić AB, Brown JH, Cameron TC, Da Costa F, Donnan DW, Ewers C, Fortibuoni T, Galimany E, Giovanardi O, Grancher R, Grech D, Hayden-Hughes M, Helmer L, Jensen KT, Juanes JA, Latchford J, Moore ABM, Moutopoulos DK, Nielsen P, Von Nordheim H, Ondiviela B, Peter C, Pogoda B, Poulsen B, Pouvreau S, Roberts CM, Scherer C, Smaal AC, Smyth D, Strand Å, Theodorou JA, Zu Ermgassen PSE (2024) Records reveal the vast historical extent of European oyster reef ecosystems. *Nature Sustainability* 7:1719–1729.

Toone TA, Benjamin ED, Hillman JR, Handley S, Jeffs A (2023) Multidisciplinary baselines quantify a drastic decline of mussel reefs and reveal an absence of natural recovery. *Ecosphere* 14:e4390.

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. *Journal of Sea Research* 64:145–165.

Van Der Ouderaa IBC, Claassen JR, Van De Koppel J, Bishop MJ, Eriksson BK (2021) Bioengineering promotes habitat heterogeneity and biodiversity on mussel reefs. *Journal of Experimental Marine Biology and Ecology* 540:151561.

Vismann B, Wejlemann Holm M, Davids J, Dolmer P, Pedersen M, Blanda E, Christensen H, Nielsen P, Hansen B (2016) Field clearance of an intertidal bivalve bed: relative significance of the co-occurring blue mussel Mytilus edulis and Pacific oyster Crassostrea gigas. *Aquatic Biology* 25:107–119.

Waldock C, Stuart-Smith RD, Albouy C, Cheung WWL, Edgar GJ, Mouillot D, Tjiputra J, Pellissier L (2022) A quantitative review of abundance-based species distribution models. *Ecography* 2022:ecog.05694.

Ward JE, Sanford LP, Newell RIE, MacDonald BA (1998) A new explanation of particle capture in suspension- feeding bivalve molluscs. *Limnology and Oceanography* 43:741–752.

Westerbom M, Jattu S (2006) Effects of wave exposure on the sublittoral distribution of blue mussels Mytilus edulis ina heterogeneous archipelago. *Marine Ecology Progress Series* 306:191–200.

Wrange A-L, Valero J, Harkestad LS, Strand Ø, Lindegarth S, Christensen HT, Dolmer P, Kristensen PS, Mortensen S (2010) Massive settlements of the Pacific oyster, Crassostrea gigas, in Scandinavia. *Biological Invasions* 12:1145–1152.

Zettler ML, Friedland R, Gogina M, Darr A (2017) Variation in benthic long-term data of transitional waters: Is interpretation more than speculation? *PLoS ONE* 12:e0175746.

Zu Ermgassen PSE, McCormick H, Debney A, Fariñas-Franco JM, Gamble C, Gillies C, Hancock B, Laugen AT, Pouvreau S, Preston J, Sanderson WG, Strand Å, Thurstan RH (2024) European Native Oyster Reef Ecosystems Are Universally Collapsed. *Conservation Letters*:e13068.

Zwerschke N, Emmerson MC, Roberts D, O’Connor NE (2016) Benthic assemblages associated with native and non-native oysters are similar. *Marine Pollution Bulletin* 111:305–310.