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**A temporal investigation of Europe-wide
drivers of cockle *Cerastoderma edule* biology,
health and population dynamics**

Thesis presented by

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for the degree of

Doctor of Philosophy

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DECLARATION

The thesis submitted is my own work and has not been submitted for another degree, either at University College Cork or elsewhere.

Kate Mahony

Dedicated to my Dad.

Charles Mahony

2nd June 1964 – 18th September 2014

Author Contributions

The work in this thesis was performed by the author (Kate Mahony), with the following exceptions:

In addition to data searches by the author, historic data were also provided by Sara Cabral (MARE, Universidade de Lisboa), Xavier de Montaudouin (Université de Bordeaux), Alice Fitch (UK Centre for Ecology & Hydrology), Luísa Magalhães (Universidade de Aveiro) and Mélanie Rocroy (GEMEL) (**Chapter 2**).

Sampling and sample processing (morphometrics and dissection) were assisted by Sara Albuixech-Martí, Katie Costello, Rebecca Laffan and Qifang Wang at University College Cork (**Chapters 3, 4 and 5**).

Sampling and tissue fixation from Arcachon Bay was conducted by Xavier de Montaudouin and Nathalie Mesmer-Dudons at Université de Bordeaux (**Chapter 3, 4, and 5**).

Morphometric data for Wales were obtained by Emily Groves and Shelagh Malham at Bangor University (**Chapter 5**).

Sampling, histology and screening for gametogenesis (training provided by the author) from Ria de Aveiro was conducted by Simão Correia and Rosa Freitas at Universidade de Aveiro (**Chapter 3**).

Sampling from Dundalk Bay and Carlingford Lough was assisted by Martin Hoey and Brian McGill (**Chapter 3, 4 and 5**).

Stable isotope analysis and density measurements were carried out by Anouk Goedknecht, Hugues Blanchet and Nicolas Savoye at Université de Bordeaux (**Chapter 5**).

Abstract

The common cockle *Cerastoderma edule* is an economically, ecologically and culturally important bivalve species and provides a range of ecosystem services. However, increasing reports of cockle mass mortalities, coinciding with reduced harvests, are a concern for various stakeholders. The factors responsible for these mass mortalities (e.g. parasites, weather extremes) are likely to be exacerbated by climate change, making it necessary to examine past and present trends in cockle biology, in order to make plans for the future protection of this species.

To examine the key drivers of cockle populations, historic analysis and current field surveys were conducted. Historic data were collated to understand past trends of abundance, spawning and harvesting, at both a local and global scale. The current impact of biotic (parasites) and abiotic (latitude, environment and fishing) factors on cockle populations were investigated in a 19-month survey. This field study was conducted across latitudinally varying European sites (Ireland to Portugal) and combined histological techniques and morphometric analysis to examine gametogenesis, health and growth, and the key biotic and abiotic modulators of these characteristics. The evident trends were then considered in the context of future climate change.

The variability in cockle populations was affirmed, particularly at a local scale. At a global scale, climate was found to historically influence cockle populations, with warmer waters resulting in reduced abundance. However,

historic data collection was lacking in coordination across borders and between stakeholders. The current study, which was more coordinated, also demonstrated the potential influence of climate. In terms of reproduction, cockles at warmer southern sites exhibited prolonged spawning. Additionally, growth was found to be reduced at warmer temperatures, likely due to a diversion of energy to gametogenesis. This highlights a potential impact on the growth and spawning of northern cockles as a result of climate change. Furthermore, trematodes (both metacercariae and sporocysts) were found to negatively impact gametogenesis and growth. Previous studies highlighted the influence of climate change on increased trematode transmission, and this was supported in this thesis, with increased sporocyst prevalence linked with warmer water. Furthermore, additional information was discovered relating to the potential influence of climate change on a range of mortality inducing parasites (e.g. bacteria, *Trichodina* ciliates, sporocysts, metacercariae), which are likely to increase as a result of the previously predicted warming seas and increased precipitation.

The results presented in this thesis have a number of implications for the protection of cockles and ensuring future sustainability of European populations. In particular, regular monitoring at a local scale is necessary, due to the evident micro-variability of cockle population characteristics. This regular monitoring, in particular of reproduction and growth rates, was shown to be necessary in creating management strategies, in particular for setting minimum harvest size. A lack of data mobility was noted between scientists,

managers, conservationists and the public, highlighting the necessity of data sharing efforts not just for cockles, but for all commercially exploited species. Finally, climate change is evidently a major threat to cockles, however this study and the future resulting research, which has been widely disseminated to a variety of stakeholders, will assist the protection of the common cockle.

Chapter 1: Introduction

1. The ocean and its resources

The world's oceans, coasts and estuaries are arguably the most important natural resource for humans, supporting life, influencing weather, providing food and transport, as well as inspiring awe (Costanza, 1999). However, the world is changing and oceans are facing increasing pressure as a result of climate change, habitat alteration, pollution and over-exploitation (Halpern *et al.*, 2015). The demand for seafood is increasing due to a growing population (United Nations, 2019) and it is crucial to protect the oceans to ensure food security (Jennings *et al.*, 2016), as well as to protect the vital ecosystems and organisms that lie within.

The oceans support an abundance of biodiversity, which contributes to successful ecosystem functioning. Many bivalves support various ecosystem functions, ranging from nitrogen removal (Carmichael *et al.*, 2012), to coastal protection (Smaal *et al.*, 2019). In addition to their vast ecological importance, bivalves are of great commercial importance. Although contributing about 2% to all global fisheries, they compensate with a high price per unit, making them important commercially (Gosling, 2015). Many coastal communities rely on shellfish, which are generally easy to access and valuable (McCay and Jenks, 1998), and are particularly important economically at a local scale, especially for women (Kyle *et al.*, 1997; Frangoudes *et al.*, 2008; Zhao *et al.*, 2013). However, bivalves are vulnerable to many threats, including fishing damage (Vasconcelos *et al.*, 2011), acidification (Waldbusser *et al.*, 2015) and climate

change (Gosling, 2015). These vast examples of bivalve importance, along with the threats they face, highlight the necessity of studying these organisms. Of the many wild harvested bivalve species, cockles are one of the most iconic species in Europe (Carss *et al.*, 2020).

2. The common cockle

Cockles (*Cerastoderma* spp.) are commercially and ecologically important bivalve species found along Atlantic and Mediterranean coasts from Norway to West Africa (Hayward and Ryland, 1995). The two species of *Cerastoderma*, *C. edule* and *C. glaucum*, are commonly found in Europe and north Africa across similar latitudes (Hayward and Ryland, 1995). *C. edule*, the common cockle, tends to be found in coastal and estuarine areas, with *C. glaucum*, the lagoon cockle, generally inhabiting non-tidal locations (Reise, 2003). These species differ in morphology with *C. glaucum* possessing fewer ribs and a thinner shell than *C. edule* (Boyden, 1973). *C. glaucum* is posteriorly elongated unlike *C. edule*. However, this is a characteristic that is difficult to quantify so is not beneficial in discriminating the two species (Boyden, 1970). It is also possible to distinguish the two species using histology, with monophasic digestion (all digestive tubules at the same phase) occurring in *C. edule* (Morton, 1970; Carballal *et al.*, 2016) in comparison with the different digestive stages occurring simultaneously in *C. glaucum* (Carballal *et al.*, 2016). Genetic techniques now make speciation more accurate (André *et al.*, 1999; Freire *et al.*, 2011; Maroso *et al.*, 2019).

Cerastoderma edule (the common cockle or edible cockle, henceforth referred to as “cockle”) is greatly important ecologically. Cockles act as ecosystem engineers (Carss *et al.*, 2020) that maintain and create habitats (Jones *et al.*, 1997) for species such as *Hydrobia* (Morgan *et al.*, 2013), as well as influencing hydrodynamics (Ciutat *et al.*, 2007; Fernandes *et al.*, 2007). Dead cockle shells provide a substrate for species such as mussels (*Mytilus* spp., Figure 1), as well as the polyps of Scyphozoan jellyfish (van Walraven *et al.*, 2020). As bioturbators, they modify sediment dynamics by burrowing and valve abduction (Ciutat *et al.*, 2007) and are an important prey source for many species, including crabs and birds (Sanchez-Salazar *et al.*, 1987). As well as being ecosystem engineers, cockles provide a range of ecosystem services such as nutrient cycling and exchange, oxygenating sediment and increasing ammonia for primary consumers (Morgan *et al.*, 2013). The faecal pellets and pseudofaeces of cockles contain higher metal concentrations than those found in surface sediments, possibly playing an important role in element cycling (Brown, 1986). *C. edule* also releases ammonium and phosphate to the water, which stimulates microphytobenthos production (Swanberg, 1991).



Figure 1. *Mytilus* sp. living inside an empty shell of *Cerastoderma edule* obtained from Carlingford Lough, Ireland (Photo Kate Mahony).

In addition to the large contributions to ecosystem functioning, *C. edule* is also a valuable species for European fisheries, with capture production reaching over 100,000 tonnes per year in the 1980s and early 1990s (FAO, 2018), but harvests have more recently reduced to 19,878 tonnes in 2018 (FAO, 2019). Cockle meat is a valuable resource, and if its ecosystem services were fully utilised, cockle harvests could value an additional US\$11.5 million annually (Carss *et al.*, 2020). The cockle has been important throughout history, acting as an important food source in areas where they are common today. Cockle shells have been found in shell middens (historic refuse sites with large deposits of shells) and burial sites across Europe, and are still represented in art and culture today (Ó Nualláin, 1989; Carss *et al.*, 2020).

3. Threats to cockles

While cockles are evidently a well-studied species, many aspects of their population cycles remain unclear. Numerous cockle mortality events have been

reported in recent years, resulting from multiple possible causes (Burdon *et al.*, 2014; Figure 2). Historically, mortalities have been attributed to a range of factors including density dependence, heavy precipitation, poor weather, storms, algal blooms and heat waves (Hancock and Urquhart, 1964; Ottway *et al.*, 1979; MacKenzie *et al.*, 1997; Parada and Molaes, 2008; Verdelhos *et al.*, 2015a). The negative effects of floods or temperature extremes can be increased due to compounding stressors such as eutrophication or low oxygen levels (Cardoso *et al.*, 2008; Burdon *et al.*, 2014).

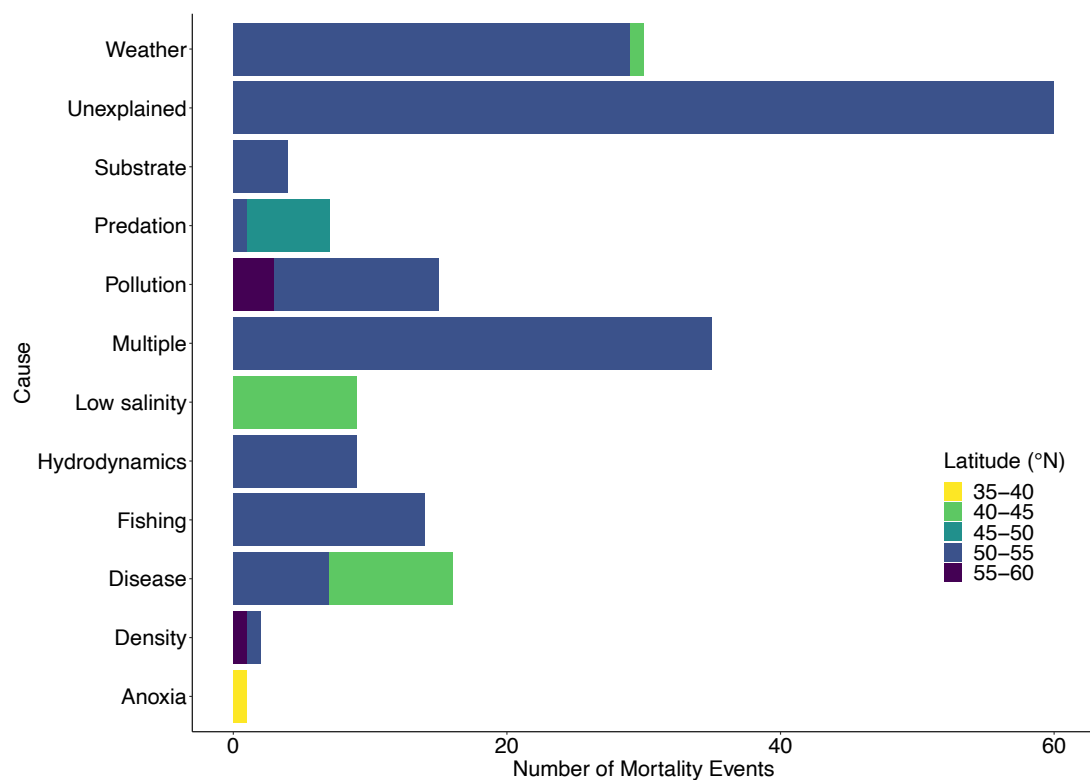


Figure 2. Mortality events and their causes as reported in historic literature (n= 202; Graph Kate Mahony).

Many of the discussed climate-related factors are anticipated to increase in frequency over the coming decades (Beniston *et al.*, 2007), causing serious

concern for cockle populations. The niche of *C. edule* is predicted to narrow in response to climate change (Singer *et al.*, 2017) and its range may shift to the north in response to increasing temperatures (Verdelhos *et al.*, 2015a). Climate change may also impact parasite-host interactions in aquatic animals, which in turn may create problems due to a cascade through food webs (Marcogliese, 2008). These predictions and initial findings suggest that cockle mortality events may increase in the future, highlighting the importance of studying cockles both historically, and currently, in order to make informed predictions.

4. Cockle fisheries

Methods of cockle fisheries vary across its range, from recreational hand picking to suction dredging (Figure 3) with the lethal and sublethal impacts on cockles assumedly varying depending on fishing type and management style. Hydraulic suction dredges function by using water jets to liquidise the sand before removing the sediment and cockles (Hall and Harding, 1997). This can alter sediments, such as in areas of muddy sand, where an anoxic layer of mud may be brought to the surface. This affects the benthic community (Ferns *et al.*, 2000), in particular the cockles themselves (Piersma *et al.*, 2001). Shell damage also occurs from mechanical harvesting due to the free falling of cockles (Coffen-Smout, 1998). In response to harvesting, the reburial response in *C. edule* is delayed, with cockles reburial faster in shallow pools compared with wet sand (Coffen-Smout and Rees, 1999). Cockles also overlap with other fisheries, which can indirectly impact cockle populations. Digging of lug and rag worms for bait can cause mortality in cockles, particularly smaller ones as they

cannot regain their position in the sediment (Jackson and James, 1979). Cockles are also harvested by hand, but this is considered to be a low impact activity (McLaughlin *et al.*, 2007). However, as management regimes differ across the range of cockles (number of licences, harvesting times, no harvest areas (e.g. Leitão and Gaspar, 2007; Ponsero *et al.*, 2009; Boldina and Beninger, 2013)), it is also likely that the impacts of hand harvesting vary.

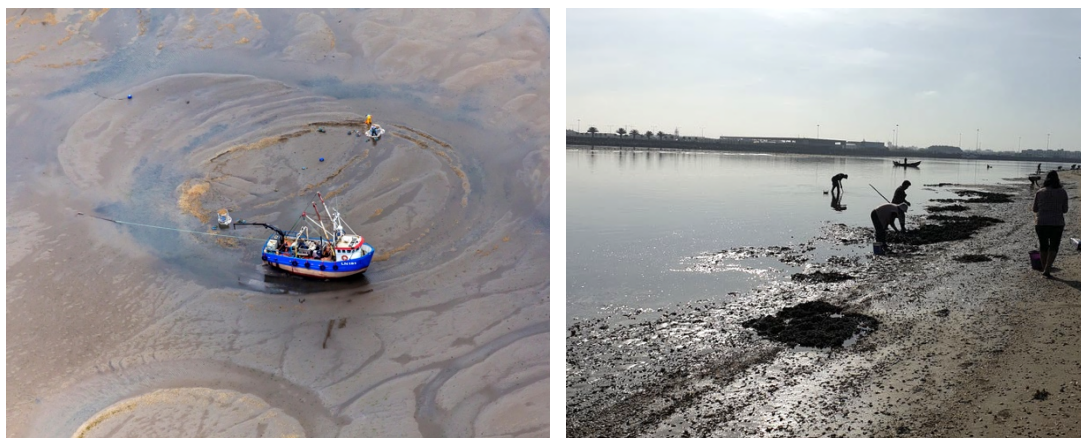


Figure 3. (A) Suction dredging for cockles in the Wash, Wales (Photo Rodger Tamblyn/Alamy Stock Photo) and (B) Women hand raking for cockles on intertidal sands in the Ria de Aveiro Lagoon, Portugal (Photo Kate Mahony).

In order to protect cockle fisheries, many fisheries operate minimum capture sizes, which are important for allowing adequate recruitment to the population (Gosling, 2015). This capture size should be related to the average growth rate (Hancock, 1967). However, cockle growth is another varying aspect of cockle life history. *C. edule* typically grows to about 50 mm (Hayward and Ryland, 1995) but this is variable, even within a single bed (Hancock, 1967). Growth is influenced by a number of factors, including position with respect to

the river mouth, tidal exposure (Hancock, 1967) and tide level (de Montaudouin, 1996; de Montaudouin and Bachelet, 1996), due to the higher food supply when cockles are immersed for longer (de Montaudouin, 1996). Growth rate is also affected by latitude, with historic growth rates tending to increase further south (Iglesias and Navarro, 1990). However, no work has been conducted on the impact of latitude on cockle growth since the 1990s. This is concerning given the shifting Atlantic Multidecadal Oscillation to a warmer, positive phase in the interim (NOAA, 2019).

5. Cockle reproduction

Reproductive processes in bivalves include gametogenesis, the development of larvae, and metamorphosis (Bayne, 1976). Typically, the dioecious *C. edule* (Boyden, 1970) begins spawning in its second year at a shell height of 15-20 mm (Seed and Brown, 1977). However, the reproductive process in cockles has been shown to vary greatly across studies. While spawning generally occurs at the end of spring or early summer (Honkoop and van der Meer, 1998), timing varies by location (Hancock and Franklin, 1972) and within populations. These variations are potentially due to environmental conditions such as temperature (Honkoop and van der Meer, 1998) and climate (Morgan *et al.*, 2013), as well as feeding conditions in prior seasons (Navarro *et al.*, 1989).

Recruitment of cockles is also variable, resulting from variations in reproduction. Recruitment is also determined by factors including current, which impacts the movement of cockle larvae, additionally influencing population genetics (Coscia *et al.*, 2020). At a local scale, while it is common for

successful settlement years to be interspersed by years of poor settlement (Boyden, 1970), declines in recruit densities may result from climate change, in addition to predation pressure or changing sediments (Beukema and Dekker, 2005).

Evidently, a large body of work has been conducted relating to cockle reproduction, however a lot of research typically occurs in one particular region or country per study, rather than a comparison across the geographic range of cockles (e.g. Seed and Brown, 1977; Navarro *et al.*, 1989; Beukema and Dekker, 2005; Morgan *et al.*, 2013). Additional knowledge relating to the latitudinal variation of cockle reproduction, including associated environmental differences, would provide beneficial knowledge for protecting cockle populations in the future.

6. Parasitism and pathology of cockles

Cockles are host to a range of viruses, bacteria and fungi (Longshaw and Malham, 2013), with previously unreported or novel species documented within the last decade (Carrasco *et al.*, 2013, 2014; Bookelaar *et al.*, 2020). These new discoveries, along with our prior knowledge of cockle parasite diversity, highlight the ecological role of cockles as a host-parasite system. A high diversity of parasites is found in complex ecosystems such as the Ria de Aveiro, Portugal, where the entire life cycle of the parasite is possible (Freitas *et al.*, 2014). While not all cockle parasites are detrimental, some parasites are known to impact cockle life history. Digenean trematodes (Phylum Platyhelminthes, Class Trematoda) are a common parasite group impacting

cockles (Longshaw and Malham, 2013). The impacts of parasites such as trematodes may have a wider impact on the food web due to the importance of cockles as a food source (Marcogliese, 2008). Other detrimental pathogens and diseases are found in cockles. Of particular note, the cercozoan parasite *Marteilia cochillia* has caused substantial impacts on Galician cockle fisheries (Villalba *et al.*, 2014).

To date, many investigations of influencing drivers or stressors have been experimental, rather than in the field (e.g. Verdelhos *et al.*, 2015a, 2015b; de Montaudouin *et al.*, 2016; Ong *et al.*, 2017; de Fouw *et al.*, 2020). Many studies have focused on single ecosystems, rather than across the range of cockles, as well as focusing on single parasite groups, in particular trematodes. However, to understand future potential impacts on cockle populations, it is necessary to examine cockles across varying latitudes, in different environmental conditions and under different fishing scenarios in order to incorporate the different combinations of drivers across its range.

7. COCKLES Project

The work undertaken for this PhD was part of the COCKLES Project (“Co-Operation for Restoring Cockle Shellfisheries and its Ecosystem Services in the Atlantic Area (AA)”). This Interreg Atlantic Area project was a collaboration between experts in Ireland, the UK, France, Spain and Portugal. The aims of this industry-driven project were to quantify the importance of cockle ecosystem services, provide new techniques for aquaculture and bed restoration, as well as providing recommendations for stakeholders.

8. Aims and objectives

- Identify suitable methods for examining historic trends in population dynamics and reconstruct the past of the common cockle throughout Europe based on literature and data searches (Chapter 2)
- Understand modern trends in European cockle populations by examining gametogenesis, parasites and growth in the Atlantic Area (Chapters 3, 4 and 5)
- Synthesise these results and make recommendations for protecting future populations (Chapter 6)
- Disseminate these findings to various stakeholders (Appendix A)

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Chapter 2: Mobilisation of data to stakeholder communities. Bridging the research-practice gap using a commercial shellfish species model

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Abstract

Knowledge mobilisation is required to “bridge the gap” between research, policy and practice. This activity is dependent on the amount, richness and quality of the data published. To understand the impact of a changing climate on commercial species, stakeholder communities require better knowledge of their past and current situations. The common cockle (*Cerastoderma edule*) is an excellent model species for this type of analysis, as it is well-studied due to its cultural, commercial and ecological significance in west Europe. Recently, *C. edule* harvests have decreased, coinciding with frequent mass mortalities, due to factors such as a changing climate and diseases. In this study, macro and micro level marine historical ecology techniques were used to create datasets

on topics including: cockle abundance, spawning duration and harvest levels, as well as the ecological factors impacting those cockle populations. These data were correlated with changing climate and the Atlantic Multidecadal Oscillation (AMO) index to assess if they are drivers of cockle abundance and harvesting. The analyses identified the key stakeholder communities involved in cockle research and data acquisition. It highlighted that data collection was sporadic and lacking in cross-national/stakeholder community coordination. A major finding was that local variability in cockle populations is influenced by biotic (parasites) and abiotic (temperature, legislation and harvesting) factors, and at a global scale by climate (AMO Index). This comprehensive study provided an insight into the European cockle fishery but also highlights the need to identify the type of data required, the importance of standardised monitoring, and dissemination efforts, taking into account the knowledge, source, and audience. These factors are key elements that will be highly beneficial not only to the cockle stakeholder communities but to other commercial species.

1. Introduction:

Knowledge does not transmit well (Young *et al.*, 2013), resulting in a gap between research and end users, with information not always translating from researchers to policy makers, the public and resource managers (Shanley and López, 2009). This has led to the study of knowledge mobilisation, which relates to the flow and application of information (Young *et al.*, 2016). Such transfer of information improves outcomes in sectors such as health (Ferlie *et al.*, 2012), education (Levin, 2011) and conservation (Cook *et al.*, 2010). However, obstacles to knowledge mobilisation and exchange exist, including difficulties such as secrecy of data by certain institutions (Young *et al.*, 2013), lack of open data (Cvitanovic *et al.*, 2014) and a shortage of collaboration between all relevant stakeholder groups (Young *et al.*, 2016). Such sharing of information should be intuitively easier on a well-studied topic, due to an abundance of literature.

The common cockle (*Cerastoderma edule*, Mollusca: Bivalvia: Cardiidae) is an extensively studied species. Its populations have a large geographic range, being found along European Atlantic coasts from Norway to Senegal (Hayward and Ryland, 1995; Honkoop *et al.*, 2008). Cockles provide a wide range of services, including cultural and ecosystem services (Carss *et al.*, 2020). As an ecosystem engineer, it alters its habitat by bioturbation and influencing hydrodynamics (Ciutat *et al.*, 2007; Fernandes *et al.*, 2007). Additionally, cockles are a valuable species to European fisheries, with capture production reaching over 100,000 tonnes per year in the 1980s and early 1990s. However,

in similarity with other fisheries (Kirby, 2004), the production of cockles has since reduced (FAO, 2018), coinciding with reports of changing fisheries policy, significant overfishing, variable recruitment and mass mortalities (Burdon *et al.*, 2014). Some of these reported mortalities are a result of climate related events (e.g. high precipitation, storms and heat waves), which are anticipated to increase in frequency over the coming decades (Beniston *et al.*, 2007; Peteiro *et al.*, 2018; Domínguez *et al.*, 2020). The cockle is also impacted on by a wide range of parasites and pathogens (de Montaudouin *et al.*, 2009; Longshaw and Malham, 2013; Rowley *et al.*, 2014). For instance, the recent discovery of the pathogen *Marteilia cochillia* is causing significant mortalities in Galicia, Spain (Villalba *et al.*, 2014).

The ecological niche of *C. edule* is predicted to narrow in response to climate change (Singer *et al.*, 2017) and its range of distribution may shift northwards in response to increasing temperatures (Verdelhos *et al.*, 2015). Global trends in cockle densities have been observed previously, such as densities increasing towards higher latitudes (Bocher *et al.*, 2007). Decreases in abundance have also been documented at a regional level, for example in the Wadden Sea in the Netherlands (Beukema *et al.*, 2010), possibly due to overfishing and eutrophication (Kraan *et al.*, 2011). Changes in reproduction of cockles have been observed at regional levels as a result of climate variability, with cold winters causing an acceleration of gametogenesis, as well as extending its duration (Morgan *et al.*, 2013). At an estuary scale, in southern Portugal overfishing of cockles has resulted in disruptions to population structure due to

the removal of larger individuals (Crespo *et al.*, 2010). This highlights the importance of examining cockles temporally at a metapopulation level, as well as across their distribution in a single comprehensive study that can be communicated effectively to relevant stakeholders.

In order to understand the ecology and status of current and future marine populations, including cockles, an understanding of past events, such as mortality events, changes in population structure and dynamics, as well as health and disease related impacts, is required. Marine historical ecology "is an emerging field of study that uses historical data sets to describe what marine ecosystems might have looked like in the past" (Campbell *et al.*, 2009). Pauly (1995) raised the issue of the "shifting baseline syndrome" in which fishery scientists focus and generate data from their own career span to determine changes and baseline shifts across generations (Pauly, 1995). However, to get a longer, less biased perspective of marine resource status, it is important to familiarise oneself with the data and mobilise knowledge from a wide range of archival sources, including natural sources such as fossils and documentary records, including maps (Patton *et al.*, 1998; Swetnam *et al.*, 1999). These techniques have been successfully incorporated into previous studies on commercially important species. In a study directed at the scientific community, fishers' logbooks were used as a data source for cod biomass to understand the health of stocks prior to the industrialisation of the fishery (Rosenberg *et al.*, 2005). With 64 citations it is valid to say that this study had substantial impact on the scientific audience. Historical studies have also been

conducted on bivalve species, primarily oysters, to understand their historic distribution and abundance (Zu Ermgassen *et al.*, 2012), as well as to examine potential causes for declines, such as disease and over harvesting (Gillies *et al.*, 2018).

In this study, a review was conducted of the available historical information on a commercially important species, the common cockle. Using this review, the aim was to gain an understanding of (1) the regional and national focus of past studies (“the knowledge”), (2) the sources of knowledge available on cockles, (3) the vested stakeholder communities (“audience”) and (4) to identify some of the key drivers and inhibitors of cockle populations - both on a macro and micro level (“knowledge mobilisation”). Historical data are inherently fragmented and variable in size and quality, but with data cleaning techniques, these data can provide invaluable information on some of the previous factors that have influenced cockle population growth or decline. Factors such as differences in legislation, fishing intensity, level of protection, minimum landing size, disease, reproduction and environmental variables were examined in this study. Based on these differences, case studies (micro level) of three key production sites were also examined, to determine if trends varied at a local scale. Data were also analysed on a macro level to examine the impacts of climate on cockle populations. Findings from this study will contribute to knowledge mobilisation for a commercially and ecologically important species and will further reduce the research-practice gap in this sector.

2. Materials and methods

2.1. Rationale

To understand “the knowledge”, i.e. the knowledge of cockles from past studies at both a regional and global scale, a review of secondary data (obtained from historic literature reporting original data) was conducted, as described in detail in Section 2.2. As these data were gathered for other purposes (e.g. to inform industry, for publication) it was deemed important to understand the “audience”, i.e. stakeholders this knowledge was intended for, as well as the stakeholder community providing the data, i.e. the “source”. These sources provide records of cockle populations, which were examined on a macro and micro level to depict trends, as well as the efficiency of “knowledge mobilisation” in this sector.

2.2. Literature review, data set creation and standardisation

Data sets detailing density, biomass, spatial distribution, spawning duration and landing records were created by carrying out a web-based literature search. Searches of both grey and published literature were conducted through Google Scholar, using the synonyms “*Cardium edule*” or “*Cerastoderma edule*”, as well as through individual search tools (ScienceDirect, JSTOR and Wiley). Literature was accessed to 2018 inclusive. Authors’ personal libraries were also searched for relevant literature. Not all of these data were readily accessible on the internet due to pay walls, lack of digitisation and language barriers. It is important to set explicit criteria when creating data sets from

multiple studies (Houlahan *et al.*, 2000). In the case of this study, key inclusion criteria were as follows: biomass and density minima and maxima, biomass and density estimates, parasite records, spawning period, capture production, and presence data from museum records and newspapers. Efforts were taken to ensure data were clean, with studies excluded if they were experimental, lacked a stated time period or location, or if the area that biomass was measured over was not clearly indicated. Each individual quantitative measure was referred to as a record, e.g. if two time periods were recorded in one piece of literature, this counted as two records. Care was taken to omit studies focusing on the lagoon cockle (*Cerastoderma glaucum*), also present in Europe, and studies were only included if *C. edule* was specifically stated.

Studies were classed according to the “stakeholder community” from which they originated (Figure 1). Literature sourced from the “Science” community originated in the published literature or from scientific reports. The “Management/Industry” community was assigned if the literature originated from a body overseeing a fishery. Knowledge was classed as “Public” if it originated from public media and “Conservation” was assigned in cases where literature related to conservation objectives, such as protected areas. Literature was further classified according to its topic, e.g. ecosystems, fisheries, parasites (Figure 1, Appendix B S1 Table). No ambiguous cases were noted, i.e. all studies were easily assigned to a community.

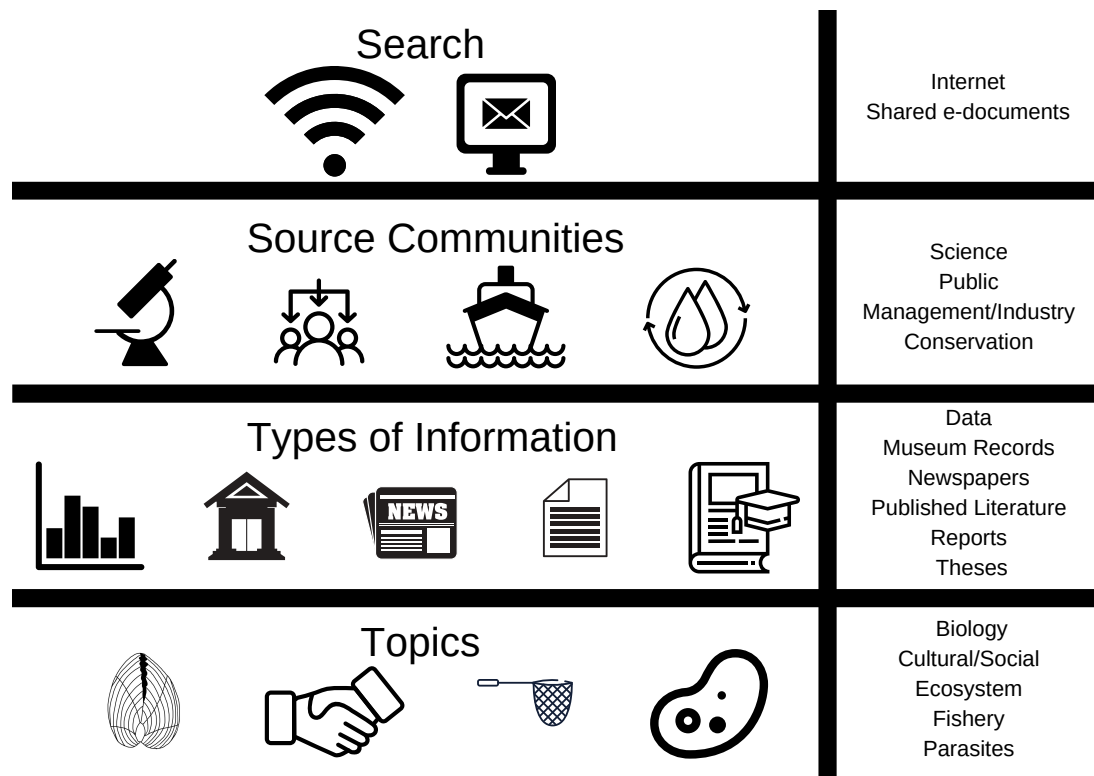


Figure 1. Overview of the data types, sources and topics collated to facilitate knowledge mobilisation of common cockle *Cerastoderma edule* research to key stakeholder communities. This figure illustrates the methodology used and provides a template for carrying out such a study.

Additional data cleaning was conducted prior to interpretation, where abundance data (biomass and density) were converted and standardised, so all figures were reported as the same unit (g wet weight/m² and individuals/m² respectively). Due to lack of reporting of sampling methods and the variety of methods used, it was not possible to standardise for fishing or sampling effort. Biomass was reported in many ways in the literature. The principal units were ash free dry weight (AFDW) and wet weight. All biomass data were converted to wet weight, as this was the most commonly reported unit. AFDW was converted using the following equation from Wijsman *et al.*, (2009):

$$WW = \frac{AFDW}{\phi AFDW_{ww}}$$

where WW = wet weight, $AFDW$ = ash free dry weight and, $\phi AFDW_{ww}$ = conversion factor.

A conversion factor of 0.12 was used to convert ash free dry weight to wet weight (van der Veer *et al.*, 2006).

For the climate analyses, Atlantic Multidecadal Oscillation (AMO) data, ranging from 1956 to 2018 were obtained (NOAA, 2019). The AMO is a cycle of variability of Atlantic climate over an extended timescale. A negative AMO index corresponds with a cooler Atlantic sea surface temperature, conversely a positive AMO corresponds with a warmer Atlantic sea surface temperature (Enfield *et al.*, 2001). These data were averaged yearly to determine the annual AMO Index. Precipitation and maximum and minimum average temperatures were obtained from national weather forecasts, from nearest weather stations (Klein Tank *et al.*, 2002; Met Éireann, 2019; Meteo Galicia, 2019).

2.3. Analysis

Linear mixed effects models fit by restricted maximum likelihood were employed to investigate fluctuations in cockle densities. Models were generated in R (R Core Team, 2019) using the `lme` function in the `nlme` package (Pinheiro *et al.*, 2019). The fixed factors included were AMO index, season, year, cockle age, sampling type and latitude (Appendix B, S2 Table) and the random factors were year and latitude (in order to account for the spatial and temporal

variation in the reports). The final model was chosen according to top down selection (Zuur *et al.*, 2009), using a combination of AIC and *p* values to determine the most suitable model, and subsequently removing the over-specified fixed factors (Appendix B, S3 Table). Homoscedasticity (homogenous variance of residuals) and normality (normally distributed residuals) assumptions were visually checked.

Due to the variation of sampling techniques in the reported/detected cockle studies, as well as the infrequent reporting of density and biomass on a global scale, it was impossible to conduct a statistical analysis for the remainder of the study. Instead, data were analysed descriptively to determine potential trends across the distribution of the common cockle. Case studies (micro level) were also conducted on a regional scale (Dundalk, Ireland; Bay of Somme, France; Ria de Arousa, Spain) to determine the climate related factors influencing cockles. These sites were chosen from three latitudinal areas based on the amount of data available.

3. Results

3.1. Overview of results and sources

The total number of records obtained was 9,997 from 193 sources (e.g. museum records, published literature, reports etc.). Of these records, 2,814 were quantitative, detailing the abundance of cockles, harvest amounts or spawning duration. A total of 7,183 records were presence data, which were used in combination with the quantitative data to determine the spatial

distribution of cockles. The oldest record of cockles was from a museum specimen from Lough Hyne, Ireland in 1859, the most recent record included was from 2018 harvest data in Galicia, Spain. Museum and newspaper records were only obtained from Irish sources, with the majority (7,105) of these records from Ireland (294) and the UK (6,811). The Irish sources also documented records from other countries, with the remainder of these records obtained from Spain (43), France (29) and Portugal (6).

The majority of literature provided was obtained from the scientific community (Figure 2), covering a large range of topics. The least amount of literature was provided in the context of conservation. Management and industry provided literature regarding the fishery, primarily reporting landings statistics. However, small quantities of literature sourced from management and industry related to cockle biology and their parasites. No qualitative information was provided from the public realm, as fisheries related literature primarily discussed the dangers of cockle fishing, or simply the presence of a fishery in a specific area.

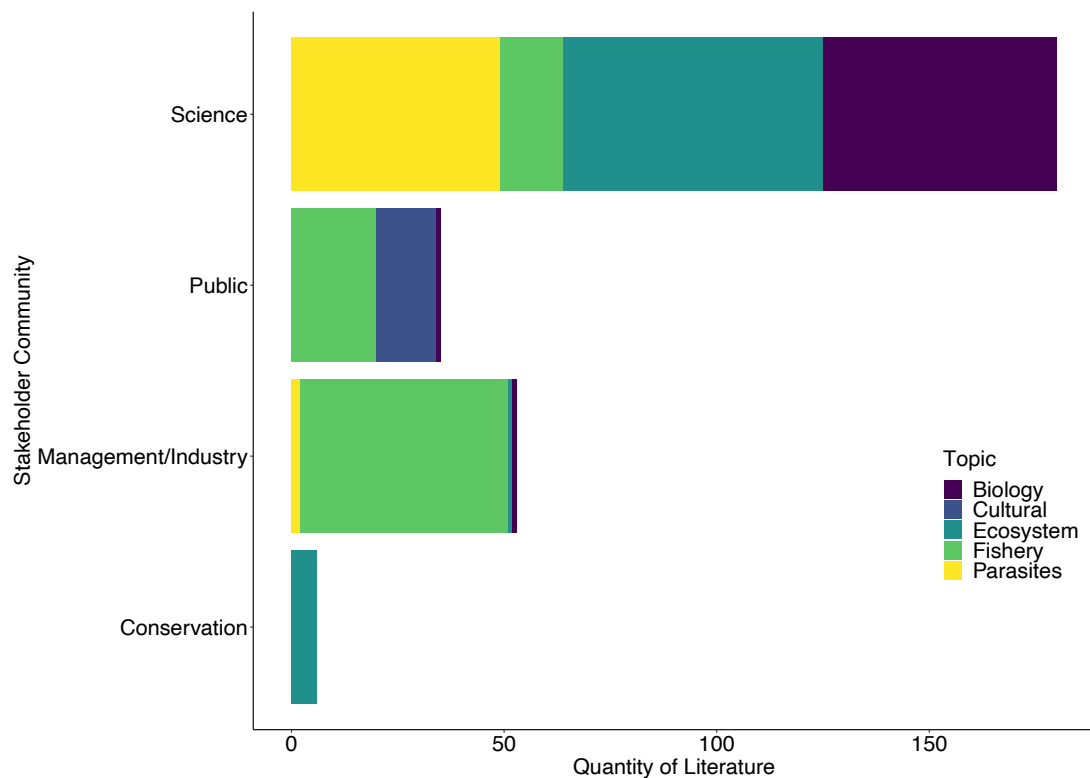


Figure 2. Stakeholder communities providing literature for this study, including the topic of the literature/dataset. The topic of “Biology” refers to the biology and natural history of cockles. The topic of “Cultural” dealt with the relationship between people and cockles (e.g. gastronomy). “Ecosystem” related to the interaction between cockles and their environment (e.g. sediment) and other species (e.g. predators). The topic “Fishery” related to cockle harvest levels and “Parasites” was classified as literature reporting parasites in cockles.

3.2. Cockle and stakeholder community distribution

All historical records were used to determine the documented distribution of *C. edule* (Figure 3), which also highlighted the regional/local geographic range of stakeholder communities/studies carried out. Cockles were recorded as far as Russia (Genelt-Yanovski *et al.*, 2010; Nazarova *et al.*, 2015)

and Iceland (Ingólfsson, 1999) in the north, to Senegal in the south (FAO, 2018). *C. edule* was reported to be found on the Mediterranean coasts of Spain (Carrasco *et al.*, 2011). Whereas no reports of cockles came from the Mediterranean coasts of France, Italy or further eastern areas (Figure 3). No records were observed over a large distance between Morocco and Senegal, with the exception of one study (Honkoop *et al.*, 2008).

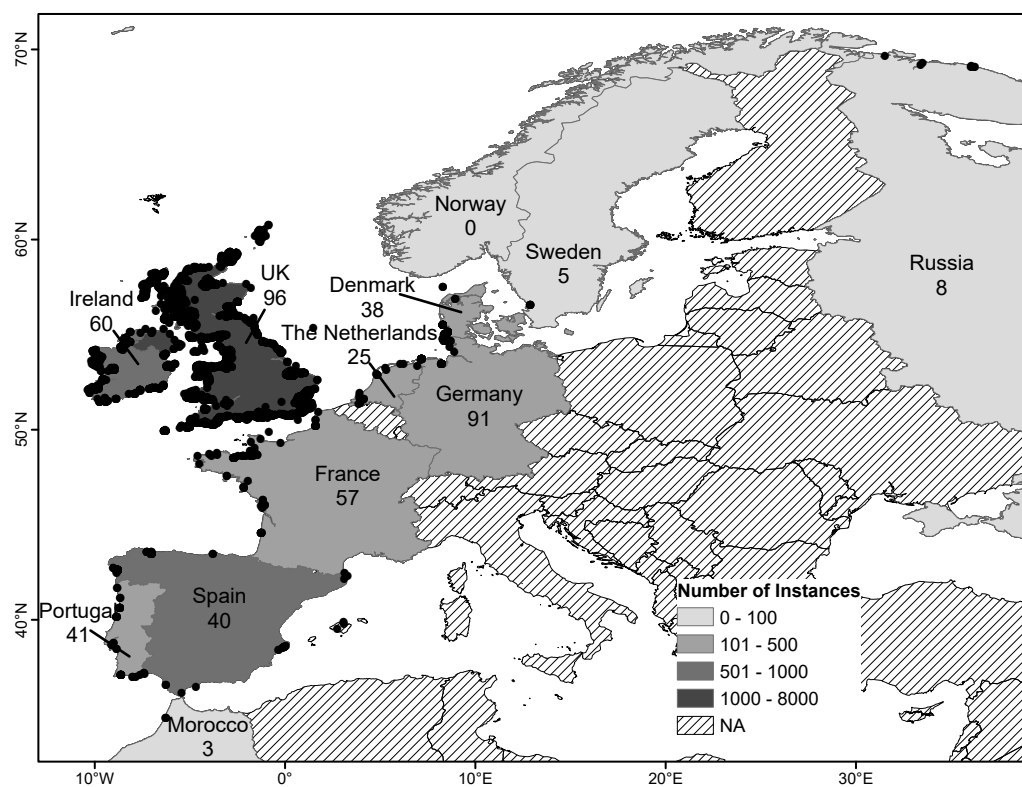


Figure 3. European distribution of cockles from all data gathered regarding *Cerastoderma edule*. The total number of reports (presence, production, abundance) are indicated by grey colour as seen in the legend. The number of reports including a quantitative measure of abundance (i.e. density or biomass) are represented by text within the map. Note: records were obtained from Iceland, southern Morocco, Mauritania and Senegal but omitted for clarity.

3.3. Historical abundance (macro level analysis)

Abundance (i.e. the number or weight of cockles per m²) was recorded as either biomass or density and varied spatially and temporally in the analysed studies. The south coast of Ireland and the Wadden Sea were amongst the most frequently studied areas (Figure 4). The countries with the most records of cockle abundance were the UK (96 records), followed by Germany (91 records) (Figure 3). Ireland (60), France (57), Portugal (41), Spain (40), Denmark (38) and the Netherlands (25) also had a significant number of reports on cockle abundance (Figure 4). Countries with small/no cockle fisheries had the lowest numbers of reports e.g. Russia (8), Iceland (1) and Senegal (0) (Figure 4).

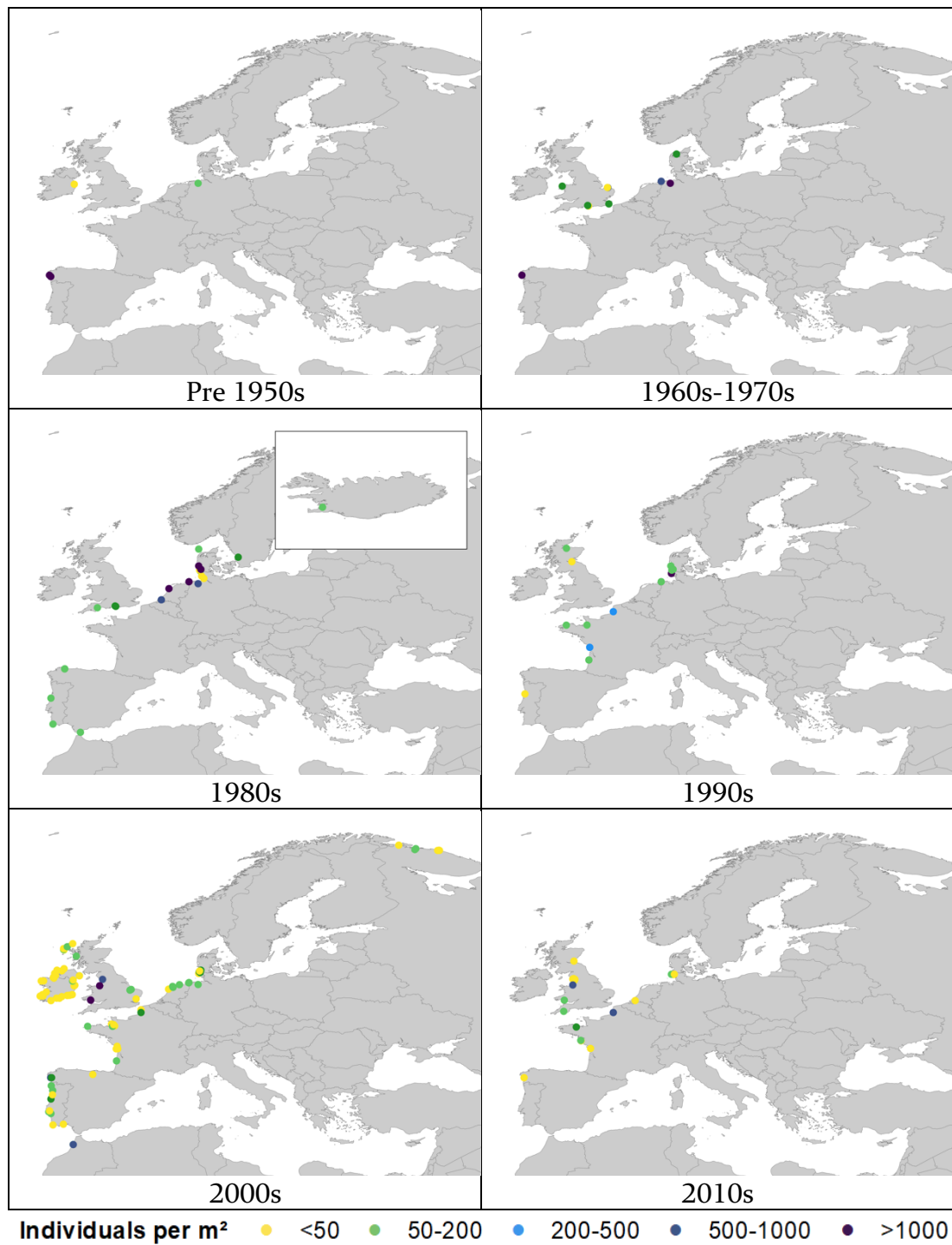


Figure 4. Density of cockles reported across Europe between the 1940s and 2010s. The colours of dots indicate the number of individuals per m^2 .

Records of biomass (g wet weight/m²) varied spatially and temporally. The earliest biomass record (15.5 gWW/m²) was from Dublin Bay, Ireland, in 1971 (West and Partridge, 1979). Few records exist from the 1970s, while many surveys detailed biomass in the 2000s. The south coast of Ireland and the Wadden Sea were amongst the most frequently studied areas, with no records from the south of Portugal. Biomass dramatically varied in certain locations, even within the same decade. For example, in the east of Ireland, where biomass ranged from 134 gWW/m² in 2008 to 30.59 gWW/m² in 2010 in a single bay (Marine Institute and Bord Iascaigh Mhara, 2011), or in Arcachon Bay, France, where values ranged from 0 gWW/m² to 460 gWW/m² between 1997 and 2014, with no temporal trend (Magalhães *et al.*, 2016).

Examining the density of cockles by decade, most areas appear to have similar cockle densities temporally. However, spikes in reported densities appeared in the 1980s in the Wadden Sea and in the 2010s in the south of the UK. Density appeared lower in areas at the north of the cockles' range, including Ireland, northern UK, Iceland and Russia. The highest reported densities were in key fishing areas in the UK, the Wadden Sea, Galicia and southern Portugal (Figure 4).

In examining densities with respect to AMO fluctuations, the AIC of models one and two did not differ significantly (3795 and 3791, $p > 0.9$). Therefore, the random intercept model was deemed the most appropriate, as it assumed that the strength of the relationship between density and the other variables changed randomly between years and latitudes (thus accounting for

spatial and temporal variation of density reports). There was a negative correlation between density and the AMO index ($p<0.001$): in positive, warm phase years, cockle densities were lower (Figure 5). The sampling season also had an impact on the density records ($p<0.01$). In the summer, spring and autumn, the densities recorded were significantly lower ($p<0.01$ for each, Figure 5).

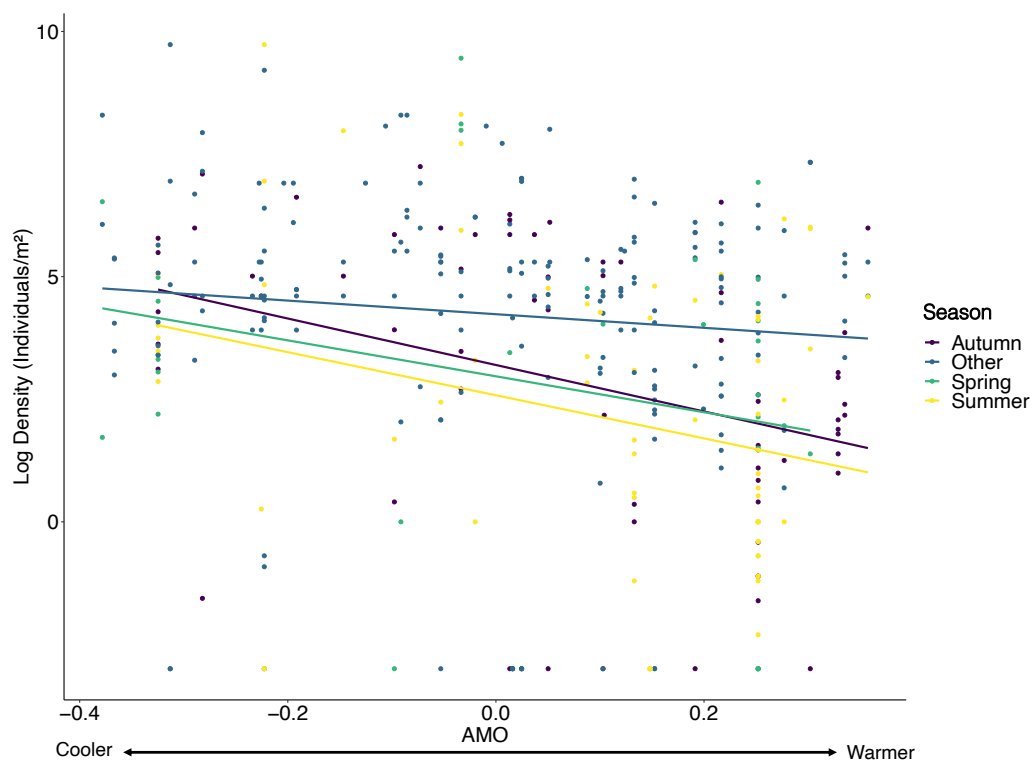


Figure 5. Relationship between $\log_{10}$ density of cockles (*Cerastoderma edule*) and the AMO index. The AMO index and sampling season had a significant impact on cockle density.

3.4. Historic reproduction patterns (macro level analysis)

Following the application of exclusion criteria, 20 records of cockle spawning times were obtained. These ranged in latitude from Trondheim in Norway (63°N, 10°E; Rygg, 1970) to the Ria de Vigo, Spain (42°N, 8°W; Martínez-Castro and Vázquez, 2012). The first record of spawning was in 1954 in the UK (Creek, 1960). Few records were obtained from the 1950s to the 1960s (Figure 6). However, spawning duration appeared to vary greatly, with the longest spawning periods recorded from the 1980s onwards (Figure 6). Spawning was observed for most of the year in the case of cockles in the French Channel in 1987 (Guillou *et al.*, 1990), when the AMO Index was in a cold phase. One of the shortest spawning periods was noted in the northernmost record, with Trondheim cockles only spawning during the month of July in 1967 (Rygg, 1970), during an AMO warm phase. A month-long spawning was also observed in south Wales in 1958 (Hancock and Franklin, 1972). Periods of spawning also varied within sites. For example, in south Wales complete spawning occurred in spring and summer 1982. However, following a severe winter in the next year, partial repetitive spawning occurred between summer and autumn (Yankson, 1986).

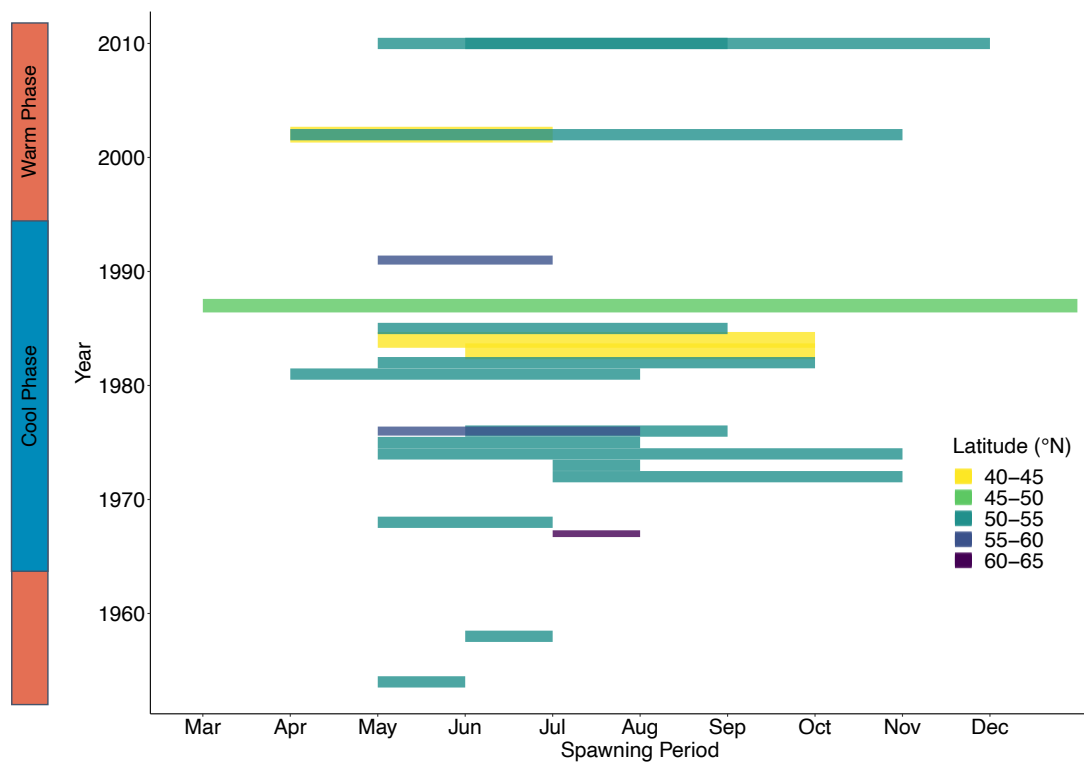


Figure 6. Historic spawning period of *Cerastoderma edule*, across various latitudes in Europe. AMO phase is indicated next to the vertical axis.

3.5. Case studies (micro level analysis)

Three case study sites were chosen from the northern, central and southern latitudes of the main distribution of cockles. Dundalk Bay (53°57'N, 6°18'W), the Bay of Somme (50°13'N, 1°35'E) and the Ria de Arousa (42°35'N, 8°52'W) were each chosen due to their importance as regional fisheries. The following factors were examined: fishing types, conservation, management, legislation, parasites, mass mortality and weather. Comparable data were not always available for each site.

3.5.1. Dundalk Bay, Ireland

Dundalk Bay, located on the east coast of Ireland, has 44.5 km² of fished cockle beds. In the 1970s, infrequent documents of landings from Dundalk Bay emerged (Fahy *et al.*, 2004), with hydraulic suction and non-suction dredging, as well as hand gathering, being used in the fishery (Fahy *et al.*, 2004; Clarke and Tully, 2014). Dundalk Bay has been the dominant source of cockles in Ireland since 2001 (Hervas *et al.*, 2008).

As a Special Area of Conservation (SAC) and a Special Protected Area (SPA), the bay is subject to an assessment, prior to the opening of the fishery (Tully and Clarke, 2016). Regulations (SI No 532) and a Total Allowable Catch (TAC) were first introduced in 2007. Subsequently, additional, more formal, legislation was introduced in 2011 as a result of the Fisheries Natura Plan, required under the EU Habitats Directive (HD, 92/43/EEC; Tully and Clarke, 2016). The annual TAC was set according to the stock biomass, which was assessed prior to the fishery annually. This legislation also outlined details on minimum landing size and gear specifications. In 2007, approximately 668 tonnes of cockles were commercially harvested, lower than the agreed 950 tonne TAC (Hervas *et al.*, 2008). A TAC of zero was enforced in 2008, 2010, 2013 and 2014 due to small size or low density (Tully and Clarke, 2016). A second five-year Fishery Natura Plan is in place since 2016. Its principle aim is to ensure protection of the habitats within Dundalk Bay, particularly to protect the cockle beds as a food source for oystercatchers (*Haematopus ostralegus*) (Tully and Clarke, 2016).

At Dundalk Bay, no mass mortalities have been observed and no studies have detailed the presence of parasites and disease in the area. However, a number of parasites were observed at the nearby Dublin Bay in 2005 (Ferreira *et al.*, 2011), including digeneans, which have been implicated in mortalities elsewhere in Europe (Longshaw and Malham, 2013).

Records show that climatic changes are influencing the health and biomass of cockles in Ireland. A severe cold spell was experienced in 2010 (Met Éireann, 2010). The entire year was generally cooler, with a mean temperature of 8.2°C, compared with the average of 9.6°C from 1942 to 2018 (Met Éireann, 2019). This coincided with lower precipitation and a decrease in cockle biomass (Figure 7). In general, years with higher minimum average temperatures, and years with lower precipitation, resulted in larger cockle harvests at Dundalk (Figure 7). However, an exception to this was noted in 2010. The highest biomass (and density) were observed in 2006, a year which was, on average, warmer than any other year between 2003 and 2011 (Met Éireann, 2019).

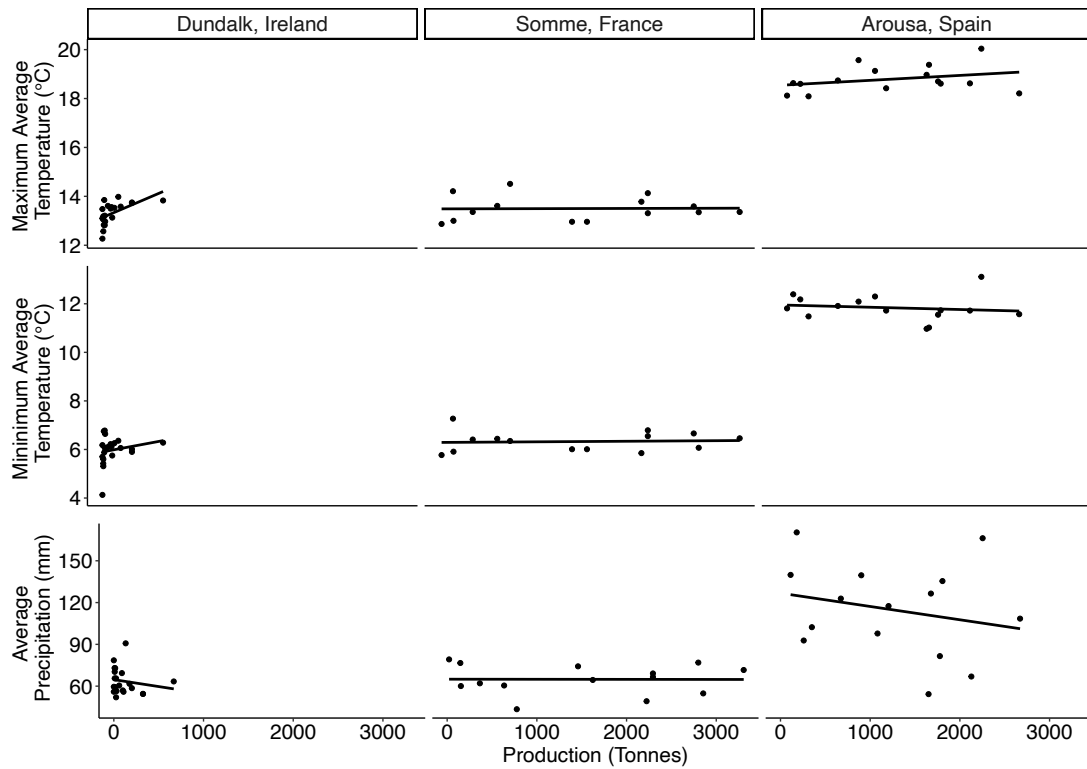


Figure 7. Relationships between climatic variables (minimum and maximum average temperature and annual average precipitation) and cockle production in the three key production areas in Ireland, France and Spain. Climate data were sourced from nearby weather stations (Klein Tank *et al.*, 2002; Met Éireann, 2019; Meteo Galicia, 2019).

3.5.2. Bay of Somme, France

The Bay of Somme estuary contains 72 km² of intertidal habitat and is the largest estuary in northwest France (Thomas *et al.*, 2014). Cockles are gathered here by professional shore-fishers (Thomas *et al.*, 2014). There are some discrepancies between data from different sources in the Bay of Somme. An absence of capture information was reported by the FAO between 1950 and 1977, while other reports state that cockle harvesting was occurring during this

time (Desprez *et al.*, 1987). For 2010, Thomas *et al.* (2014) reported a higher volume of cockles harvested than was reported by the FAO (FAO, 2018) (2855 vs 1496 tonnes). Despite the differences in data, the Bay of Somme accounted for a large proportion of French cockle harvests, both now and historically (Lambert, 1943; Desprez *et al.*, 1987; FAO, 2018).

The bay is provided with a number of protections as an SPA, Marine Protected Area, Nature Reserve and Ramsar Convention site (Thomas *et al.*, 2014). The first available record of legislation in the Bay of Somme exists from 2013, where the minimum capture size was 30 mm for cockles, and the fishery opened traditionally from September to December, with 339 fishers active. Since 2017, the legal fishing size was reduced to 27 mm for professional fishers, followed by recreational fishers in 2019.

Mass mortalities were reported in the Bay of Somme from 1981 to 1990, as a result of eutrophication (Desprez *et al.*, 1987), and further mortalities were reported in 2012, 2015 and 2018 due to the pathogenic bacteria *Vibrio aestuarianus* (ICES, 2013). While some parasitological surveys have been conducted in France, these are primarily towards the south of the country and may not be representative (de Montaudouin and Lanceleur, 2011; Magalhães *et al.*, 2017). The landings in the Bay of Somme did not appear to be influenced by any of the three examined variables.

3.5.3. Ria de Arousa, Spain

Ria de Arousa is one of the four largest estuaries in Galicia, Spain, covering an area of 230 km² (Otto, 1975). It supported an MSC certified cockle fishery from 2013 to 2018 (Marine Stewardship Council, 2013). Cockles here are fished by hand and boat, while recreational fishing is not permitted (Xunta de Galicia, 2008). Three types of exploitation are allowed under the management regime of Galicia. Two are territorial concessions, which are leased to fishers' guilds. There are also free access areas, which are directly managed by the government and require a license to operate in (Xunta de Galicia, 2008).

As the Ria de Arousa is a *Marteilia* impacted area, the free access fishery has a lower daily quota in comparison with other fisheries in Galicia. By 2018, cockle production had yet to recover following a *Marteilia* related mass mortality in 2012 (Villalba *et al.*, 2014). This is unlike the recovery that followed a mortality in 2006, which occurred after the end of the fishing season, the highest year of production for the Ria de Arousa on record (Villalba *et al.*, 2014).

No apparent relationship was observed between the environmental variables (minimum/maximum average monthly temperature or precipitation, Figure 7). However, decreased salinity was implicated in the mortality event of 2006, as a result of increased precipitation (Parada *et al.*, 2012).

3.6.4. Comparison between the three sites

Comparable data were not always available from each site (Table 1). Mortality events were observed at both the Bay of Somme and Ria de Arousa,

however of the three sites, only the Ria de Arousa was surveyed for parasites and pathogens (Villalba *et al.*, 2014). A key difference evident between the sites was climate. Predictably, average temperatures were lowest in Dundalk and increased towards lower latitudes (Table 1). However, the increased temperatures did not result in obvious differences between cockle densities. Decreased precipitation (and increased salinity), lead to reductions in biomass in Dundalk. Conversely, increased precipitation and decreased salinity lead to reduced production in Ria de Arousa (Figure 7).

Table 1. Key differences between three sites included in the case study of *Cerastoderma edule*

	Dundalk (Ireland)	Somme (France)	Arousa (Spain)	Sources
First Legislation	2007	2013	1973	Pesca de Galicia, 2019; Thomas <i>et al.</i> , 2014; Tully and Clarke, 2016
Mortalities	No Data	Yes (Eutrophication, Parasites)	Yes (Parasites)	ICES, 2013; Thomas <i>et al.</i> , 2014; Villalba <i>et al.</i> , 2014
Pathogens	No Data	<i>Vibrio aestuarianus</i>	<i>Marteilia</i>	ICES, 2013; Villalba <i>et al.</i> , 2014
Average Temperature	9.55°C	10.31°C	13.79°C	Klein Tank <i>et al.</i> , 2002; Met Éireann, 2019; Meteo Galicia, 2019
Maximum Harvest	668 tonnes (2007)	20,000 tonnes (1913)	2671 tonnes (2008)	Lambert, 1943; Pesca de Galicia, 2019; Tully and Clarke, 2016
Area Harvested	44.5km ²	72 km ²	*230km ²	Fahy <i>et al.</i> , 2004; Otto, 1975; Thomas <i>et al.</i> , 2014
Max. Mean Density (ind/m ²)	36 (2009-2010)	27.74 (2014)	527 (1997-2004)	Parada and Molaes, 2008; Ruellet <i>et al.</i> , 2014; Thomas <i>et al.</i> , 2014
Max. Mean Biomass (g/m ²)	134.8 (2008)	34.62 (2014)	No Data	Ruellet <i>et al.</i> , 2014; Thomas <i>et al.</i> , 2014

*Not all of this area is covered in cockle beds

4. Discussion

The gathering of historical data can be a difficult endeavour for several reasons, as observed in this study: data gaps, complexity, or incomparable data collected for other purposes. This analysis of secondary data provides a holistic overview of cockle populations, however it is very difficult to examine detailed trends due to the complexity of derived datasets. A large amount of research was reactive, focusing on issues impacting fisheries at a particular time, e.g. mortality causes or recruitment issues. Data collected to-date on cockle populations have often been sporadic, disjointed and lacking in intra- and cross-border coordination. Studies focused on one or only a few parameters and, understandably, were not carried out with the vision of future analysis. These findings of gaps in the dissemination of knowledge highlight the gaps that also exist between the research and practice communities.

It is important to evaluate the rationale used in this study. In terms of “the knowledge”, a large volume of secondary data was obtained detailing cockle populations in the past. This knowledge however was limited in space and time, with some areas/times demonstrating greater detail than others. In terms of “the source”, the scientific community was at the centre, with a large quantity of this presumably aimed at an industry or scientific “audience”. At a macro level, it appeared that knowledge mobilisation was unsuccessful and this was further evidenced in the lack of choices for case study locations. At the micro level, which examined important areas for cockle fisheries, it was evident

that knowledge mobilisation was sometimes happening at a local level, resulting in successful fisheries monitoring translating to management plans.

Many of the sources of data included in this study, such as newspaper articles, are generally not considered in scientific studies (McClenachan *et al.*, 2012), despite such resources being accessible to a larger audience, across a range of disciplines and sectors. However, in this well studied species it was evident that a research-practice gap exists. Very little information was derived from conference proceedings or workshops, highlighting the lack of active engagement between all relevant stakeholders. This study was larger in geographical scope than other marine historical ecology studies (Rosenberg *et al.*, 2005; Connell *et al.*, 2008), which brings another issue to the fore. Lack of cross border communication was evident with most studies only dealing with local issues, rather than a comparison across the range of the species. This highlights the requirement to improve knowledge mobilisation not just among local audiences, but across borders. However, the examination of the case studies highlights the benefit of bridging the gap between research and practice, as scientific monitoring in all three case study sites was shown to feed the management and policies there.

In many cases examined by this study, important factors such as gear type and sampling effort were not reported. Furthermore, sampling schemes (e.g. transect vs quadrats) varied between studies. It has previously been reported that sampling schemes and effort can impact density estimates (Van Wynsberge *et al.*, 2016). However, even when these confounding effects are not

taken into account, estimates in changes of cockle abundance may still be determined (Patton *et al.*, 1998), although should be considered cautiously when examining trends in species. A common approach to sampling, using similar equipment, time periods and reporting, would provide more informed robust data for decision making.

Typically, marine historical ecology is conducted not just through internet and electronic methods (as in this study), but through methods including physical searches and interviews (Swetnam *et al.*, 1999). Only using electronic means would be beneficial, reducing the costs, time and effort related to field work, particularly when examining the entire range of a species. When gathering data for this study, a lack of accessible data was discovered in the public realm. It would be more worthwhile to conduct more local scale case studies, and acquiring physical archival information and local knowledge, which would provide a more determinate overview of the factors impacting cockles. Such case studies would have more in-depth information than reported here and could be pooled to provide a holistic overview of fisheries. However, it must be noted that such a project would require greater financial investment.

In cockles, the study species, it appeared that climate had an impact on a global scale, with an overall increase in density in years with a negative AMO (“cooling” trend, Figure 5). There is currently an emerging trend of a negative AMO index in the northern Atlantic (Frajka-Williams *et al.*, 2017), which may lead to cooler sea surface temperatures and thus be beneficial to cockle

populations. However, when examining local trends (micro level) using historical data, deriving a trend is much more difficult.

While it is known that environmental factors can play a major role in influencing cockle populations (Malham *et al.*, 2012; Peteiro *et al.*, 2018; Domínguez *et al.*, 2020), it was found that management regimes and legislation also impact cockles at a regional level. It was evident that fishing methods vary across the range of cockles (Appendix B, S4 Table), some of which are more destructive than others (e.g. dredging vs hand picking). Conversely, management and legislation can have a positive impact on cockle densities and biomass. This was particularly evident at Dundalk, where a TAC was implemented (Table 1, Tully and Clarke, 2016). This measure prevented uncontrolled fishing, even when biomass was very high, facilitating improved recruitment and population expansion. Acquiring information on legislation detailing fishing techniques and management regimes for historic populations was difficult, thus making it difficult to properly examine trends at specific fisheries.

In spite of some of the limitations, a number of unexpected findings were encountered during this study. Distribution of *C. edule* was well known along Atlantic coasts of European countries, evidence of the established fisheries (Figure 3). However, modern reports of *C. edule* were recorded in the Mediterranean (Figure 3), despite the lack of reported fisheries in this region (FAO, 2018). This is a difficulty encountered in other studies, where taxonomic issues have led to errors (Mackey *et al.*, 2012). While it is possible that this was

due to difficulty in differentiating *C. edule* from *C. glaucum*, this is an interesting finding that is undergoing investigation (Maroso *et al.*, 2019). In addition, the findings concur with previous literature stating that densities of cockles tend to be higher towards higher latitudes (Figure 4, Bocher *et al.*, 2007). While Senegal (the southernmost record of cockles) has previously reported cockle fisheries (FAO, 2018), the dearth of reports from southern Morocco to Senegal (Figure 3) may be an indicator of low densities of cockles in this region (Kirby, 2004), lack of funding for this research topic, or low interest in this fishery. Such findings highlight the advantages to carrying out secondary data analyses.

A number of further recommendations can be made to improve knowledge mobilisation in commercially important species like cockles. Searches in this study were conducted via electronic means and with other scientific researchers. However, collaborating with stakeholders, including fishers and managers would allow for access to “closed knowledge sharing networks” (Young *et al.*, 2016). Open science is also a vital factor in examining the impacts of climate on species (Wolkovich *et al.*, 2012). It is essential that information is open and easily shareable, particularly in the case of an important resource (Young *et al.*, 2013). This study highlights the necessity of a “one stop” online resource where those gathering data (regardless of their community), can digitise new and pre-existing information. Incentives for the sharing of data are widely lacking (Shanley and López, 2009). Such incentives should be provided, as demonstrated by the COCKLES Project (COCKLES Project, 2020), to facilitate easier sharing and access to data. Further incentives

to promote the impact of collaborations should be encouraged through publishing this impact or including a chapter in dissertations (Brewer, 2006; Shanley and López, 2009).

The knowledge and information compiled in this study offers an insight to knowledge mobilisation in commercially fished species. While the variability of cockle populations is affirmed in this study, a more in-depth analysis was not achievable due to the lack of access to concise data. Nonetheless, the knowledge and information compiled offer many opportunities for improved, evidence-based, fisheries management and conservation. It was apparent that, previously, studies were not conducted with the intention of large-scale comparisons. To allow for more accurate predictions in the future, it would be worthwhile to employ a standardised protocol for surveying cockle populations and create a common web portal for these results. Simplifying the delivery channel will enable a more reliable relay of cockle data (i.e. knowledge) to a broader audience of stakeholders, allowing more consistent reporting of results. These recommendations are necessary for fisheries management, conservation and science to support the future sustainability of not only this industry, but other fish and shellfish species, that many European coastal communities depend on for their incomes and culture.

Data availability statement:

Data used in this study is available in the Dryad Digital Depository

<https://doi.org/10.5061/dryad.x69p8czgd>.

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Chapter 3: Latitudinal influence on gametogenesis and host-parasite ecology in a marine bivalve model

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Abstract

Boom and bust cycles have significant impacts on marine animal populations globally. Biological and environmental processes that drive population dynamics can vary geographically. Reproductive development is one process associated with the boom stage of an animal population, while parasites are connected with the bust stage. This study aimed to investigate the associative effects of host reproductive health and a host-parasite interplay on a bivalve ecosystem engineer, along a geographic gradient of latitude. Cockles *Cerastoderma edule* were sampled from five fished and unfished European sites (54°N to 44°N), between April 2018 and October 2019. A histological survey provided data on trematode (metacercaria and sporocyst life stages) prevalence and cockle stage of gametogenesis to assess the influence of a latitudinal gradient, and associated ecology, on both interplays. Sex ratios at the

northernmost sites were skewed towards females and spawning size and age were reduced at the lower latitudes. Trematode infection did not follow a latitudinal gradient. Localised site-related drivers, namely seawater temperature varied spatially, having an impact on cockle-trematode interactions. Spawning was related to elevated temperatures at all sites. Prolonged spawning occurred at southern latitudes, where seawater temperatures were warmer, and spawning was correlated with seawater temperature at the northern sites. Trematode prevalence and the impact of trematodes on gametogenesis were found to be spatially variable, but not latitudinally. Energy was likely allocated to reproduction rather than somatic growth in southern populations, with less energy allocated to reproduction in the larger, northern cockles. This awareness of the spatially varying drivers of populations is crucial considering the potential for these drivers/inhibitors to be exacerbated in a changing marine environment.

1. Introduction

Boom and bust cycles associated with population growth and decline are commonly reported phenomena, particularly in species exploited for fisheries and aquaculture (e.g. Hofmann and Powell, 1998; Korman *et al.*, 2017; You and Hedgecock, 2019). These cycles are particularly evident in marine invertebrates (e.g. van der Meer *et al.*, 2001; Uthicke *et al.*, 2009; Gamboa-Álvarez *et al.*, 2020), which play vital roles ecologically. To understand the spatial variability in population dynamics, the common cockle (*Cerastoderma edule*, Cardiidae), is a suitable model organism, due to its wide geographic range, and well-studied

biological characteristics (Malham *et al.*, 2012), as well as ecological and commercial significance (Carss *et al.*, 2020). This marine keystone species, has previously been shown to experience some biogeographical variation in these cycles on a small scale (Morgan *et al.*, 2013). However, recently, the boom and bust cycles impacting cockles are escalating temporally with mortality events increasing as a result of factors including parasitism and climate change (e.g. extreme temperatures, increased precipitation, variability in water quality) (Burdon *et al.*, 2014). Therefore, examining the reproduction of cockles is vital, in order to adjust minimum landing size and harvest amounts, to provide protection for the fisheries and ecosystems into the future.

In bivalves, including cockles, many variables impact recruitment temporally (Yankson, 1986; Beukema *et al.*, 2001), and spatially, influencing population dynamics and distribution. *C. edule* is a dioecious species (Cardoso *et al.*, 2009) that can undergo both epidemic and repetitive spawning. Generally cockles exhibit a 1:1 sex-ratio (Boyden, 1971), with age/length at first spawning differing across studies (Hancock and Franklin, 1972; Cardoso *et al.*, 2009; Elliott *et al.*, 2012). Typically, cockles begin gametogenesis in the spring and spawn in the summer (Longshaw and Malham, 2013). Variation is evident in this regime, with cockles in Trondheim, Norway (63°N), spawning for a single month in summer (July; Rygg, 1970) and cockles in the French Channel (49°N) spawning throughout most of the year (Guillou *et al.*, 1990). Previous multi-process studies on marine invertebrates have found mesoscale variation in reproduction (Lester *et al.*, 2007). Furthermore, the timing of spawning and

gametogenesis differs temporally even in cockles at the same geographic locations (Navarro *et al.*, 1989). Many factors have been proposed as the drivers of spawning and gametogenesis in cockles, including temperature (Gam *et al.*, 2010), water quality (Lusher *et al.*, 2017), immersion time (Honkoop and van der Meer, 1998) and feeding conditions in the previous season (Navarro *et al.*, 1989). A particular cause for concern is the impact of changing climate on cockle reproduction, which is intensifying regionally at an irregular rate. In fact, it has already been shown that extreme events in the Wadden Sea such as hot summers and cold winters negatively impact cockle recruitment, as well as survival (Beukema and Dekker, 2020).

Cockles are also crucial ecologically due to their role as host to a large range of parasites (Longshaw and Malham, 2013), with digenean trematodes being particularly dominant (Thieltges, 2006). Trematodes impact tissue structure and morphology due to their size relative to the host. Trematodes exhibit a complex life cycle and cockles act as primary (sporocysts) and/or secondary (metacercariae) hosts (de Montaudouin *et al.*, 2009), which can have detrimental impacts on their health (de Montaudouin *et al.*, 2012; Longshaw and Malham, 2013). For example, *Bucephalus minimus* (infecting as a first intermediate host) causes castration (Carballal *et al.*, 2001) and starvation (Dubois *et al.*, 2009). *Gymnophallus choledochus* (first and/or second intermediate host) also causes castration in cockles by eliminating gonad structure (Thieltges, 2006). It is essential to study parasites as climate change is likely to impact parasite-host interactions, which will not only impact the

individual species, but the entire ecosystem due to trophic cascades (Marcogliese, 2008). Furthermore, the expanding northern range of some parasites (e.g. rhizocephalans) may cause local increases in transmission (Gehman *et al.*, 2018) and increasing water temperature may result in year-round trematode infection (Marcogliese, 2001; de Montaudouin *et al.*, 2016). Such changes in parasite-host dynamics may prove disadvantageous to cockles.

The interplay between the reproductive and parasitic processes can have far-reaching impacts, associated with other spatially and temporally varying drivers. Energy allocation is a fine balance in bivalves, with energy needed for functions including somatic growth, reproduction and immune response. This energy balance is intertwined with a range of external/environmental factors including temperature, latitude (Clarke, 1987) and parasitism (Lafferty and Kuris, 2009). Parasites commonly cause castration, preventing the reproduction of first intermediate hosts (Lafferty and Kuris, 2009). However, it is difficult to differentiate this from the strategy of a host, diverting energy from reproduction in order to fight the parasite (Hurd, 2001). Host populations experiencing high rates of castration may exhibit altered life histories, with expedited maturity (Lafferty and Kuris, 2009).

This 19-month study aimed to examine the influence of latitude, as well as the associative influence of trematode infection and site-specific drivers (environment and fishing type), on cockle reproductive health and population characteristics across a large proportion of its range. These findings will be vital

for understanding this host-parasite system, particularly in the context of climate change.

2. Materials and methods

2.1. Sample sites

Five sites were surveyed from Carlingford Lough in the north, to Ria de Aveiro in the south (Figure 1, Table 1). Only occasional hand harvesting occurs at Carlingford, but the area is important for mussel *Mytilus* spp. and Pacific oyster *Crassostrea gigas* aquaculture (Ferreira *et al.*, 1998). Cockles are fished at Dundalk Bay from July to October (Tully and Clarke, 2016). Cockle fishing does not occur at Cork Harbour. Cockle density at Arcachon Bay is variable (de Montaudouin and Lanceleur, 2011). Since 2019, reported densities have been very low. Cockle densities at Ria de Aveiro are also variable (<10 to approx. 1200 individuals per m²) due to year-round harvesting.

Table 1. Key details of the study sites examined, along with information on individual beds. Available data on density or biomass (abundance) were obtained from previous literature.

Site	Bed	Coordinates	Seawater		Abundance
			temperature (°C)	Salinity	
Carlingford Lough	Oyster Farm	54°02'N, 6°10'W	8.2-15*	19.8*	-
Dundalk Bay	Annagassan	53°52'N, 6°20'W	6-17*	33.4-34*	1875 tonnes in 2018†
	Riverstown	54°00'N, 6°17'W			
Cork Harbour	Cuskinny	51°51'N, 8°15'W	6.9-17.6*	33.1-34.8*	<10 per m ²
	Ringaskiddy	51°49'N, 8°18'W			
Arcachon Bay	Banc d'Arguin	44°35'N, 1°14'W	9.5-21.1‡	32-35‡	Reaching 2390 ind/m ² §
Ria de Aveiro	Mira Channel	40°38'N, 8°44'W	11-22¶	0-36#	Reaching 1200 ind/m ²

*Copernicus, 2020

†The Marine Institute and Bord Iascaigh Mhara, 2018

‡de Montaudouin and Lanceleur, 2011

§Magalhães *et al.*, 2016

¶Vaz *et al.*, 2005

#Lillebø *et al.*, 2015

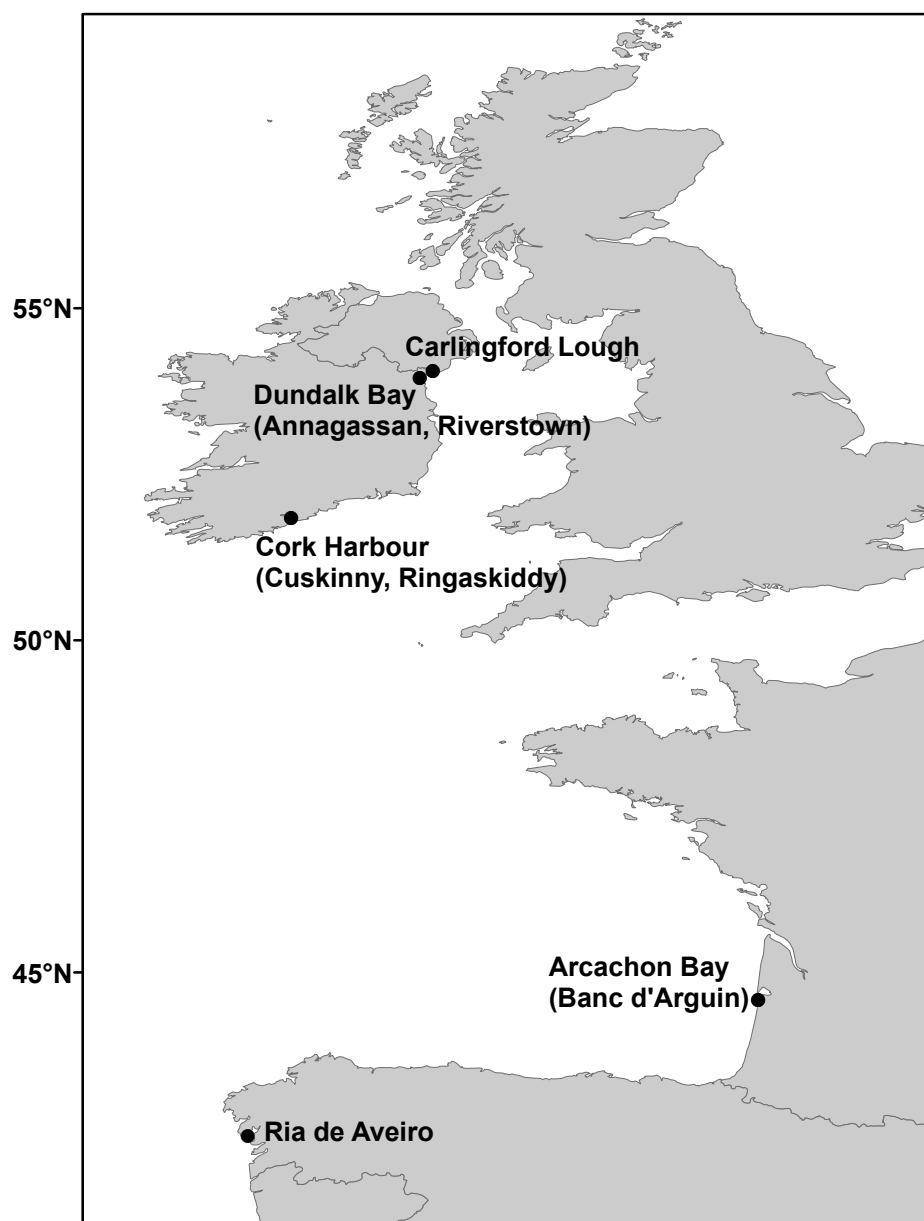


Figure 1. Geographical range of the study sites in Ireland, France and Portugal (bed names indicated in brackets).

2.2. Sample Collection

In this study, 1,636 cockles were sampled from intertidal areas (Table 2). The aim was to collect 30 samples from each location every other month, from April 2018 until October 2019 (19-month time period). Bi-monthly sampling was deemed appropriate, following the slow reproductive development of

cockles observed in the monthly sampling regime of Morgan *et al.* (2013). Some deviation occurred due to difficulty in locating cockles or where cockle densities were low. In rockier substrates (Carlingford and Cork), surfaced cockles were gathered. This method was deemed more appropriate and time effective with time constraints associated with tidal exchange. At the remaining sites, where sandy and muddy substrates were present, surfaced cockles were opportunistically gathered by hand, in combination with collection of buried cockles using a rake. The total number of cockles examined via histology was less than the number collected in the field, due to occasional issues with fixation and tissue integrity.

Table 2. Descriptive statistics of all cockles examined in this study and number of males, females and indeterminate *Cerastoderma edule* from three Irish sites, one French site and one Portuguese site. Sex ratio is presented as male:female. For the chi square results, there was one degree of freedom in each case.

Site	Male	Female	Indeterminate	Total	Sex Ratio	Chi Square Test	Length (mm)		Growth Rings	
							Range	Mean	Range	Mean
Carlingford	58	102	69	229	1:1.7	$\chi^2=12.1$, $p<0.001$	21 - 45.8	33.8	1 - 11	4.2
Dundalk	138	178	163	479	1:1.3	$\chi^2=5.06$, $p=0.02$	18.1 - 49.1	32.7	0 - 9	2.9
Cork	168	177	62	407	1:1.1	$\chi^2=0.23$, $p=0.63$	9.5 - 49.9	32.9	0 - 13	3.6
Arcachon	100	113	26	239	1:1.1	$\chi^2=0.80$, $p=0.37$	16.2 - 40	28.6	1 - 7	3.7
Aveiro	123	116	43	282	1:0.9	$\chi^2=0.21$, $p=0.65$	7 - 36	25.8	-	-
Total	587	686	333	1636	1:1.2	$\chi^2=7.7$, $p=0.006$	7 - 49.9	31.1	0 - 13	3.4

2.3. Cockle processing

(i) Morphometrics

Prior to histology, the whole weight (shell and tissue) of each cockle was measured before dissection. Cockle morphometric measurements were gathered (Figure 2). External growth rings in cockles are set down each winter (Orton, 1926) although sometimes lines may be hard to distinguish due to warm winters or short cold spells (Ponsero *et al.*, 2009). Therefore, easily distinguishable external growth rings were counted to estimate cockle age.

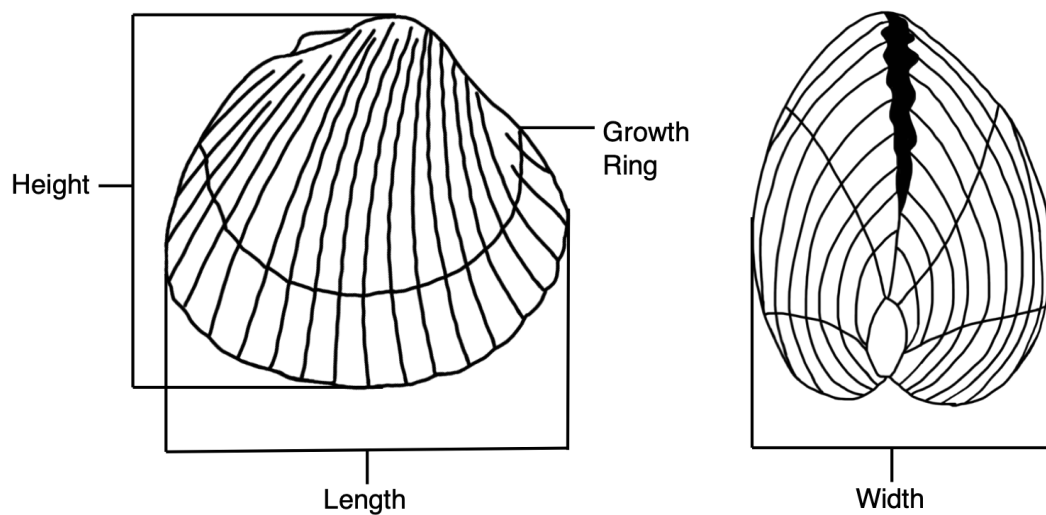


Figure 2. Measurements taken for cockle morphometrics.

(ii) Histology

Cockle tissues were removed from the shells and fixed in Bouin's solution (Arcachon samples) and Davidson's solution (all other samples) for 24-48 hours (Shaw and Battle, 1957). They were then prepared for embedding in wax by a

20-hour cycle through graded volumes of ethanol for dehydration (adapted from Howard *et al.* (2004)). The samples were sectioned to at least 5 μm (3 μm if possible) before staining with Haematoxylin and Eosin (Humason, 1979). Gonad staging was conducted according to the scale described by Morgan *et al.* (2013), where the gonad was classed into five stages: early developing, late developing, ripe, spawning/partially spent and spent. When one individual exhibited multiple stages, or an intermediate between two stages, the dominant stage was assigned. Cockles that did not have identifiable gonad were classed as indeterminate. Presence or absence of trematodes (either sporocysts or metacercariae stages) was also determined.

2.4. Analysis

The sexual cycle was described at each site and compared with the seawater temperature. These temperature data were derived from the Atlantic-Iberian Bay Irish-Ocean Physics Analysis and Forecast (Copernicus, 2020). All subsequent analyses were conducted in R (R Core Team, 2019).

To examine pairwise differences in spawning length, spawning age and proportion of indeterminate individuals between sites, Kruskal Wallis tests were conducted followed by a Dunn test with a Bonferroni correction. Significance was determined at a 97.5% probability level. These tests were chosen following evaluation using Levene's test for homogeneity of variance and the Shapiro-Wilk normality test.

Pearson's chi square tests with Yate's continuity corrections were employed to examine the following hypotheses:

1. Did sex ratio differ from 1:1 overall, and at each site/latitude?
2. Did the proportion of trematode infection vary across sites/latitudes?
3. Did the percentage of individuals exhibiting each stage of gametogenesis vary according to trematode infection at the sites/latitudes?

As appropriate, a post hoc analysis comparing the adjusted critical value with the adjusted residuals was conducted to determine which variables were significant at the 5% level.

Finally, an ANCOVA was employed to determine if seawater temperature was associated with the percentage of individuals spawning. The full statistical results are detailed in Appendix C.

3. Results

3.1. Spatial variation in seawater temperature

Sea surface temperature did not follow a strict latitudinal gradient. In the months studied, mean temperatures at Carlingford ranged from 8.2°C to 13.6°C, with a mean of 11°C. Despite the close proximity of Dundalk with Carlingford, water temperature ranged from 6.5°C to 17.4°C, with a mean of 12.4°C. Water temperature at Cork ranged from 8.5°C to 15.4°C, with a mean of 12.2°C. The mean water temperature at Arcachon Bay was the highest of all of the sites studied (15.6°C) and ranged from 11.1°C to 21.5°C. Despite being

the southernmost site, water temperatures were lower at Ria de Aveiro than at Arcachon Bay, and had the narrowest range, from 12.6°C to 16.4°C, with a mean of 14.8°C.

3.2. Relationship between sex ratio and indeterminate individuals with latitude

The two northernmost sites were the only locations where sex ratio deviated from the expected 1:1 (Carlingford (1:1.7) and Dundalk (1:1.3)). Indeterminate individuals were found at all sites, with the percentage varying spatially ($\chi^2=13.7$, $df=4$, $p=0.008$, Table 2). Higher percentages of indeterminate individuals were observed at Carlingford (the northernmost site), compared with Ria de Aveiro ($p=0.04$, trend at significance level of 0.025) and Arcachon Bay ($p=0.03$) (the southernmost sites). Proportions of indeterminate individuals appeared to vary over time, with expected peaks of indeterminate individuals during the winter months when a resting period in gametogenesis occurred (Figure 3). However, the mid latitude site of Arcachon Bay, in particular, had a shortened resting period during the summer after massive spawning when the majority of cockles were indeterminate.

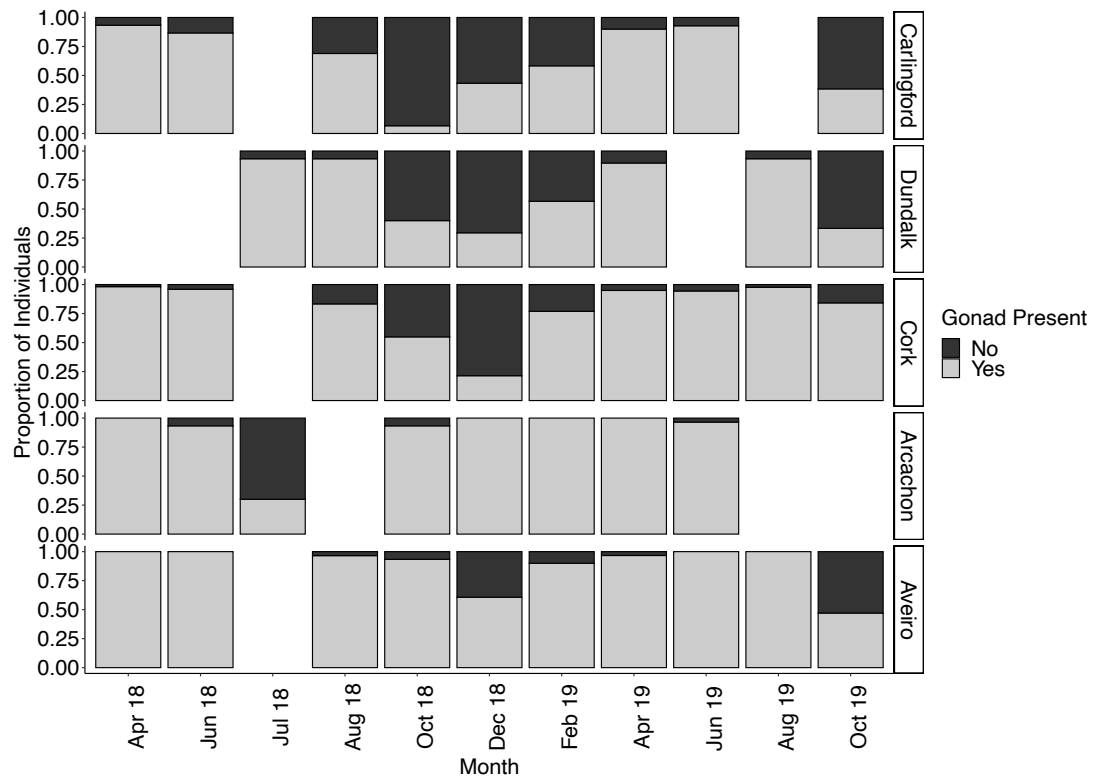


Figure 3. Proportion of *Cerastoderma edule* with and without evident gonad at each site. Months without a column indicate that sampling did not occur.

3.3. Relationship between cockle size, age and spawning

Spawning size was reduced at the southern latitude sites. Cockles spawning at the more southern sites of Arcachon Bay and Ria de Aveiro were significantly smaller than all of the other sites ($p < 0.001$ in all cases, Figure 4A). Full size distributions are reported in Chapter 5 and Appendix E, S3 Figure. However, age did not follow the same gradient, with large variations of spawning age within the Irish sites (Figure 4B).

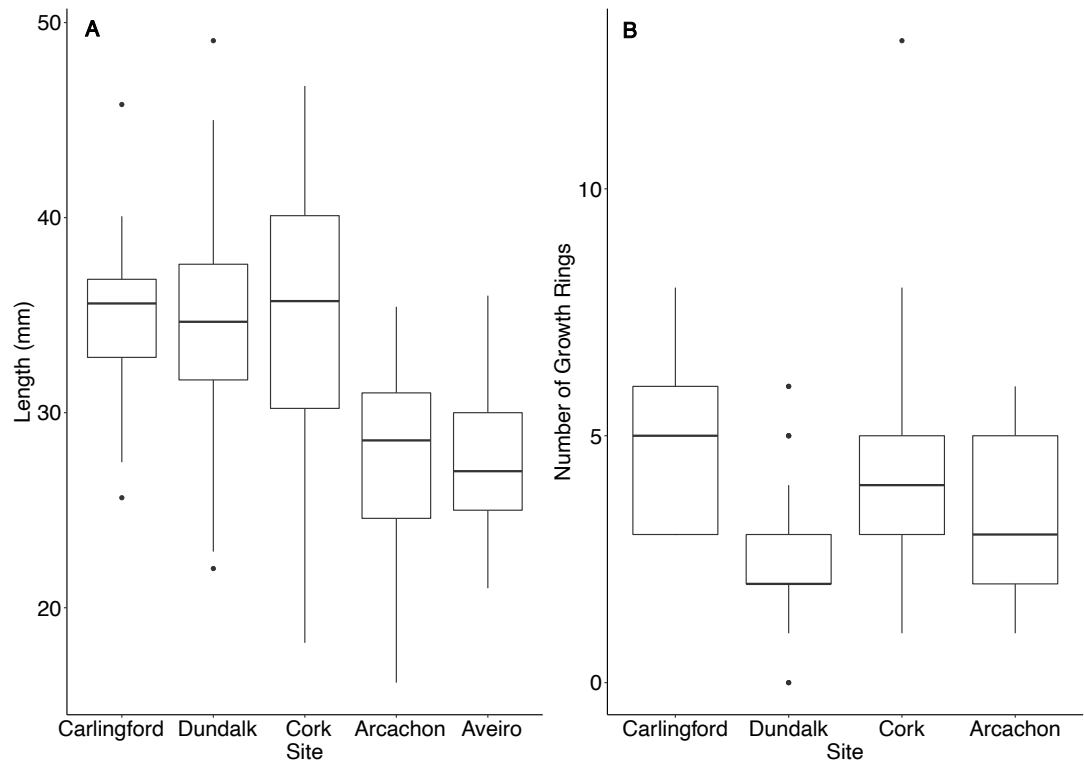


Figure 4. (A) Median length at spawning (i.e. all individuals at the spawning/partially spent stage) for cockles at all sites and (B) Median number of growth rings at spawning for cockles at all sites (excluding Ria de Aveiro). Boxplots demonstrate the median values, boxes extend from the 25th to 75th percentile of each group's distribution of values, and whiskers show the largest and smallest values within 1.5 times the interquartile range. Outliers are indicated by individually plotted points.

3.4. Sexual cycle and seawater temperature

Spawning duration and frequency varied between the Irish sites, between countries and inter-annually. At Carlingford, only one spawning period was observed in each year, commencing by April and ceasing by October of both years. In 2018, spawning in Dundalk cockles continued until August in

females, and October in males, with development recommencing by October 2018 in both sexes. A second, smaller spawning in 2018 was observed in males (20%) in December but did not continue throughout the winter (Figure 5). At Cork, in 2018, a single spawning event was noted, ceasing during the winter, indicated by an absence of spent males in February 2019 (Figure 5). However, in 2019 at Cork, spawning individuals were observed in all sampled months, until the end of the sampling period (October). At the southern sites (Arcachon Bay and Ria de Aveiro), resting periods appeared to be shorter (Figure 5), with spawning observed during the majority of sampled months (and likely during the interim months due to the numbers of spent individuals observed).

At the northernmost sites, a synergy between seawater temperature and spawning time was evident (Figure 6). At Dundalk there was a positive correlation between percentage of individuals spawning and temperature ($p=0.002$, $F=14.2$). At Cork there was a similar trend ($p=0.061$, $F=3.994$). While no significant correlation was observed at the other sites, there did appear to be an overall positive trend between increased spawning and increased temperature (Figure 6).

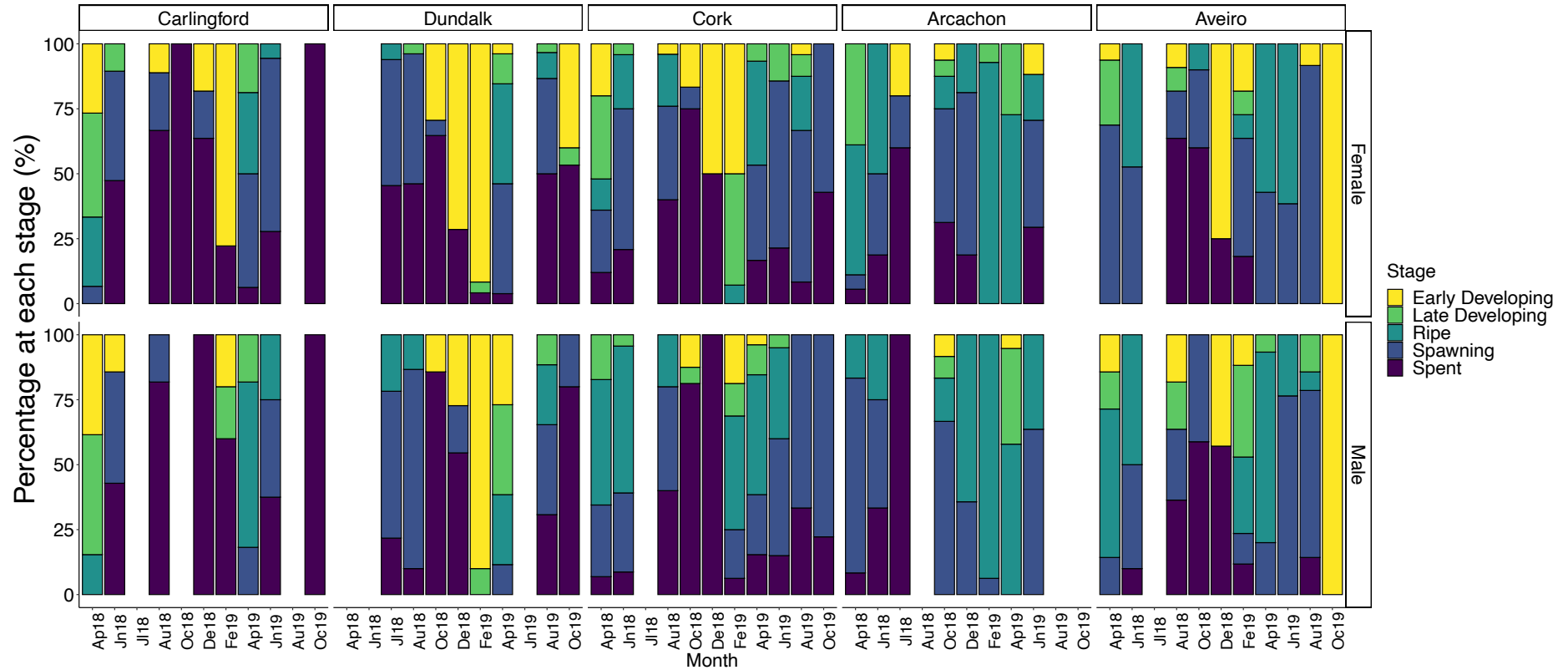


Figure 5. Percentage of *Cerastoderma edule* at each stage of gonadal development at French, Portuguese and Irish sites. Sampling commenced in April 2018 (Ap18) and was completed in October 2019 (Oc19). Indeterminate individuals were omitted and included in Figure 3. Months with no bar indicate that sampling was not conducted.

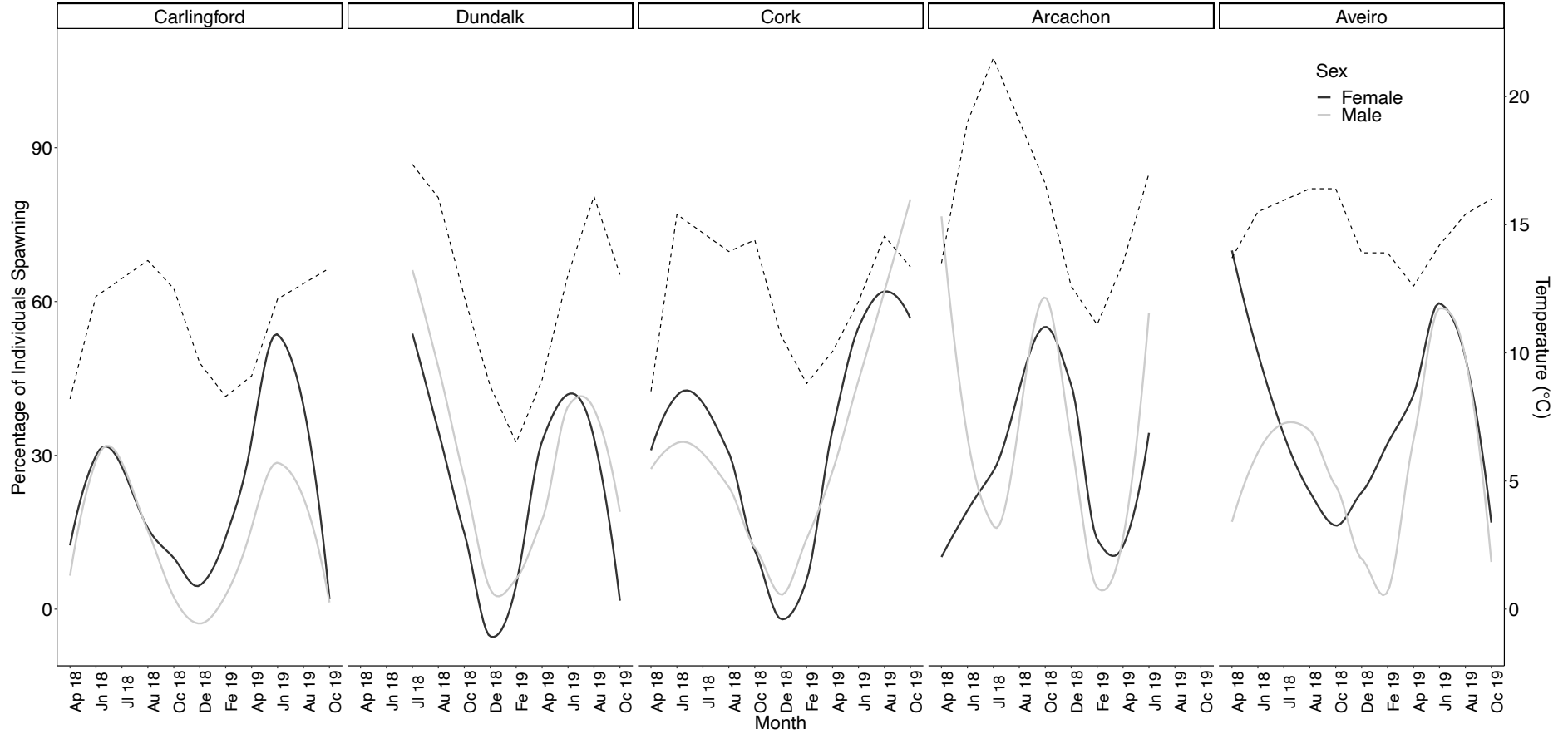


Figure 6. Percentage of males and females at the spawning/partially spent stage of gametogenesis during each month of the study, compared with sea surface temperature (dashed line), at each site.

Differences in the synchronicity of gametogenesis were observed between sites. At Carlingford spawning generally appeared synchronous between sexes, although more females than males were spawning in 2019 (Figure 6). At Cork, one of the other northern sites, it appeared that more females were spawning in 2018, with the converse occurring in 2019. At Arcachon Bay, more males were spawning in early 2018 (Figure 6) and at the southernmost site, Ria de Aveiro, spawning of both sexes was less synchronous in 2018 than in 2019, where similar numbers were spawning in both sexes by June (Figure 6). Spawning at the Ria de Aveiro appeared to be initiated by females in both years (Figure 6).

3.5. Patterns of trematode infection and impact on cockle gametogenesis (reproductive cycle)

Trematode infection varied spatially, with both sporocysts and metacercariae present at all sites but variation did not follow a latitudinal gradient. Sporocyst prevalence was highest at Arcachon Bay (12.1%) and metacercarial prevalence was highest at Carlingford (81.7%). However, prevalence of both stages was lowest at the southernmost site (Ria de Aveiro: sporocysts = 2.1%, metacercariae = 9.6%). Prevalence of infection by metacercariae generally increased with higher water temperature, peaking between approximately 13.5°C and 17.5°C (Figure 7). Arcachon Bay was the exception, therefore a latitudinal gradient was not obvious. Metacercarial prevalence at Arcachon Bay decreased gradually over the summer months, when the temperature reached a monthly mean of 22.2°C in July 2019,

exceeding that of all other sites, peaking in December at 60% infection (mean temperature at Arcachon = 12.6°C) (Figure 7).

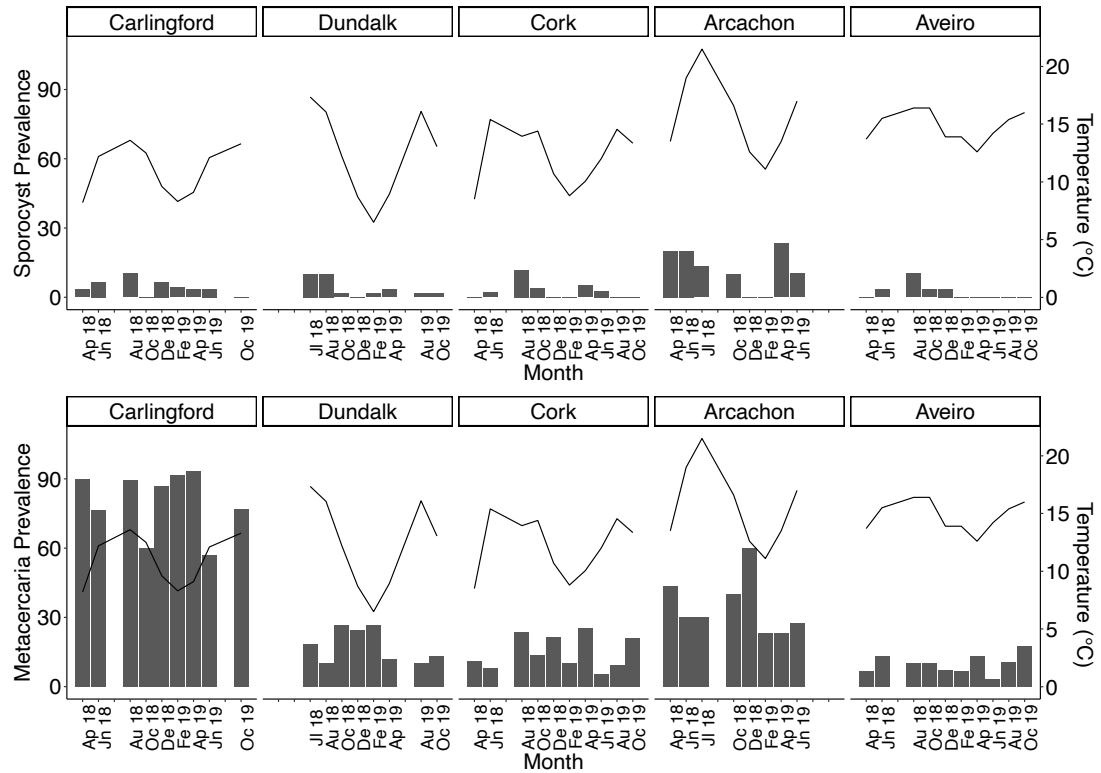


Figure 7. Time series of trematode prevalence (metacercariae and sporocysts) recorded in *Cerastoderma edule* at all study sites, compared with seawater temperature (solid line). Individuals coinfecting with metacercariae and sporocysts were included in both graphs. Months without a label indicate that sampling did not occur.

Overall, a trend was observed where metacercaria infected individuals were more likely to be indeterminate than to be ripe or spawning ($p=0.08$, in both cases). Similarly, coinfecting individuals were more likely to be indeterminate, rather than ripe or spawning ($p=0.008$, in both cases, Figure 8). No significant relationship was observed between cockles solely infected with

sporocysts, and the stage of gametogenesis. Similar patterns of gametogenesis were noted in both males and females uninfected by trematodes, and those with single infection of sporocysts and metacercariae (Appendix C, S7 Figure). For coinfecting individuals, the majority were indeterminate (n=15), with fewer males observed (n=3). However few individuals were coinfecting by both trematode stages (n=29).

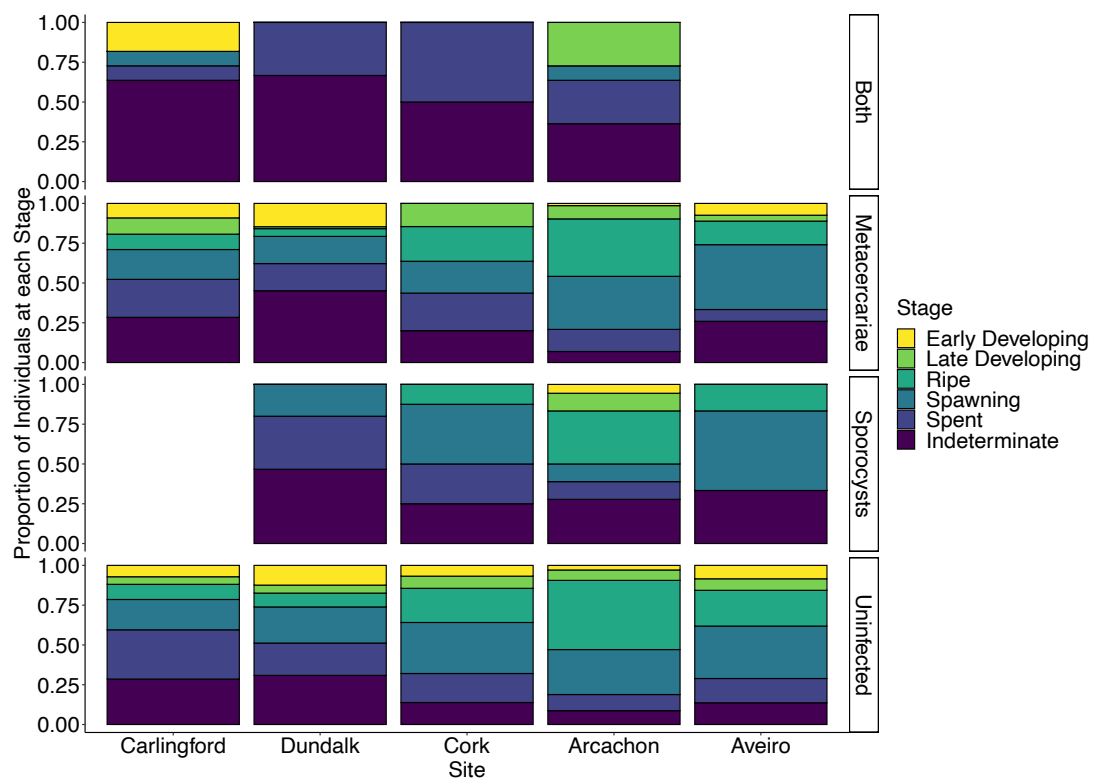


Figure 8. Proportion of *Cerastoderma edule* at each stage of gametogenesis for individuals infected and uninfected by sporocysts and metacercariae. Infection state is indicated on the right of the graph, and “Coinfection” indicates that an individual was coinfecting by sporocysts and metacercariae.

4. Discussion

This study highlighted the biogeographical differences in cockle populations, showing that there is an associative influence of trematode infection, temperature and latitude on population dynamics and reproduction characteristics. Increased seawater temperatures potentially influenced trematode prevalence, until a threshold temperature was reached (approximately 20°C, Figure 7), when prevalence decreased, potentially impacting cockles at more southern, warmer locations. Trematodes may have had a deleterious effect on reproduction, with a reduced proportion of spawning individuals and higher numbers of trematode infected cockles exhibiting no gonad regardless of latitude or other local factors. Latitude appeared to influence the reproductive cycle of cockles, with the northernmost sites exhibiting spawning peaks at similar times in the year. Furthermore, spawning occurred almost year-round at the two southernmost sites, despite variations in average seawater temperature between them. It is also important to note that while bi-monthly sampling sufficed at the Irish sites and Aveiro (cooler sites), more frequent sampling may be necessary at Arcachon (and possibly other warmer sites), to examine the more accelerated gametogenesis here.

A potential link between sex ratio and latitude was found, with the northernmost latitudes experiencing skewed sex ratios, despite varying in terms of fishing pressure and trematode infection. Significantly higher numbers of females were found at these northerly, nearby sites of Carlingford and Dundalk, a phenomenon also seen in other cockle populations (Boyden, 1970; Martínez-

Castro and Vázquez, 2012). A number of explanations may be suggested. First, deviation from a 1:1 sex ratio can result from sex specific mortality (Longshaw and Malham, 2013) and it is possible that trematode infection was higher in males, as suggested by a previous study (Morgan *et al.*, 2012). However further research would be required to test this hypothesis, considering the many species of parasites found in cockles (Longshaw and Malham, 2013), including trematodes (de Montaudouin *et al.*, 2009). Another possibility is that a genetic element of sex determination is at play, with large genetic diversity recorded spatially in cockles previously (Martínez *et al.*, 2015). However, further studies would be required to determine this.

Significant site related differences were found in both the age and size of spawning cockles. Latitude appeared to be an influencing factor, but fishing activity may also have a role. Older as well as larger spawning cockles were found at Cork as might be expected due to the lack of cockle fishing activity. Cockles at Carlingford, a site also free of large-scale commercial fishing, reached similar ages to Cork cockles. The heavily fished sites had smaller and younger spawning cockles than unfished sites. At the southern sites (Ria de Aveiro and Arcachon Bay), this may be because cockles allocate more energy towards longer spawning periods, rather than growth. Such variations in reproductive and life history strategies, through differing energy allocation, have been found in other shellfish (Egerton *et al.*, 2020). However, it is also possible that temperature, food availability and water quality are impacting growth and

maturity in cockles (Gosling, 2015) and it would be beneficial to further investigate these drivers.

Although seawater temperature (and likely resulting food availability), and a range of other local factors, influenced trematode prevalence, it did not follow a latitudinal gradient. Trematode infection levels varied across sites, with the highest prevalence detected at Carlingford. However, it is important to consider that histological methods, such as those used in this study, may result in an underestimation of trematode prevalence, as not all tissue is screened (Morgan *et al.*, 2012). Similar to previous observations relating age and parasites (de Montaudouin *et al.*, 2000), at Carlingford there was a high metacercarial prevalence, as well as a high abundance of old cockles. However, metacercarial intensity was not examined and may in fact have been low due to the dilution effect of sympatric *Crassostrea gigas* (Krakau *et al.*, 2006). Another driver of differences at these sites may be the presence of intermediate and final host species (Hechinger and Lafferty, 2005; Thieltges and Reise, 2006, 2007; Byers *et al.*, 2008; de Montaudouin and Lanceleur, 2011). At Carlingford, birds may not be the factor driving prevalence, due to high human activity on the oyster farm, but it would be worth examining abundance and trematode infection in gastropod species here (Longshaw and Malham, 2013). Interestingly, high numbers of barnacles were observed fouling cockles at Carlingford (Personal Observation). These fouling organisms potentially keep cockle shells from closing entirely, thus increasing the potential for trematode infection, but conversely can predate cercariae (Welsh *et al.*, 2017). Cockle

density also differed greatly between Cork and Carlingford, the two sites with low fishing impact. Notably, a lower density of cockles at Cork coincided with lower trematode prevalence. However, it is difficult to ascertain the relationship between host density and trematode prevalence (Magalhães *et al.*, 2017). For example, Cork and Ria de Aveiro, sites with a large density difference, both reported low trematode prevalence. It may be that these factors are acting additively or synergistically, explaining the differences between sites.

Cockles may go through an over-wintering stage when their gonad is undifferentiated (Boyden, 1970) and unsurprisingly, high levels of indeterminate individuals were found at all sites, mostly from autumn to winter, when food availability is lower. However indeterminate individuals were observed year-round at the northern sites (Carlingford, Dundalk and Cork). Many trematode species cause castration (Carballal *et al.*, 2001; Thieltges, 2006) and in this study a higher proportion of infected cockles were of indeterminate sex, compared to at a ripe or spawning stage. It is generally believed that parasites infecting as sporocysts (reproductive stage) are likely to cause more damage than those infecting as metacercariae (encystment stage) (Wegeberg and Jensen, 1999). However, it was evident that both metacercariae and sporocysts had a deleterious effect on reproduction, with reduced spawning and higher numbers of indeterminate individuals in trematode infected cockle communities.

Findings from this study indicate the influence of geographical variation on cockle reproduction, with temperature, seasonal energy availability,

trematode infection and gametogenesis acting associatively. Spawning appeared to be prolonged at the southern sites (Ria de Aveiro and Arcachon Bay), potentially causing a re-allocation of energy resources from individual growth, denoting varying life history strategies amongst different genetic groups, and sites. Trematode prevalence was potentially related to seawater temperature and it would be worthwhile to examine further sites to confirm this relationship. Gametogenesis and spawning were likely impacted by trematodes and water temperature (and associated seasonal peaks in food availability), as shown in this study, as well as by a range of biotic and abiotic factors influencing energy reserves and cockle production (Rueda *et al.*, 2005). These results indicate the potential for significant changes in cockle reproduction and host-parasite ecology related to warming seas. These findings are not limited to cockles (Lester *et al.*, 2007), and many of the factors impacting commercially exploited marine species at both a local and regional scale are likely to change as a result of a changing environment - thus highlighting the importance of regular monitoring to follow shifting population dynamics.

Data availability statement:

Data used in this study is available in the Dryad Digital Depository

<https://doi.org/10.5061/dryad.slrn8pk7b>

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Chapter 4: Extrinsic and intrinsic drivers of parasite prevalence and parasite species richness in an ecosystem engineer

Abstract

Parasite species richness is influenced by a range of drivers including host related factors (e.g. host size) and environmental factors (e.g. seawater temperature). However, identification of modulators of parasite species richness remains one of the great unanswered questions in ecology. The common cockle *Cerastoderma edule* is renowned for its diversity and abundance of parasites, yet drivers of parasite species richness in cockles have not been examined to investigate the association of both macro and microparasite communities. Using cockles as a model species, some of the key drivers of parasite prevalence and parasite species richness were investigated. The objectives of this 19-month survey were to determine the influence of the environment, host-parasite dynamics and parasite associations on parasite species richness and prevalence at two different geographic latitudes, chosen based on environmental differences. The highest parasite species richness was recorded in the northern sites, and this was potentially influenced by a range of interactions between the host, the pathogens and the environment. Parasite prevalence increased with host size and age, and parasite species richness increased with reduced salinity. A number of interactions between parasites,

and between parasites and pathologies may be influencing parasite infection dynamics. New and concerning information is also presented regarding interactions between parasites and their environment. A number of parasites and potential pathogens (bacteria, *Trichodina* ciliates, metacercariae, sporocysts) may be advantaged under climate change conditions (warming seas, increased precipitation), increasing disease incidence, which may prove detrimental not just for cockles, but for other bivalve species in the future.

1. Introduction

Parasites are ubiquitous in the marine environment (Torchin *et al.*, 2002). Some marine parasite species are topical due to their detrimental effects on the global economy, impacting both wild and reared species (Lafferty *et al.*, 2015). As well as having economic impacts, parasites play important ecological roles. Disease outbreaks are becoming increasingly common in the marine environment (Ward and Lafferty, 2004), and parasitism and disease are likely to be influenced by climate induced variations in temperature, salinity and oxygen (Byers, 2021). Parasite species richness and biodiversity within a given host is one of the key questions in modern ecology (Kamiya *et al.*, 2014). Despite this, the drivers of parasite species richness is a topic that remains largely unanswered (Dallas *et al.*, 2020). Across a diverse range of taxa, parasite species richness may be driven by a range of host characteristics including host size, geographical range and population density (Kamiya *et al.*, 2014). For parasite clades with complex life-cycles (e.g. cestodes, trematodes), parasite species richness is also often correlated with free-living diversity in their habitat

(Hechinger and Lafferty, 2005; Hechinger *et al.*, 2007). However, environmental factors, such as exceeded host tolerance, and those resulting from climate change (e.g. warming seawater, weather extremes) may also influence patterns of parasitism, potentially causing extinctions or conversely increasing species richness in certain areas (Carlson *et al.*, 2017). Moreover, these climate related influences on parasite-host interactions may create problems due to a cascade through food webs (Marcogliese, 2008; Galaktionov, 2017; Mouritsen *et al.*, 2018).

The common cockle *Cerastoderma edule* is a commercially exploited ecosystem engineer, located along the Eastern Atlantic, from west Russia to west Africa (Hayward and Ryland, 1995; Honkoop *et al.*, 2008; Mahony *et al.*, 2020). This species is renowned for its diversity and abundance of parasites, including viruses, bacteria, microsporidia, apicomplexa, ciliophora, haplosporidia, turbellaria, digenea and crustacea (Lauckner, 1983; Longshaw and Malham, 2013). While parasitology in cockles is a centuries old field (Huet, 1888), previously unreported cockle parasites are still being described (Bookelaar *et al.*, 2020). Furthermore, novel species, such as the mortality inducing *Marteilia cochillia*, have been reported within the last decade (Villalba *et al.*, 2014). The impact of parasites infecting cockles may be detrimental depending on parasite species (Longshaw and Malham 2013), or interactions with poor environmental conditions (e.g. temperature extremes) (Longshaw and Malham 2013). Mass mortalities are increasingly reported in cockles, and pathogenic organisms are one of the most commonly reported causes (Jonsson

and André, 1992; Longshaw and Malham, 2013; Burdon *et al.*, 2014; Villalba *et al.*, 2014). While not all of these parasites are pathogenic, some have been implicated in mortalities or sub-lethal effects, for example apicomplexan gregarines, infecting as oocysts, have been linked to destruction of cells within gills, which may contribute to mortality (Azevedo and Cachola, 1992).

Large diversity also exists within parasite groups, evidenced by the sixteen documented trematode species, which infect cockles as first (sporocysts) and secondary (metacercariae) intermediate hosts (de Montaudouin *et al.*, 2009). These can co-occur within a single individual (Thieltges and Reise, 2007; Magalhães *et al.*, 2018a). While not all trematode species found in cockles cause negative effects (Longshaw and Malham, 2013), lethal and sublethal impacts have been caused by a number of species (Goater, 1993; Thieltges, 2006; Dubois *et al.*, 2009). These negative impacts may be worsened due to interaction with unsuitable environmental conditions (Desclaux *et al.*, 2004; Gam *et al.*, 2009). As variation in environmental factors occurs between different sites, particularly over large geographical ranges, it is necessary to account for this effect when studying parasite dynamics.

Previous studies of cockles focused on select parasite groups, trematodes in particular, leaving many questions unanswered regarding the interactions between cockle pathogens and driving factors. Few studies investigated coinfection within a clade (de Montaudouin *et al.*, 2000; Magalhães *et al.*, 2015, 2020). As an example, coinfection between *Monorchis parvus* and *Gymnophallus choledochus* was lower than expected from mono-infection

prevalence (Magalhães *et al.*, 2020). Studies dealing with coinfection among different parasite clades are even rarer. For example, coinfection between digeneans and *Perkinsus* sp. have been examined, but no association was discovered (Lassalle *et al.*, 2007). Additionally, some previous studies have detailed interactions with the environment in other parasite groups. Interaction between *Vibrio tapetis* (bacteria) and *Himasthla elongata* (trematode) was studied in an experimental cadmium contaminated context (Paul-Pont *et al.*, 2010). In terms of non-trematode species, *Mycoplasma*-like bacteria can also have detrimental impacts on cockles at higher temperatures (Azevedo, 1993). Furthermore, mortality associated haplosporidians (Longshaw and Malham, 2013) exhibit lower prevalence in areas of reduced salinity (Albuxech-Martí *et al.*, 2020).

While it appears that parasite studies in cockles often focus on trematodes, this well-studied digenean community makes cockles a suitable model for examining dynamics of parasite-host systems in the climate change scenario (de Montaudouin *et al.*, 2016). Moreover, cockles are also an appropriate model species for examining both macro and microparasites for a variety of additional reasons. Cockles are often found in intertidal areas (Malham *et al.*, 2012) and as a result, are likely to come in contact with a variety of organisms, which act as hosts to parasites, such as birds (Longshaw and Malham, 2013). Therefore, the dynamics of parasitism are easily studied in cockles due to the potential for contact with a wide array of pathogens. Finally, and importantly for a model species, the cockle is a well-studied, economically

and ecologically vital organism, for which it has been deemed a suitable model in previous studies (Morgan *et al.*, 2013; Carss *et al.*, 2020; Mahony *et al.*, 2020).

The overarching aim of this study was to provide knowledge on parasite species richness using a marine bivalve model (the common cockle *Cerastoderma edule*). This study is novel due to the vast geographic range (Ireland to France), the long sampling time (19 months, bimonthly) and the differences in anthropogenic activities (fishing impact, aquaculture, shipping, conservation) at the sample sites. The objectives were to: i) determine parasite species richness across sites, ii) determine if associations exist between the observed parasite groups, and iii) determine if intrinsic (host size) or extrinsic (environmental) factors drive prevalence of pathogens. A number of hypotheses were devised based on previous studies on single parasites/parasite groups. It was expected that species richness would vary depending on host size (de Montaudouin *et al.*, 2000). Furthermore it was hypothesised that associations would occur between parasites due to the stress of detrimental pathologies, which may increase susceptibility (Díaz *et al.*, 2010, 2016). Similarly it was hypothesised that suboptimal temperature and salinity would result in greater parasite prevalence, due to the impact of stressors on immune function (Coates and Söderhäll, 2020). This study will provide knowledge on the impact of environmental drivers on parasite prevalence and parasite species richness, and the potential impacts of climate change in the future.

2. Materials and methods

2.1. Study sites

The northernmost site was Carlingford Lough (Table 1, Figure 1), which covers an area of 49 km². Samples here were obtained from a cockle bed in the vicinity of a Pacific oyster *Crassostrea gigas* farm. The second Irish study site was nearby at Dundalk Bay (Figure 1, Table 1). The final Irish site examined was Cork Harbour (Figure 1, Table 1), a sheltered bay on the south coast of Ireland. The southernmost sample site was Arcachon Bay in France (Figure 1, Table 1). Cockles came from a bed at the 25 km² Banc d'Arguin, a moderately sheltered sandflat located in the south of Arcachon Bay (de Montaudouin and Lanceleur, 2011).

Table 1. Description of the four sites and the beds examined within. Typical activities occurring in the general area of the sites are described.

Site	Bed	Coordinates	Water Quality	Activities	Cockle Fishery
Carlingford	Oyster Farm	54°02'N, 6°10'W	Unassigned*	Agriculture, aquaculture, shipping	Occasional small scale hand harvesting
Dundalk	Riverstown	54°00'N, 6°17'W	Moderate*	Fishing	Hydraulic suction dredging
	Annagassan	53°52'N, 6°20'W	Good*		
Cork	Cuskinny	51°51'N, 8°15'W	Moderate*	Industry shipping	Wild
	Ringaskiddy	51°49'N, 8°18'W	Moderate*		
Arcachon	Banc d'Arguin	44°35'N, 1°14'W	Good*	Agriculture, aquaculture, forestry, tourism	None†

*Assigned under the Water Framework Directive (EPA, 2020)

†No fishing during the studied period

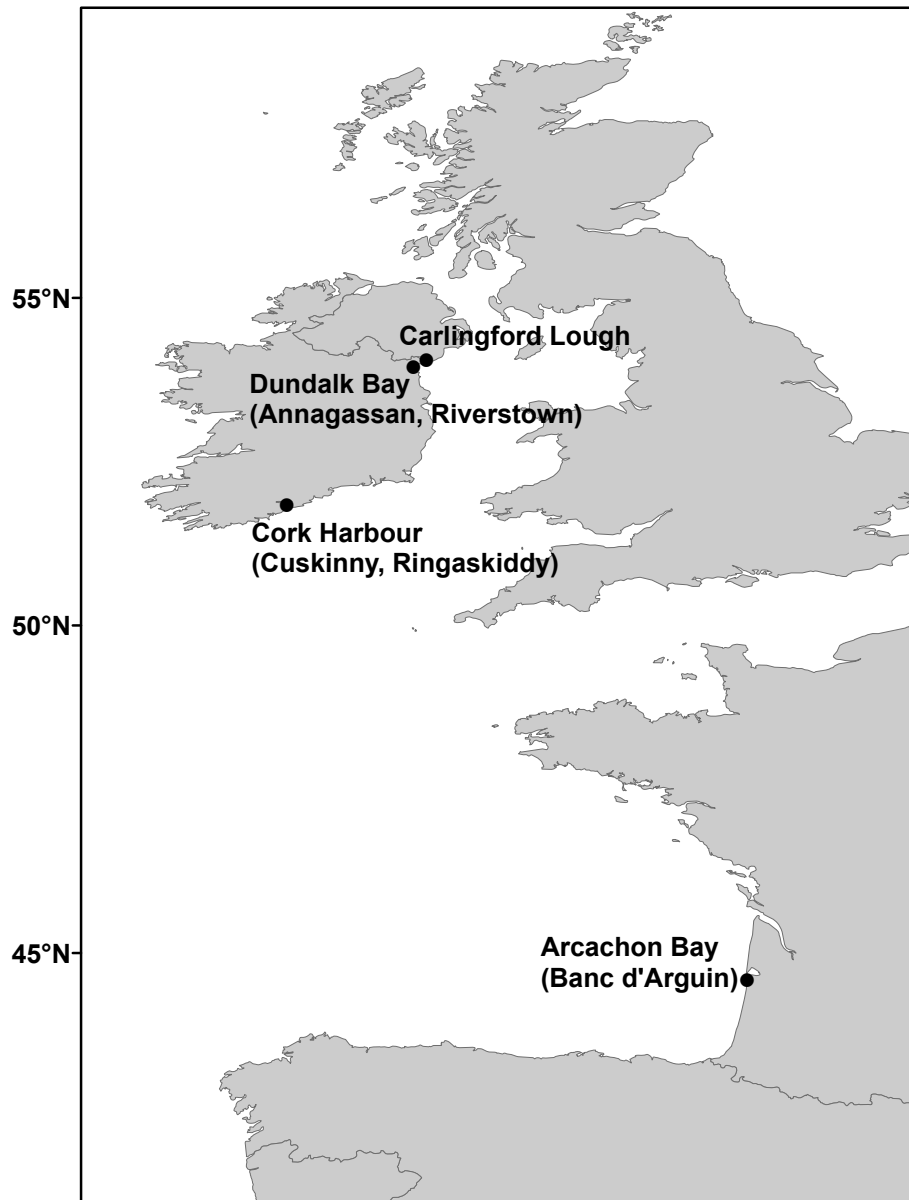


Figure 1. Map of the study sites. In some cases multiple beds were surveyed within a single site, indicated within brackets.

2.2. Sampling

Between April 2018 and October 2019, approximately 30 cockles were collected from each bed, every other month. Sampling was carried out opportunistically, with both hand collection and raking of buried and surfaced cockles, depending on sampling constraints. At Arcachon, sampling ceased in

June 2019, due to lack of cockles in the area. Lower numbers of approximately 20 per sample were obtained in Cork due to low densities and rocky substrate.

2.3. Histology

In total, 1,353 cockles were examined histologically (Carlingford=229, Dundalk=478, Cork=407, Arcachon=239). Prior to dissection for histology, the whole weight (dried with laboratory paper) and length of each individual was obtained. Cockles lay down rings each winter (Orton, 1926). These rings were counted as an estimation of age, with each ring equivalent to a year's growth.

For histology, large individuals were divided and the tissue fixed included a representation of the major tissue groups (mantle, visceral mass, digestive system, foot, gill). Smaller cockles were placed whole into tissue embedding histocassettes. After 24-48 hours in Bouin's solution (Arcachon samples) or Davidson's solution (all other samples) (Shaw and Battle, 1957), the tissues were prepared for paraffin embedding by undergoing a 20-hour cycle through graded ethanol volumes, adapted from Howard *et al.* (2004). Finally, slides were prepared by sectioning the embedded tissue to at least 5µm, followed by staining with Haematoxylin and Eosin (Humason, 1979). Screening for pathologies, macroparasites, and microparasites (Longshaw and Malham, 2013) was conducted using a NikonEclipse 80i light microscope, at 4X, 10X and 40X. Presence or absence of internal parasites and lesions were recorded for each individual.

2.4. Statistical analysis

2.4.1. Patterns of parasite species richness

In this study, total species richness for each site was determined as the total number of parasite species recorded, over the sampling period. Mean species richness per individual was calculated as an average species number per individual cockle. Species richness in this study actually refers to minimum species richness, as in some cases it was impossible to classify parasites to species level. While a variety of indices can be used to describe species patterns, this method of species richness was chosen for easy comparison with previous studies of parasites in cockles (e.g. de Montaudouin and Lanceleur, 2011; Thieltges and Reise, 2006). Kruskal Wallis tests (following assessment of normality and homogeneity of variance) were employed to determine if the species richness differed across beds. Post hoc Dunn tests were applied if a variable was significant, to determine which beds differed from each other. The relationship between individual species richness with length was assessed using linear regression.

2.4.2. Associations between parasites

Probabilistic species co-occurrence analysis was conducted in R using the ‘cooccur’ package (Griffith *et al.*, 2016) to determine if associations existed between parasites, and between parasites and pathologies. The ‘cooccur()’ function within this package examines all pairwise combinations to determine

the probability of these combinations co-occurring more or less frequently than expected.

2.4.3. Site related differences of environmental variables

Environmental data (dissolved oxygen, sea temperature and salinity) were obtained from the Atlantic-Iberian Bay Irish-Ocean Physics Analysis and Forecast (Copernicus, 2020). All analyses were conducted using R Version 1.2.5033 (R Core Team, 2019). The difference between environmental variables across beds was determined using Kruskal Wallis and Dunn tests.

2.4.4. Relationship between intrinsic and extrinsic variables, and parasite prevalence

To determine if environmental variables (sea temperature, dissolved oxygen, salinity), site or host length influenced parasite prevalence, binomial generalised linear models were applied, using the 'lme4' package in R (Bates *et al.*, 2015). Models were run separately for each key parasite/parasite group. Prior to testing, explanatory variables with correlations greater than ± 0.5 were omitted due to high collinearity. Additionally, due to the possibility of autocorrelation between length and age, as well as the absence of age data for 106 individuals, age was not included as an explanatory variable in these models. Sites were included as contrasts to examine differences between locations.

3. Results

3.1. Patterns of parasite species richness

A variety of both macro and microparasites (Appendix D, S1 Table) were observed in this study. Macroparasites included crustacea, fungi (in one cockle), trematodes (*Parvatrema minutum* and unidentified metacercariae and sporocysts) and turbellaria (*Paravortex* spp.). Microparasites included apicomplexa (coccidia and gregarina), bacteria (in the gill and digestive gland), ciliates (*Trichodina*-like and *Rhynchodida*-like) and haplosporidia. Haplosporidian infection (observed as sporonts in the connective tissue) was detected at all sites, except Arcachon. Pathologies were also observed during sampling. Granulomas were observed at all sites, typically in the gills or mantle. A low prevalence of necrosis was detected at Carlingford, Dundalk and Cork. Finally, neoplasia was observed at all sites with the exception of Dundalk.

Total parasite species richness was similar at each of the sites (Carlingford=11, Dundalk=13, Cork=12, Arcachon=10). Median individual parasite species richness differed significantly across beds ($H=273.14$, $df=5$, $p<0.001$, Figure 2A). A post hoc Dunn test found that individual species richness was highest at Carlingford (3.24 ± 1.28), compared with all other sites ($p<0.001$ in all cases). When examining beds within the same site, parasite species richness differed significantly between Ringaskiddy, Cork (1.16 ± 1.24 ; mean $\pm$ SD) and Cuskinny, Cork (1.77 ± 1.24 , $p<0.001$). Individual parasite species richness also increased significantly in longer ($F=64.67$, $p<0.001$, Figure 2B) and older cockles ($F=82.15$, $p<0.001$). However the adjusted R^2 was 0.05

and 0.06 respectively, indicating that a large proportion of the variance in species number was not explained by length or age.

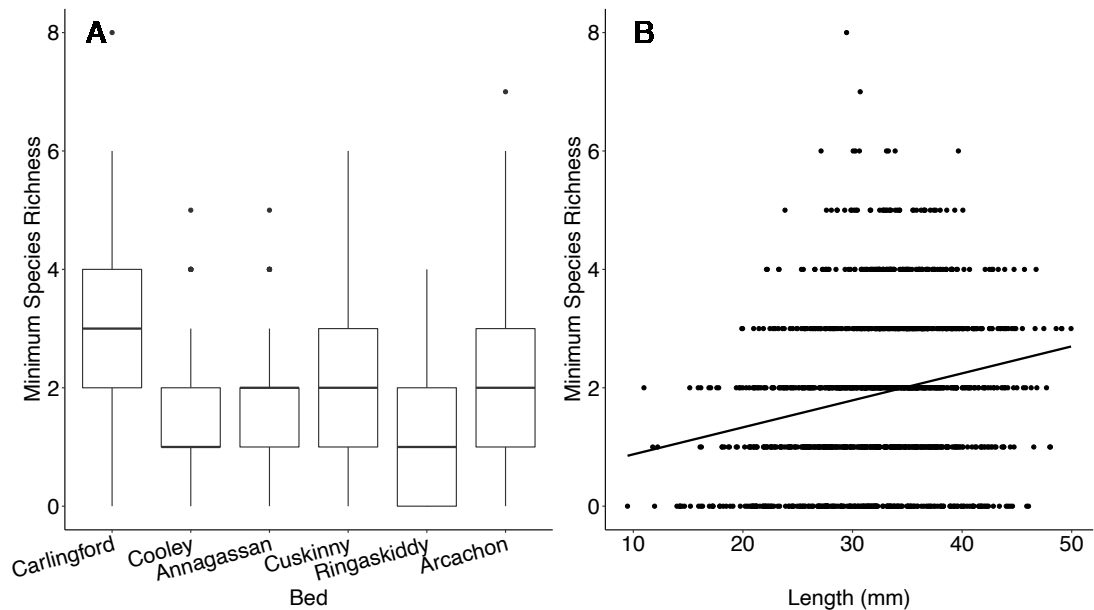


Figure 2. Relationships between minimum parasite species richness (not all identified to species level) and (A) cockle beds and (B) cockle length, between April 2018 and October 2019. Boxplots in (A) demonstrate the median values, boxes extend from the 25th to 75th percentile of each group’s distribution of values, and whiskers show the largest and smallest values within 1.5 times the interquartile range. Outliers are indicated by individually plotted points.

3.2. Associations between pathogens

3.2.1. Association between pathogens and pathologies

Following species co-occurrence analysis, some significant associations were detected, of which 25% were positive and 6% were negative. The remainder of the pairs (69%) were random. As a threshold was applied to remove pairs which co-occurred once, 16.7% of pairs were removed from the

analysis (Figure 3). A number of associations were detected between pathogens and cockle pathologies (Figure 3). A positive association was detected between granulomas and *Rickettsiae*-like infection ($p=0.014$), gregarines ($p<0.001$), *Trichodina* ciliates ($p=0.018$), *Rhynchodida*-like ciliates ($p<0.001$), coccidia ($p=0.035$) and metacercariae (excluding *P. minutum*, $p<0.001$). A negative association was detected between *Paravortex* and granulomas ($p=0.042$). Necrosis was only associated with one pathogen, haplosporidia ($p=0.044$), where necrosis was more likely in infected individuals. Infiltration of haemocytes was positively associated with granulomas ($p=0.025$), gregarines ($p<0.001$) and metacercariae ($p<0.001$ for unclassified metacercariae and *P. minutum*). A negative association was observed between infiltration and *Rhynchodida*-like ciliates ($p=0.024$). Finally, neoplasia was negatively associated with gregarines ($p<0.001$), *P. minutum* ($p=0.001$) and haplosporidians ($p=0.028$). A positive association was detected between *Rickettsiae*-like infection and neoplasia ($p=0.024$), as well as neoplasia and *Trichodina* ciliates ($p=0.042$).

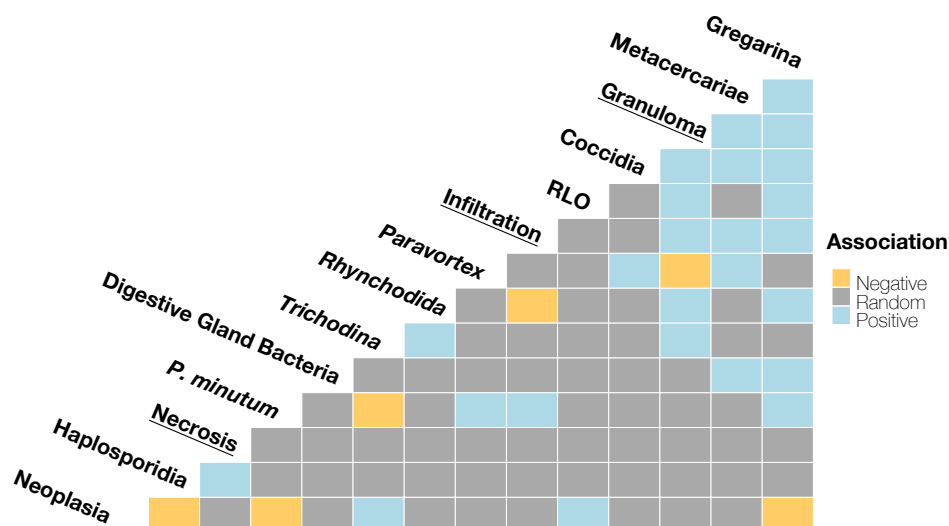


Figure 3. Heat map demonstrating a species co-occurrence matrix, showing relationships between parasite species and cockle pathologies (underlined) as determined by a probabilistic co-occurrence model from the “cooccur” package in R. Species names indicate the pairwise comparisons made.

3.2.2. Associations between parasites

A number of parasite species were found to co-occur more frequently than expected. Gregarines were positively associated with detection of bacterial foci in the digestive system ($p=0.008$), *Rickettsiae*-like infection ($p=0.009$), *Rhynchodida*-like ciliates ($p=0.010$), coccidia ($p=0.004$) and metacercariae ($p<0.001$), including *Parvatrema minutum* ($p<0.001$). An association existed between bacterial foci in the digestive system and the detection of metacercariae ($p<0.001$, not *P. minutum*). Those infected with *P. minutum* were likely to also be infected with *Paravortex* spp. ($p=0.016$). A positive association also existed between *Trichodina* ciliates and *Rhynchodida*-like ciliates ($p=0.015$), and between metacercariae (not *P. minutum*) and *Paravortex*

($p=0.005$). A negative interaction was detected between *Trichodina* and *P. minutum* ($p=0.004$). Positive associations were observed between coccidia and metacercariae ($p<0.001$), and between coccidia and *Paravortex* ($p=0.038$).

3.3. Site related differences in environmental variables

Salinity differed significantly between beds ($H=66.61$, $df=5$, $p<0.001$, Figure 4A). Salinity at Carlingford was significantly lower than all other beds (19.8 ± 10.4 ; mean $\pm$ SD), with the exception of the beds at Dundalk ($p<0.001$ in all cases, Annagassan= 30.6 ± 0.8 , Riverstown= 30.6 ± 0.7). However, the salinity range was much greater at Carlingford, compared with these beds.

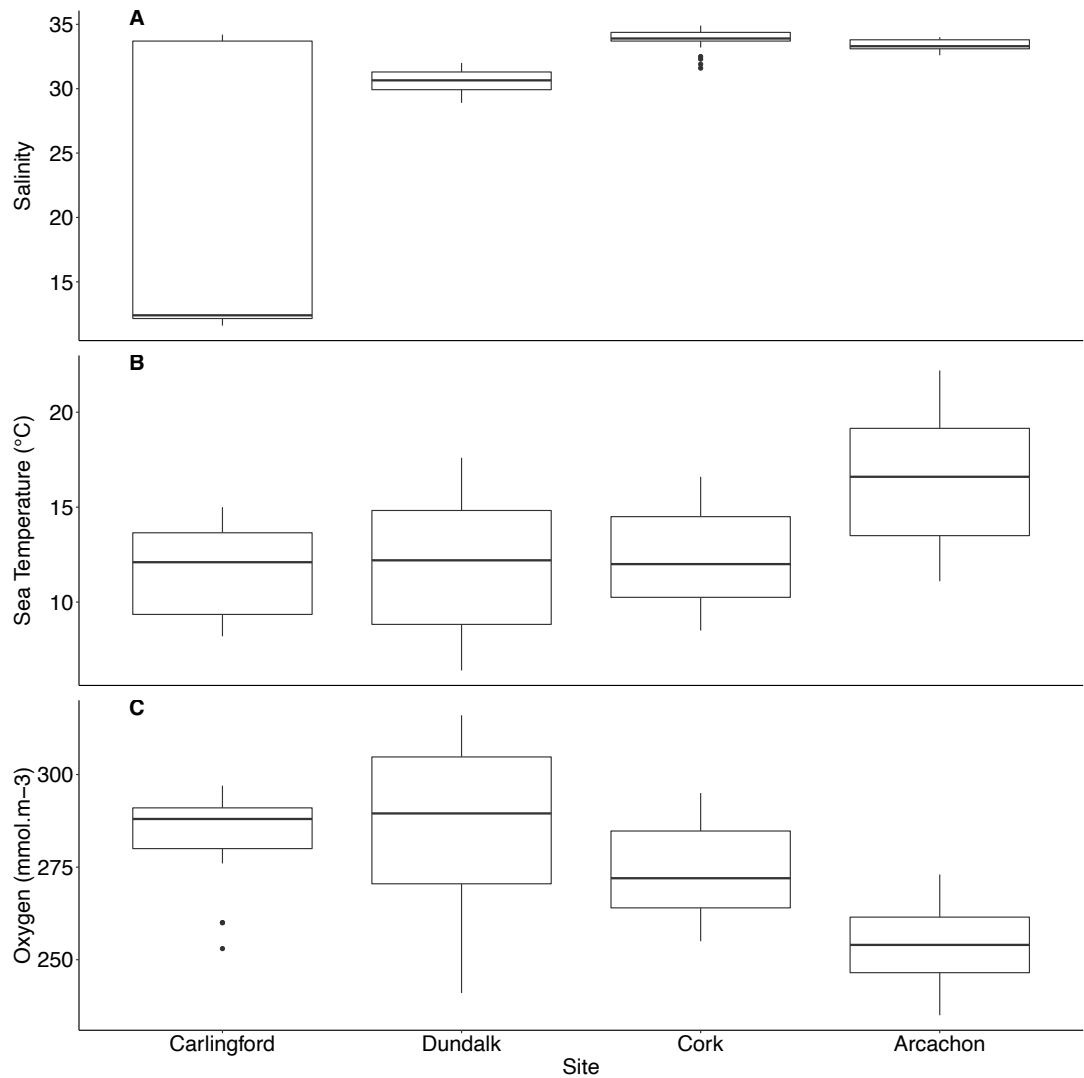


Figure 4. Boxplots describing differences in (A) salinity, (B) sea temperature and (C) dissolved oxygen for each of the beds surveyed for histological analysis of *Cerastoderma edule*. The boxplots display the median values, with boxes extending from the 25th to 75th percentile of each group's distribution of values, and whiskers demonstrate the largest and smallest values within 1.5 times the interquartile range. Outliers are indicated by individually plotted points.

Sea temperature differed significantly between beds ($H=18.75$, $df=5$, $p=0.002$, Figure 4B). While temperatures did not differ between the Irish beds, seawater at Arcachon ($16.3^{\circ}\text{C} \pm 3.5$, mean $\pm$ SD) was significantly warmer than

all the Irish sites ($p < 0.001$, with the exception of Cuskinny: $12.4^{\circ}\text{C} \pm 2.48$ SD), where a trend existed ($p = 0.0281$ at a significance level of 2.5% to correct for pairwise analysis).

Finally, oxygen levels differed significantly between beds ($H = 37.70$, $df = 5$, $p < 0.001$, Figure 4C). As was the case with temperature, Irish beds did not differ significantly. However, dissolved oxygen at Arcachon ($254 \text{ mmol/m}^3 \pm 10.8$; mean $\pm$ SD) was significantly lower than all of the Irish sites ($p < 0.025$ in all cases).

3.4. Relationship between intrinsic and extrinsic variables, and parasite prevalence

3.4.1. Cockle length and parasite prevalence

Gregarines (likely *Nematopsis* sp.) were the most commonly observed parasite, being observed mainly in the gills and mantle, but also across all tissue groups. Results from binomial generalised models indicate that gregarine infection was more likely to occur in larger host individuals ($z = 2.96$, $p = 0.004$, Figure 5). A number of other parasites were more likely to impact larger individuals: haplosporidians ($z = 3.81$, $p < 0.001$, Figure 5), *P. minutum* ($z = 2.27$, $p = 0.023$), metacercariae ($z = 3.07$, $p = 0.002$) and sporocysts ($z = 2.44$, $p = 0.015$, Figure 5).

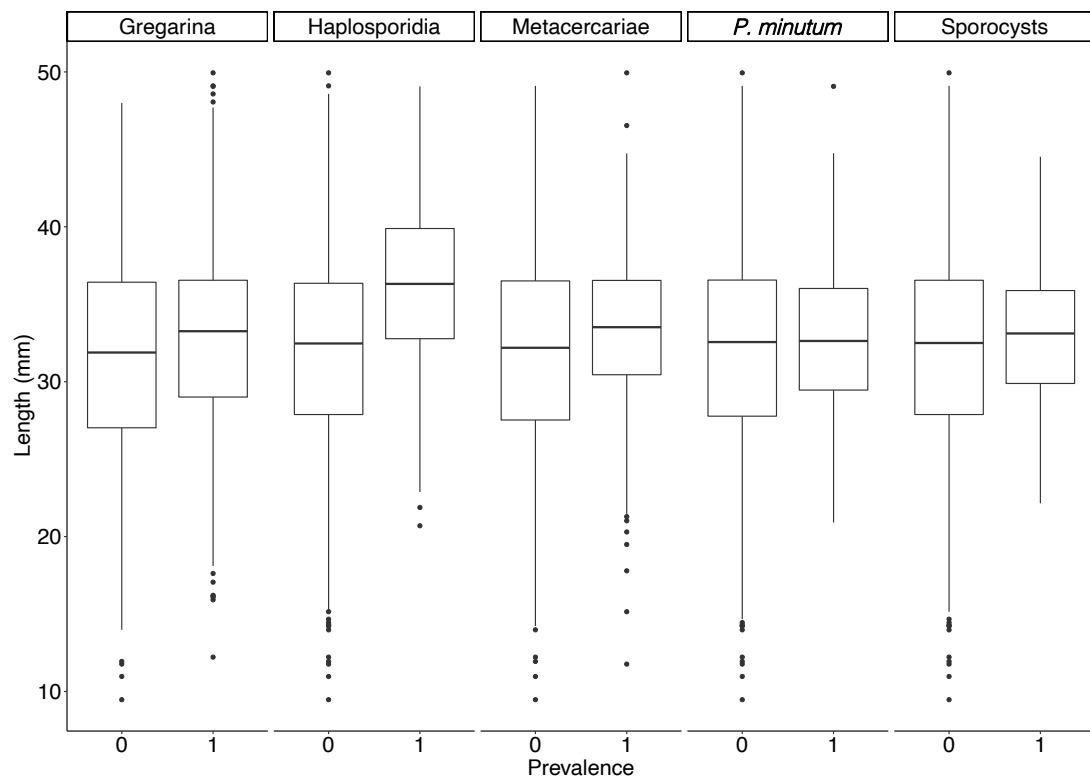


Figure 5. Boxplots demonstrating the relationship between pathogens and cockle length. Absence of pathogens is indicated by 0 and presence is indicated by 1. The boxplots display the median values, boxes extend from the 25th to 75th percentile of each group's distribution of values, and whiskers show the largest and smallest values within 1.5 times the interquartile range. Outliers are indicated by individually plotted points.

3.4.2. Environmental variables and parasite prevalence

Binomial generalised linear model outputs (previously discussed in section 3.4.1.), show that a range of parasites are more likely to occur at higher temperatures (Figure 6A): *Rickettsiae*-like infection ($z=6.36$, $p<0.001$), *Trichodina* ciliates ($z=5.23$, $p<0.001$), and sporocysts ($z=2.07$, $p=0.004$). Additionally, sporocyst prevalence was highest at the warmest site, Arcachon

($z=2.41$, $p=0.041$). *P. minutum* and other metacercariae were more likely to occur at lower temperatures ($z=-3.51$, $p<0.001$ and $z=-2.11$, $p=0.004$ respectively).

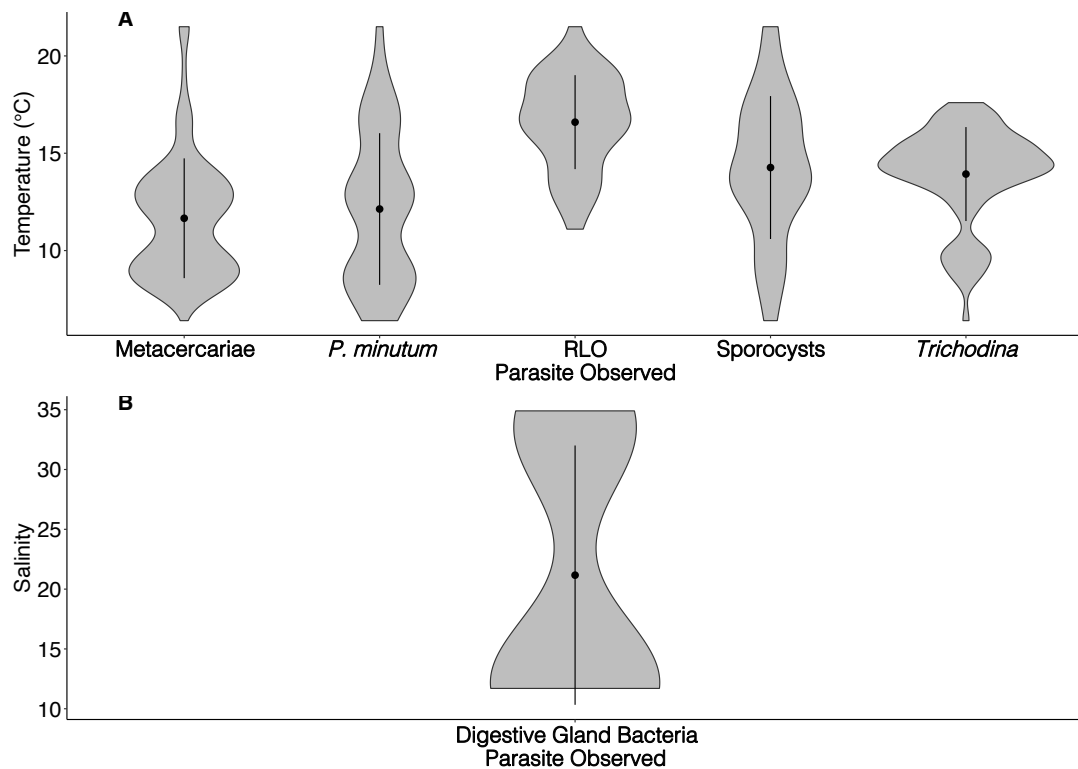


Figure 6. Violin plots (visualising the kernel probability density), demonstrating the relationship between the presence of pathogens and (A) seawater temperature and (B) salinity, at all sites combined. Mean $\pm$ 1 SD of salinity/temperature is represented by the vertical line and point within the violin plots.

Similarly, an association was detected with salinity. Bacterial foci in the digestive gland epithelium were more likely at lower salinities ($z=-4.52$, $p<0.001$, Figure 6B). Carlingford, the site with the lowest salinity demonstrated highest prevalence of coccidian infection of the kidney and the intestine, gregarines and metacercariae (results of contrasts detailed in Appendix D, S9

Table). However, site wise differences were not always related to environmental variations. For example in *P. minutum*, prevalence was lower in Cork and higher in Arcachon, compared with Carlingford (Appendix D, S9 Table).

4. Discussion

Using the common cockle *Cerastoderma edule* as a model host species, this study provides new insights into the modulators of parasite prevalence and parasite species richness in bivalves. It was found that size of the host, as well as environmental factors (in particular salinity and temperature) both drive or inhibit parasite species and prevalence. Furthermore it was shown that parasite species richness may also be influenced by interactions between pathogens. The high species richness demonstrated in cockles, the model species, affirms its important role as host to a diverse array of parasites. Overall parasite species richness at Dundalk, one of northern sites was potentially greater than 13, due to the method of trematode identification, exceeding that of previous findings (Elliott *et al.*, 2012). This high species richness is influenced by a combination of extrinsic (environmental) and intrinsic (host size) factors.

This study confirmed that the intrinsic drivers of host size (and potentially age due to the correlation) played a role in parasite prevalence and parasite species richness. Previously in cockles, the relationship between parasite prevalence and host size has been demonstrated in few parasite groups. For example, cockle length and sporocyst prevalence demonstrated a positive correlation (Magalhães *et al.*, 2015), which was supported by this study. A positive size effect on *P. minutum* was observed, which contradicts Fermer *et al.*

(2009). This size dependent effect was not isolated to trematodes, with gregarines and haplosporidia also more likely to occur in larger individuals (the latter in agreement with Albuixech-Martí *et al.* (2020)). The findings of this study support previous findings of a positive size effect on trematode richness in cockles, with adults displaying greater species richness (Thieltges and Reise, 2006). For trematodes, increased water clearance and longer exposure time in larger (and likely older cockles) increase the likelihood of infections (de Montaudouin *et al.*, 1998). Thus, it is possible that similar effects are increasing the species richness of both macro and microparasites.

Environmental characteristics were found to be an important driver of parasite prevalence. Higher seawater temperatures correlated with increased prevalence of *Rickettsiae*-like infection, *Trichodina* ciliates, metacercariae and sporocysts, while low salinity corresponded with increased prevalence of bacterial foci. While it is important to note that more sites should be examined to determine these effects, these potential relationships are concerning, considering the likelihood of increased water temperatures and reduced salinity (due to increased precipitation), resulting from climate change in many regions (Beniston *et al.*, 2007). It is therefore possible that these parasites may be advantaged in a changing climate, causing problems due to the mortality inducing potential of some parasite species (Longshaw and Malham, 2013).

Associations were observed between a number of parasites. These associations may be a direct result of the relationship between pathogens, or may be attributed to the environmental characteristics of the sites. These

associations may influence the impact of climate change on cockles. Due to the possibility of some parasites facilitating infection by others, climate change may have far reaching consequences. For example, metacercariae and bacterial foci are likely to be impacted by increased water temperature or reduced salinity. However these parasites are often associated with infection by gregarines, which have been linked to mortalities (Azevedo and Cachola, 1992). Therefore, while gregarines were not found to be influenced by environmental factors, climate change may indirectly influence the prevalence of this parasite group.

Further interactions between pathogens and the host were evident in the pathologies observed. A particularly problematic pathology noted was disseminated neoplasia, which is linked to immunosuppression and mortality in cockles (Díaz *et al.*, 2010, 2016). In the individuals studied, *Rickettsiae*-like infection of the gills was more likely in neoplasia impacted individuals. However negative associations were also discovered relating to neoplasia, most notably between neoplasia and haplosporidian infection (i.e. haplosporidian infection was less likely in individuals with neoplasia), despite combinations of this pathogen/pathology being previously attributed to mass mortality (Elliott *et al.*, 2012). The fact that neoplasia was absent from Dundalk, despite relatively high haplosporidian infection, indicates that haplosporidian infection is not linked to the aetiology of neoplasia. Furthermore in terms of neoplasia, prevalence at Cork and Arcachon was reduced since the 1980s and 2000s respectively (Twomey and Mulcahy, 1988; Le Grand *et al.*, 2010). However, as these are just two time points, it is impossible to determine if prevalence fluctuated in the

interim. These associations, along with the remaining associations discovered in this study, should be analysed experimentally to confirm these interactions, or determine if they are associated with changing climate and disease cycles.

Stressors in the environment lead to stress in shellfish, which in turn results in immunosuppression and increased disease risk (Coates and Söderhäll, 2020). In agreement with previous studies (Magalhães *et al.*, 2018b; Peteiro *et al.*, 2018; Domínguez *et al.*, 2020), low salinity was confirmed as one of the most stressful factors influencing cockles. This was most evident at Carlingford, which exhibited high overall parasite species richness and greatest individual species richness. Two conflicting scenarios may explain the impact of salinity on parasite dynamics in cockles. First, salinity may cause valve closure to prevent osmotic shock, resulting in reduced respiration (Domínguez *et al.*, 2020). Second, and conversely, stressful conditions may cause cockles to increase respiration, following depletion of initial energy reserves (Ong *et al.*, 2017). The second scenario (delayed increase in respiration) is most likely, considering cockles at Carlingford exhibit reduced growth in later years (Mahony *et al.*, 2021, Chapter 5), possibly due to energy allocation to respiration. Therefore, it appears that cockles at Carlingford, a stressful environment, allocate energy to homeostasis, rather than immune function, potentially contributing to greater parasite species richness. While diversity of host species is an important driver of trematode parasite diversity (Hechinger and Lafferty, 2005), host diversity was not quantified, therefore it was not possible to verify if birds are the key influencer. Similarly, fishing had no

detectable impact on parasite species richness, as no patterns were evident between harvested and wild areas.

This study provides an insight into the drivers of parasite species richness in bivalves, which are a complex combination of factors. Previously known relationships between size in certain parasite groups were affirmed, but evidence of this relationship was also demonstrated in gregarines. While the confounding factor of similar environments may lead to the co-presence of certain pathogens at a given site, it was probable that interactions between pathogens are a driver of infection, providing an important starting point for future experimentation. Low salinity was affirmed as a stressor, causing increased parasite species richness and prevalence. However, most importantly in terms of the environment, this study provides new insights into the potential impacts of climate change on bivalve parasite dynamics. It appears that not all parasite groups will be similarly impacted by climate change. Due to high temperatures and increased precipitation resulting in reduced salinity (Beniston *et al.*, 2007), it is likely that some parasites may be advantaged (bacterial inclusions, *Trichodina* ciliates, metacercariae, sporocysts, gregarines), either by direct or indirect effects. This is likely to have cascading impacts on cockles, their predators and the wider ecosystem. Therefore, future interactions between bivalve hosts, their parasites and the environment must be closely monitored in order to minimise potentially detrimental impacts on hosts and their ecosystems.

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Chapter 5: Drivers of growth in a keystone fished species along the European Atlantic Coast: the common cockle *Cerastoderma edule*

Abstract

A better understanding of growth drivers in shellfish populations including the common cockle *Cerastoderma edule* is essential, as their future is challenged by unsustainable fishing practices and climate change. In this 19-month study, spatial and temporal variabilities in cockle growth of Irish, Welsh and French populations were assessed and compared with historical data. Younger cockles (0-3 years) at a suction dredged site (Ireland) reached larger sizes initially, while an infrequently hand-harvested site (Ireland), impacted by low salinity and parasites (trematodes), exhibited reduced growth in later years. Wild cockles at a third Irish site attained the largest sizes. At a hand raked, mass mortality impacted site (France, warmest site), growth was lowest in cockles >2 years. Previously, cockles at that site have been shown to spawn almost year-round, possibly diverting energy to gonad development rather than growth. Previous literature contrastingly demonstrated significantly increased growth at lower latitudes. Intensively hand raked cockles in Wales slowly attained smaller maximum sizes possibly due to high densities and interspecific competition. Results also indicate that food source did not impact cockle growth. These findings predict that cockle growth and size is variable due to local abiotic

(reduced salinity) and biotic (density, trematode infection, gametogenesis) drivers. Additionally the synergistic relationship between these factors, i.e. warmer temperatures driving prolonged spawning, and the potential association between lower salinities and trematode prevalence, is concerning due to predicted climate related increases in temperature, precipitation and trematode prevalence/transmission, which may result in slower growth trajectories in northern cockles.

1. Introduction

Globally, many fisheries are under threat due to unsustainable practices (Pauly *et al.*, 2002). Assessing population dynamics is vital for predicting the future sustainability of marine populations and fishery stocks. One important parameter in the fishing industry, individual growth rate, informs policy and management about the species' energy allocation, and gives guidance in determining the minimum capture size (Bidegain *et al.*, 2013). A method frequently used in assessing growth rates in both fish and shellfish populations is the von Bertalanffy growth model (VBGM), which describes growth in relation to age and has been proven valuable in growth rate comparisons across space and time (e.g. Aragón-Noriega *et al.*, 2015; Pace *et al.*, 2018). Spatial and temporal variability in bivalve growth rates exists due to variations in both external (e.g. food supply, temperature, immersion time, density, salinity) and internal (e.g. genetics, physiology) factors (Gosling, 2015). Assessing the impact of these factors is important not only to better understand the drivers of current

spatial and temporal variability in growth rates but also to provide an indication of their variation under changing climate conditions (Kharin *et al.*, 2013).

The common cockle *Cerastoderma edule* is an ecosystem engineer that influences surrounding sediment and hydrodynamics (Ciutat *et al.*, 2007), and is an important food source for many bird and fish species (Malham *et al.*, 2012). In Europe, cockles have the potential to provide an additional \$11.5M a year from meat, ecosystem services and by-products, such as shell aggregate and nutrient removal (Carss *et al.*, 2020). Management of cockle fisheries is particularly topical, considering the increasingly frequent boom and bust cycles observed in populations of this species (Morgan *et al.*, 2013; Burdon *et al.*, 2014). In terms of fisheries, cockle management schemes typically set minimum capture sizes to safeguard future generations of cockles and landings. To critically determine these capture sizes, the monitoring of growth and morphometrics (in combination with reproductive surveys) of harvested cockle populations is essential (Froese *et al.*, 2008). Regarding large-scale patterns, cockle growth rates have been found to increase towards lower latitudes (Iglesias and Navarro, 1990) and remain relatively constant longitudinally (Genelt-Yanovskiy *et al.*, 2010). However, to our knowledge, since this study (Iglesias and Navarro, 1990), no further reports of cockle growth variations over a latitudinal gradient have been published.

Environmental factors have been recognised as important influences on cockle growth, for example; a reduction in growth has been associated with metal contamination (Savari *et al.*, 1991) and ocean acidification may lead to

the diversion of energy allocation from growth and reproduction (Fitzer *et al.*, 2012). Biotic factors such as competition (Jensen, 1992, 1993; Masski and Guillou, 1999; Beukema and Dekker, 2005; de Fouw *et al.*, 2020), predation (de Fouw *et al.*, 2020), available food sources (Iglesias and Navarro, 1990; Wijsman and Smaal, 2011; Beukema and Dekker, 2015) and parasites (de Montaudouin *et al.*, 2012) also impact cockle growth. Food availability is another influencer of cockle growth, with adults mainly assimilating organic matter and microphytobenthos (Kang *et al.*, 1999). Phytoplankton quality rather than quantity is considered a driver of growth in bivalves (Gosling, 2015). However, varying opinions exist on the role of detritus on bivalve growth (Arambalza *et al.*, 2018). Additionally, emersion time is an additional influencing factor, due to the presence of food in the water and the amount of time this water is available for feeding (de Montaudouin, 1996; Navarro *et al.*, 1998). In terms of parasites, digenean trematodes are a dominant taxa, with cockles acting as both primary (sporocysts) and secondary (metacercariae) intermediate hosts (de Montaudouin *et al.*, 2009). These parasites can negatively impact cockle condition and survival (Longshaw and Malham, 2013), particularly when coupled with environmental factors, for example high temperatures may increase the vulnerability of cockles to trematodes (Gam *et al.*, 2009).

The overarching aim of this study was to assess the past and current growth rates of European cockle populations along a latitudinal gradient and identify local abiotic and biotic factors that influence this important population characteristic. The objectives were (i) to examine the spatial variation of abiotic

and biotic factors across six sites along the western European Atlantic coast. These variables included cockle morphometrics, growth performance, sea temperature, salinity, primary productivity, fishing pressure (based on fishing types) and trematode infection. Stable isotope analysis was also conducted to determine differences in food sources between sites. Further objectives were to assess (ii) the effects that these (a)biotic variables had on growth performance in those populations, and (iii) temporal trends by comparing growth rate results of this study with historical data.

The findings of this study will bridge the 30-year knowledge gap in latitudinal cockle growth variations by providing more up-to-date information on appropriate capture sizes for fisheries management, as well as predicting the challenges faced by future cockle populations in a changing marine environment.

2. Materials and methods

2.1. Study sites and sampling

Every other month from April 2018 until October 2019, approximately 30 cockles were collected. Cockles (n=2,133) were gathered from six sites (three Irish (n=1,174), two Welsh (n=720), and one French (n=239; Figure 1). Two Irish sites (Dundalk Bay and Cork Harbour) were sampled at two distinct beds (Figure 1). At every site, cockles were randomly collected with rakes and by hand. At Carlingford and Cork, cockles were collected from the sediment

surface due to the rocky substrate making raking difficult. At the remaining sites both surfaced and buried cockles were collected.

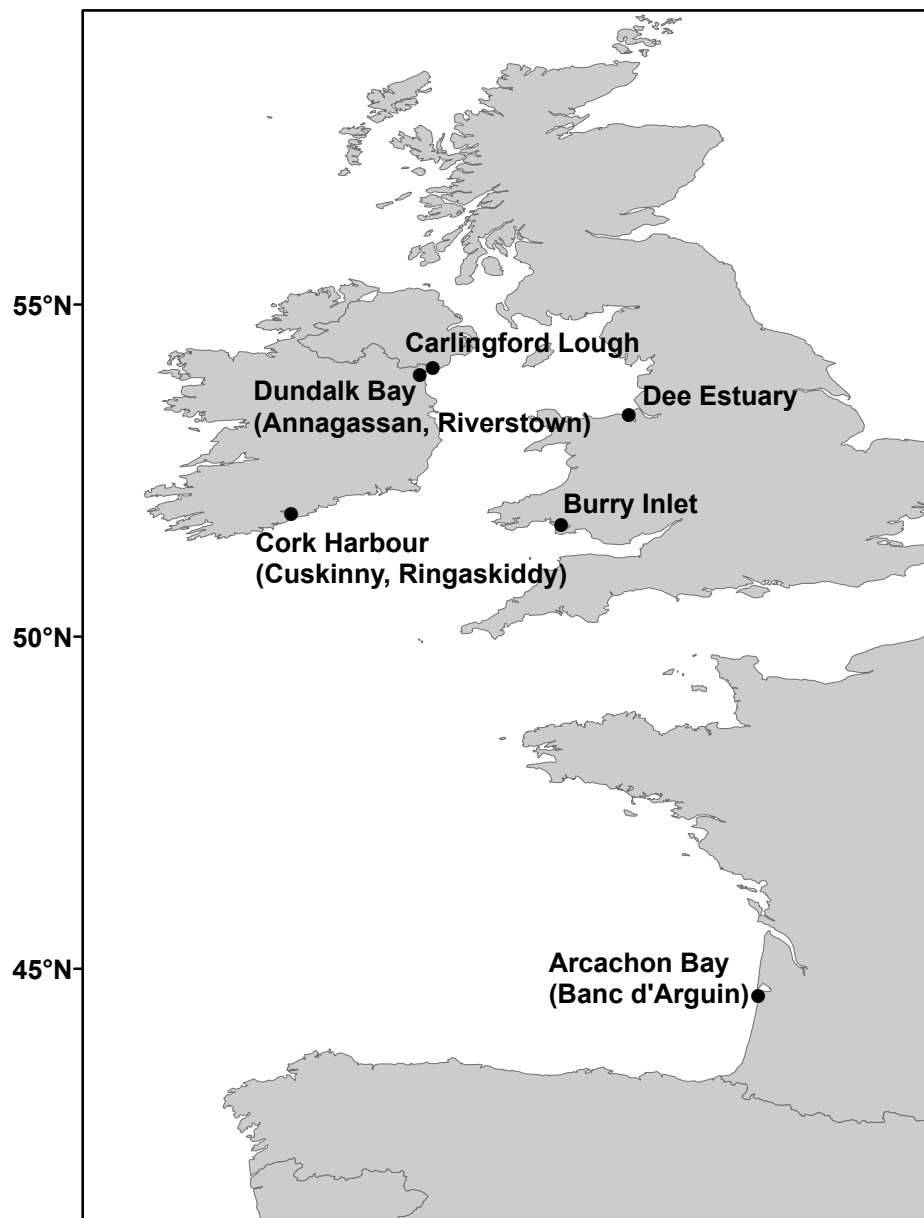


Figure 1. Sites (and beds within) studied in a 19-month survey of growth rates in *Cerastoderma edule*.

2.2. Cockle morphometrics and growth

Morphometric data were obtained for all collected cockles. External growth rings were counted as an estimation of age. The shell exterior of the cockles was dried with paper and whole wet weight (g) was determined with an electronic balance. Shell length (mm), width (mm) and height (mm) were measured by using a Vernier callipers (Appendix E, S1 Figure).

2.3. Abiotic data acquisition

Monthly means of environmental variables (sea temperature, salinity and primary productivity (net primary production of carbon, $\text{mg/m}^3/\text{day}$) were obtained from the Atlantic-Iberian Bay Irish Ocean Physics Analysis and Forecast (Copernicus, 2020).

The conservation/protected area status, land usage, and types of fishing activity were recorded (Table 1).

Table 1. Description of the five sites and the beds examined within each site (only for Cork Harbour and Dundalk Bay), including information on cockle fisheries, with the type of fishery and minimum capture size (MCS). SPA refers to a Special Protection area under the EU Birds Directive, SAC refers to a Special Area of Conservation under the EU Habitats Directive and Ramsar Reserve is designated by the Convention on Wetlands. Activities relate to that of the general area near the sites.

Country	Site	Bed	n	Coordinates	Type of fishery	MCS (mm)	Activities	Protections	Sporocyst	Metacercarial
									Prevalence (%)*	Prevalence (%)*
Ireland	Carlingford	Oyster Farm	229	54°01'N, 6°09'W	Occasional light hand-harvesting	17	Shipping, aquaculture, agriculture	SAC, SPA, Ramsar	4.80	81.66
	Dundalk	Annagassan	269	53°52'N, 6°20'W	Suction dredging	22	Razor clam fishery	SAC	2.92	20.00
		Riverstown	269	54°00'N, 6°17'W					4.60	15.48
	Cork	Cuskinny	240	51°51'N, 8°15'W	Unfished	17	Industry, shipping	SPA	2.92	19.58
		Ringaskiddy	167	51°49'N, 8°18'W					2.99	7.19
Wales	Dee	-	360	53°20'N, 3°10'W	Hand raking and sieving	20	Agriculture, industry	SPA, SAC	-	-
	Burry	-	360	51°40'N, 4°11'W	Hand raking and sieving	Variable	Agriculture, industry	SPA, SAC, Ramsar	-	-
France	Arcachon	Banc d'Arguin	239	44°35'N, 1°13'W	Hand raking	27	Aquaculture, tourism, forestry and agriculture	National Reserve	12.13	34.73

*Mahony *et al.*, 2021

2.4. Biotic data

2.4.1 Density

On one occasion during the entire sample period, in winter 2018/2019, cockle density was recorded at each site, in order to provide an estimate of cockle abundance. Density was estimated using ten 0.25 m² quadrats and a sieve. Due to logistical reasons, cockle density at Carlingford Lough, Dundalk Bay and Ringaskiddy were not measured, but substitute data from a cockle stock survey were obtained for Dundalk Bay from The Marine Institute and Bord Iascaigh Mhara (2020). Data from this survey were obtained during July 2019 using 0.25 m² quadrats. Average density was calculated from records within a 1 km radius of the sampled sites.

2.4.2. Stable isotopes of cockle tissue to analyse food sources

Stable isotopes of carbon can be used to determine the isotopic composition of organisms, inferring their potential food sources (Peterson and Fry, 1987). On a single occasion, in winter 2018/2019, 15 cockles were collected from each bed (except at Ringaskiddy and Carlingford) in preparation for stable isotope analyses. Cockles were rinsed externally with fresh water. The cockles were subdivided into three groups of five cockles with similar average size (small (juvenile), medium and large cockles), to account for variation between size classes (Kang *et al.*, 1999). Shell length (mm) was measured with Vernier calipers and the tissue was added to pre-combusted (4 hours at 450 °C and cleaned with 10% HCl) glass vials, which were stored at -20°C. Prior to the

analysis, samples were freeze-dried at -60°C before grinding with a ball mill. Inorganic carbon was removed from the ground cockle tissue intended for carbon analysis, by adding 50 µL of 10% HCl to 0.5-0.7 mg cockle powder twice, with one hour of drying (60°C) in between and one night of drying after the entire decarbonisation process.

The amount of $\delta^{13}\text{C}$ in the cockle tissue, as a proxy for the type of food source, was determined with a Thermo Scientific Delta V Plus Isotope Ratio Mass Spectrometer equipped with a Flash 2000 Organic Elemental Analyzer, at Laboratoire de Physico et Toxico-Chimie of the University of Bordeaux. Homemade casein ($\delta^{13}\text{C}$: -23.3‰; $\delta^{15}\text{N}$: 6.3‰), and the standards USGS24 Graphite (real value $\pm$ SD; $\delta^{13}\text{C}$: -16.05 $\pm$ 0.07‰) and sorghum flour ($\delta^{13}\text{C}$: -13.68 $\pm$ 0.1‰; $\delta^{15}\text{N}$: 1.58 $\pm$ 0.5) were employed as controls. Per mille (‰) differences between the reference material (Vienna Pee Dee Belemnite Limestone (VPDB)) and the sample were used to calculate the isotope ratio of $\delta^{13}\text{C}$ using the formula:

$$X = ((R_{\text{sample}}/R_{\text{standard}}) - 1) \times 1000$$

Where R is the ratio between light and heavy carbon isotopes ($^{13}\text{C}/^{12}\text{C}$).

2.4.3. Parasites

Trematode prevalence data (percentage of infected cockles in the population) were obtained from a histological survey of a previous study (Mahony *et al.*, 2021, Chapter 3, Table 1).

2.5. Literature review of historic growth data

Values of asymptotic average length (L_{∞}) and the Brody growth rate coefficient (k) were extracted from literature (obtained through Google Scholar with combinations of the search terms “*Cardium edule*”, “*Cerastoderma edule*”, “Growth” and “von Bertalanffy”), as well as information detailing study years, sites and immersion time (subtidal, intertidal).

2.6. Statistical analysis

All analyses were conducted in R Version 1.2.5033 (R Core Team, 2019). Prior to analysis of variance, homogeneity of variance was tested using Levene’s test and normality was assessed with a Shapiro-Wilk test.

2.6.1. Spatial variation

Analysis of variance was conducted using one-way ANOVA or Kruskal Wallis tests, followed by Dunn tests/Tukey’s tests, to determine if mean/median environmental variables (temperature, salinity, primary productivity), $\delta^{13}\text{C}$, shell length or total fresh weight differed between beds.

Linear and quadratic equations were examined to determine the relationship between length and weight in cockles across all sites. Both equations were fitted to the length and weight data, and the model with the lowest AIC value was deemed to be the best fit to describe the relationship between length and weight.

Many growth functions can be used to describe growth in shellfish, including the Gompertz, Logistic, Richards and Schnute functions (Ogle, 2015). As cockle growth is typically examined using the von Bertalanffy growth model (e.g. Jones and Baxter, 1987; Gam *et al.*, 2010; Magalhães *et al.*, 2016) it was chosen to describe growth in this study. The von Bertalanffy growth model is represented by:

$$L_t = L_{\infty} (1 - \exp [-k(t - t_0)])$$

where L_t is expected length at age t , L_{∞} is the asymptotic average length (the mean maximum length reached by an individual), k is the Brody growth rate coefficient (which refers to how quickly L_{∞} is approached) and t_0 (not biologically meaningful as $L=0$ does not exist) (Gosling, 2015; Ogle, 2015).

Von Bertalanffy growth parameters were estimated using the ‘FSA’ package in R, with nonlinear least squares estimates (Ogle *et al.*, 2020). Differences between growth models were then compared using the ‘fishmethods’ package (Nelson, 2019). A general model and four submodels were fitted to the length and growth rings data using nonlinear least squares. Likelihood ratios based on residual sum of squares were calculated for each submodel-general model comparison. Chi square statistics were then used to determine the most appropriate model.

Finally, growth performance indices (ϕ') were calculated for each population, using the formula:

$$\phi' = 2 \times \log_{10}(L_{\infty}) + \log_{10}(k) \text{ (Pauly and Munro, 1984)}$$

This calculation was relevant because of the negative correlation between L_{∞} and k , which can invalidate bivalve models based on individual parameters (Pauly and Munro, 1984; Magalhães *et al.*, 2016).

2.6.2. Drivers of spatial and temporal variation

Multiple regression was used to determine the impact of spatially varying factors (primary productivity, salinity, trematodes (metacercariae or sporocysts), density and $\delta^{13}\text{C}$ as a proxy of food source, on the cockle growth performance index (ϕ'). Initially, to avoid overfitting the model, submodels were examined to determine the most suitable variables for inclusion in the maximal model. Two submodels were first fitted to determine the most important environmental and biotic variables. A separate submodel was employed to examine the impact of cockle density and $\delta^{13}\text{C}$ on growth, due to the lack of availability of data from certain beds (i.e. Carlingford, Ringaskiddy). The maximal model (including all relevant factors) was then simplified using top down selection of p values (Zuur *et al.*, 2009).

Mixed effects models were employed to examine the impact of latitude and decade on historical growth parameters (L_{∞} , k). As was the case for the initial multiple regression models examining growth drivers, final models were chosen using top down selection of p values (Zuur *et al.*, 2009).

3. Results

3.1. Spatial variation in biotic and abiotic variables

3.1.1. Morphometrics

Median shell length of cockles differed significantly across beds ($H=725.91$, $df=7$, $p<0.001$). A post hoc Dunn test revealed that cockles were smallest at the Burry Inlet in Wales when compared with all other beds ($p\leq 0.001$ in all cases), with the largest cockles found at Cuskinny ($p<0.05$ in all cases, with the exception of Carlingford and Annagassan, which did not differ significantly from Cuskinny). No relationship between length and geographic proximity was observed (Table 2).

Table 2. Descriptive statistics for all variables measured in this study (April 2018 – October 2019). Wet weight refers to the weight of the cockle shell and flesh. Density estimates were gathered during winter 2018/2019. SD indicates standard deviation. Maximum values between sites for each mean variable indicated in bold, minimum indicated in italics. For trematode data see Table 1.

Site	Bed	Measure	Shell Length (mm)	Wet Weight (g)	Growth Rings	Salinity	Seawater Temperature °C	Primary Productivity mg C/ m ³ / day	Density ind/m ²	δ ¹³ C
Carlingford Lough	Oyster Farm	Mean	33.8	16.2	4.2	19.8	11.6	28.9		
		SD	3.9	4.7	1.6	10.4	2.4	30.5		
		Minimum	21.0	4.0	1	11.6	8.2	0	-	-
		Maximum	45.8	32.5	11	34.2	15	99		
Dundalk Bay	Annagassan	Mean	32.0	14.6	2.7	30.6	12.1	98.1	93.7	-18.6
		SD	6.2	7.7	1.5	0.9	3.6	63.3	156.6	0.2
		Minimum	17.2	1.3	0	28.9	6.4	6	0	-18.8
		Maximum	47.7	37	9	32.0	17.6	186	547.5	-18.4
	Riverstown	Mean	32.2	14.8	2.9	30.6	11.8	68.5	30.9	-17.9
		SD	6.0	8.2	1.5	0.7	3.3	41.9	34.9	0.3
		Minimum	20	2.1	0	29.3	6.6	6	0.25	-18.2
		Maximum	49.1	50.4	8	31.8	17.1	132	106.25	-17.6
Cork Harbour	Cuskinny	Mean	34.0	18.5	3.8	33.9	12.4	83	9.6	-18.0
		SD	8.3	10.2	1.9	0.7	2.5	47.1	8.3	0.2
		Minimum	11.8	0.8	0	31.9	8.5	9	0	-18.1
		Maximum	49.9	46.3	13	34.8	16.5	161	28	-17.7
	Ringaskiddy	Mean	31.1	15	3.2	33.8	12.3	83.7		
		SD	8.2	9.1	1.6	0.8	2.5	47.5		
		Minimum	9.5	0.4	0	31.6	8.5	10	-	-
		Maximum	46.3	47.7	8	34.9	16.6	171		
Wales	Burry	Mean	24.1	5.3	2.2	27.3	13.5	324	3525.3	-18.0
		SD	3.0	2.1	0.7	1.5	4.6	235.1	2373.0	0.2
		Minimum	17.5	1.8	1	24.2	6.4	26	201.6	-17.3
		Maximum	33.3	13.7	5	29.3	20.6	840	6933.7	-17.0
	Dee	Mean	25.8	6.4	1.5	27.7	13.3	314.2	608.7	-19.5
		SD	3.6	3.0	0.7	1.9	5.7	217.9	392.5	0.3
		Minimum	18.3	1.8	1	24.9	4.3	21	211.7	-19.6
		Maximum	35.8	17.2	5	30.9	21.9	610	1249.7	-19.1
Arcachon	Arguin	Mean	28.6	8.5	3.4	33.4	16.3	30.5	14	-17.3
		SD	4.5	3.6	1.4	0.4	3.5	23.2	14.0	0.1
		Minimum	16.2	1.4	0	32.6	11.1	6	0	-17.3
		Maximum	40.0	25.7	7	34	22.2	91	40	-17.2

Shell length and total individual weight followed a quadratic relationship, where $R^2=0.93$ (Standard Error = 0.0008). The relationship was very similar at all beds, with a slight variation observed in Carlingford, which was also characterised by more variability (Figure 2).

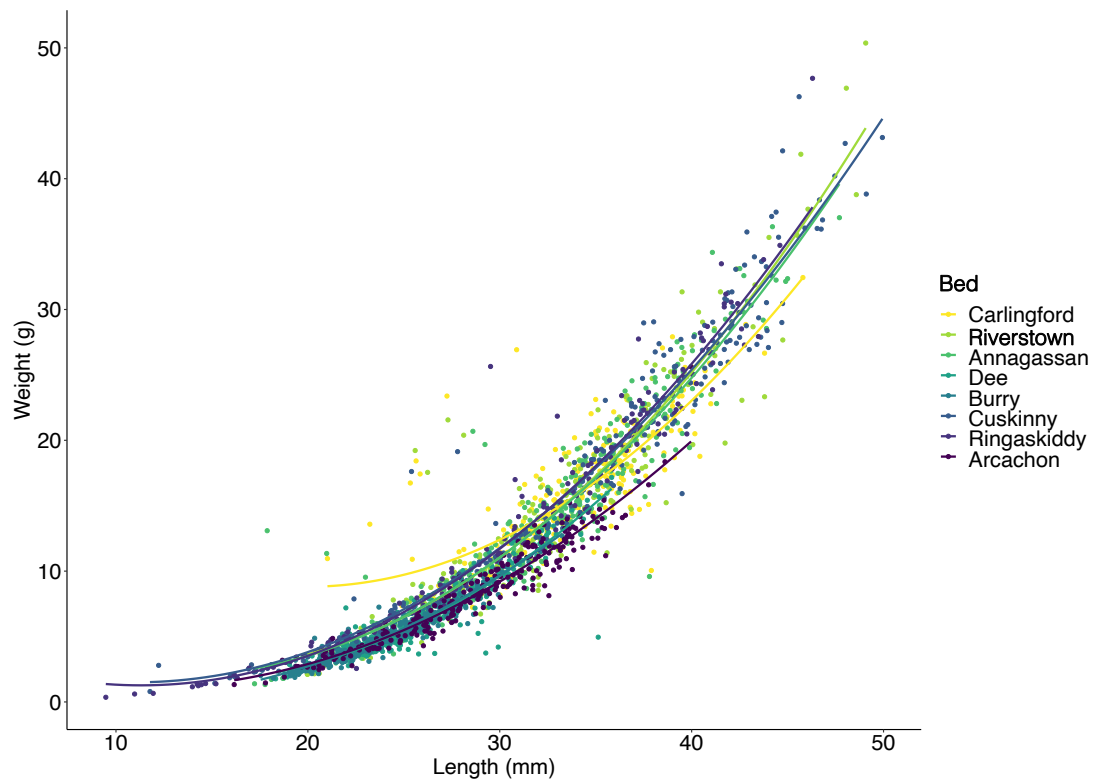


Figure 2. Relationship between shell length and total wet weight (shell and flesh), fitted with a quadratic equation, for *Cerastoderma edule* from five Irish beds, two Welsh beds (Burry and Dee) and one French bed (Arcachon).

Weight also differed significantly between beds ($H=876.44$, $df=7$, $p<0.001$). As was the case with length, mean wet weight of Welsh cockles was lower than all other beds ($p<0.001$ in all cases). Cockles at Cuskinny were significantly heavier than all other beds, except for Carlingford. Like with cockle length, no relationship was observed between wet weight and geographic proximity.

3.1.2. Potential cockle food sources

The mean $\delta^{13}\text{C}$ value of cockles differed significantly between beds ($F=41.65$, $df=5$, $p<0.001$). All beds differed significantly in $\delta^{13}\text{C}$ values according to post hoc tests, with the exception of three comparisons (Burry vs Arcachon, Riverstown vs Arcachon and Cuskinny vs Riverstown). The beds with the lowest $\delta^{13}\text{C}$ values corresponded with the highest primary productivity (Burry and Dee, Table 2).

3.1.3. Growth and environmental variability

The estimates for L_{∞} (asymptotic average length), k (Brody growth rate coefficient), t_0 (theoretical age at which size is 0) and ϕ' (growth performance index) are indicated in Table 3. Growth parameters could not be estimated for the Burry due to lack of older individuals, resulting in a linear fit. Beds within the same sites (i.e. beds within Cork Harbour and Dundalk Bay), exhibited similar growth curves (Figure 3).

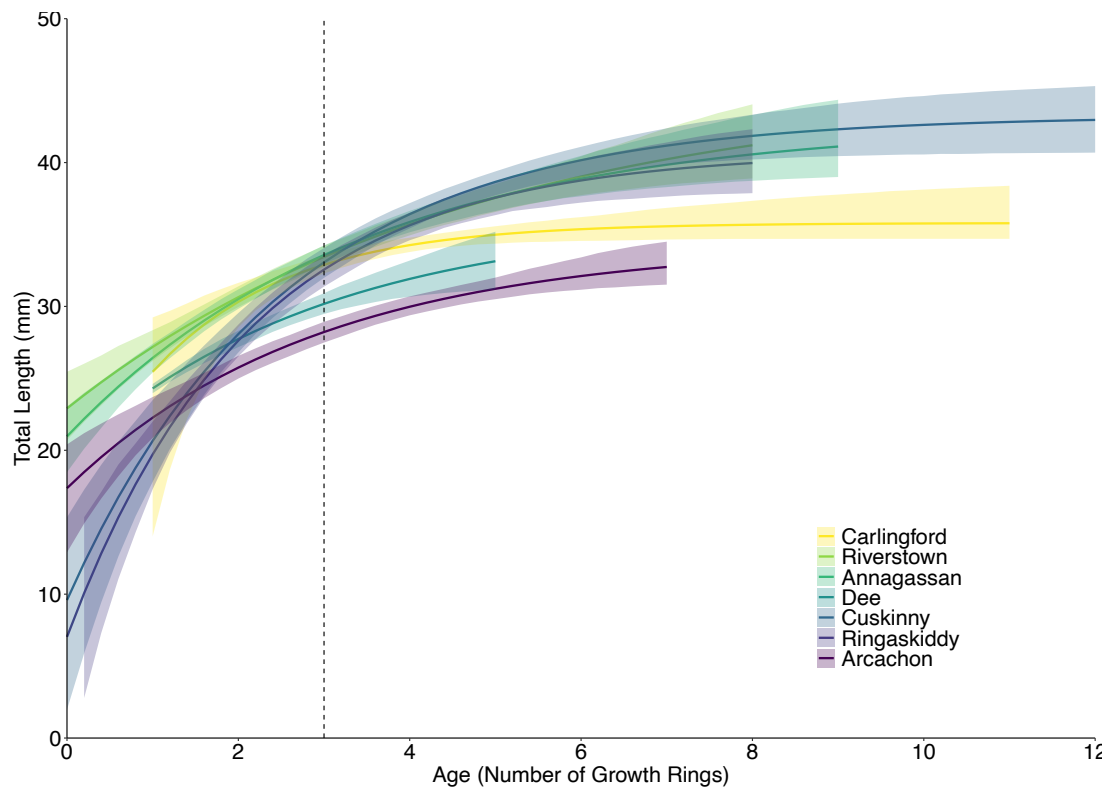


Figure 3. Estimated von Bertalanffy growth curves of cockles at five Irish beds, one Welsh bed and one French bed. Cockles <3 years are delineated by the dashed line, when variations in growth curves became evident. Shaded areas around the curve indicate the 95% confidence intervals.

Following analysis of multiple nonlinear growth models, there was a significant difference between the simplest model (where no growth parameters differed between beds), and the most complex, where all parameters differed. This suggested that growth parameters varied between beds ($\chi^2=308.29$, $df=18$, $p<0.001$, Table 3). Likelihood ratio and extra sum-of-square tests, to determine which parameters differed, found a significant difference for both k (Brody growth rate coefficient) and t_0 (age at size zero; $p<0.001$) among beds. However, L_∞ was not found to significantly differ among beds.

Table 3. Growth parameters estimated using the von Bertalanffy growth model for *Cerastoderma edule*, from five Irish beds, one Welsh bed (Dee) and one French bed (Arcachon). L_{∞} is the asymptotic average length (i.e. average maximum length), k is the Brody growth rate coefficient (i.e. “speed: at which average maximum length is reached), t_0 is the theoretical age at which size is 0, and ϕ' is the growth performance index.

Bed	Latitude	L_{∞} (mm)	k (yr ⁻¹)	t_0 (yr)	ϕ'
Carlingford	54°N	35.80	0.64	-0.95	2.72
Riverstown	53°N	45.04	0.22	-3.24	1.99
Annagassan	53°N	42.74	0.29	-2.34	2.18
Dee	53°N	36.15	0.34	-2.25	2.19
Cuskinny	51°N	43.24	0.40	-0.63	2.48
Ringaskiddy	51°N	40.74	0.47	-0.40	2.57
Arcachon	44°N	34.29	0.34	-2.07	2.13

No significant relationships were observed between the growth performance index (ϕ') and food sources (represented by $\delta^{13}\text{C}$), or any of the other environmental and biotic variables (metacercarial prevalence, sporocyst prevalence, density, sea temperature, primary productivity or salinity, all $p>0.05$).

The highest growth performance index (ϕ') and the highest Brody growth rate coefficient (k) were found at Carlingford, indicating that cockles reach the average maximum length (L_{∞}) first at this bed. However, at

Carlingford, t_0 was low initially and growth appeared relatively slow in cockles greater than three years (Figure 3). Carlingford also exhibited the lowest primary productivity (differing significantly from all beds except for Arcachon; Table 2). Mean salinity also appeared to be lowest compared to the other beds, combined with a large range (Table 2). Conversely, in terms of growth parameters, both beds at Dundalk took the longest to reach maximum average length (L_∞ ; Annagassan: 0.29 yr^{-1} and Riverstown: 0.22 yr^{-1}). However, at Dundalk cockles had reached larger sizes by year three (Figure 3). Although not significant, the highest L_∞ was observed at Riverstown (45.04 mm), followed by Cuskinny (43.24 mm) and then Annagassan (42.74 mm) while the lowest L_∞ was observed in Carlingford (35.8 mm), with a similar value at Arcachon (34.3 mm). Annual temperatures were highest at Arcachon, significantly more so than Carlingford ($p=0.004$) and Riverstown ($p=0.02$), with a trend for lower temperatures at Annagassan ($p=0.04$ at a significance level of 2.5%). Primary productivity was generally higher at the Welsh sites, and significantly higher than Arcachon ($p<0.001$) and Carlingford ($p<0.001$; Table 2), however, the growth parameters were not extremely high or low in Wales (Table 3).

3.2. Historic spatio-temporal trends of cockle growth

More work was conducted using the von Bertalanffy growth curve in the 70s and 80s at higher latitudes (Figure 4, Table 4), with lower latitudes more frequently studied since the 1990s. A total of ten papers detailing L_∞ and k were included in this analysis (Table 4). L_∞ tended to increase at higher latitudes ($p=0.068$) and significantly increased over time ($p=0.03$), with a L_∞ of 54 mm

found at a latitude of 57°N (Langerak, Denmark, Figure 4A). The Brody growth rate coefficient (k) decreased significantly at higher latitudes (i.e. cockles reached L_{∞} in less time at lower latitudes; $p=0.04$, Figure 4B). Only two sites examined in the field survey had been detailed in the previous literature regarding von Bertalanffy growth parameters, Arcachon Bay and Dundalk Bay. However, growth was detailed over nearly the entire latitudinal range of *Cerastoderma edule*, from 34°N to 69°N. At Dundalk in 2003-2004, L_{∞} was higher than in 2018-2019 (Table 4). Between 1997 and 2014, L_{∞} was 36 mm at Arcachon (Magalhães *et al.*, 2016) and between 2005 and 2007 it was 38.4 mm (Gam *et al.*, 2010), compared to a lower 34.29 mm in this study.

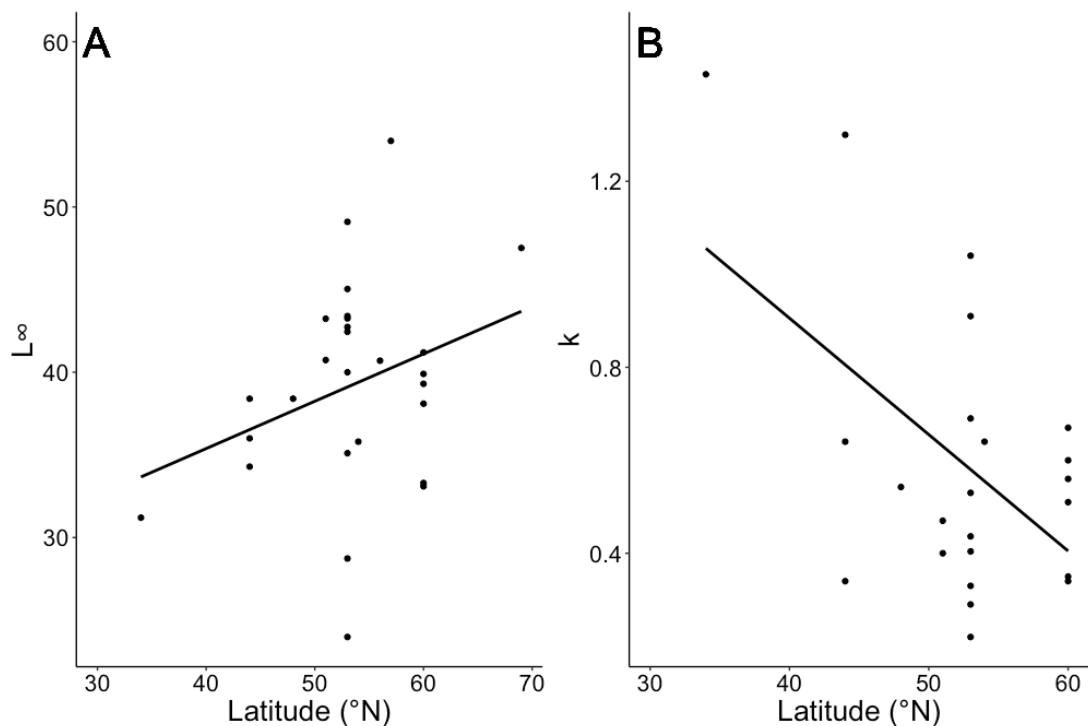


Figure 4. Relationship between latitude and (A) L_{∞} and (B) k , based on mixed effects models. Values for L_{∞} and k were obtained from the current study and historic studies.

Table 4. Von Bertalanffy growth parameters from published literature, as well as those from the present study (bold). Units of latitude are °N. L_{∞} is reported in mm and k in yr^{-1} .

L_{∞}	k	ϕ	Site	Country	Years	Latitude	Description	Source
47.52	NA	NA	Ramfjord	Norway	1975-1976	69	Intertidal	Richardson <i>et al.</i> , 1980
39.90	0.51	2.6	Gluss Voe	Scotland	1972	60	Intertidal	Jones and Baxter, 1987
38.10	0.67	2.8	Shetland	Scotland	1977	60	Intertidal	Jones and Baxter, 1987
39.30	0.60	2.7	Shetland	Scotland	1979	60	Intertidal	Jones and Baxter, 1987
41.20	0.56	2.7	Shetland	Scotland	1981	60	Intertidal	Jones and Baxter, 1987
33.10	0.35	2.1	Shetland	Scotland	1982	60	Intertidal	Jones and Baxter, 1987
33.30	0.34	2.1	Shetland	Scotland	1984	60	Intertidal	Jones and Baxter, 1987
54.00	NA	NA	Langerak	Denmark	1977-1979	57	Subtidal	Brock, 1980
40.70	NA	NA	Aggersbord	Denmark	1977-1980	56	Subtidal	Brock, 1980
35.80	0.64	2.7	Carlingford	Ireland	2018-2019	54	Intertidal	This Study
43.40	0.33	2.3	Wadden Sea	The Netherlands	2001-2003	53	Intertidal	Cardoso, 2007
43.26	1.04	3.3	Wadden Sea	The Netherlands	2001-2003	53	Subtidal	Cardoso, 2007
49.10	0.44	2.7	Dundalk	Ireland	2003-2004	53	Intertidal/Subtidal	Fahy <i>et al.</i> , 2004
42.74	0.29	2.2	Dundalk (Annagassan)	Ireland	2018-2019	53	Intertidal	This Study
45.04	0.22	1.9	Dundalk (Riverstown)	Ireland	2018-2019	53	Intertidal	This Study
36.15	0.34	2.19	Dee	Wales	2018-2019	53	Intertidal	This Study
23.98	0.91	2.7	Traeth Melynog	Wales	1986	53	High Shore	Sanchez-Salazar <i>et al.</i> , 1987
28.73	0.69	2.6	Traeth Melynog	Wales	1986	53	Mid Shore	Sanchez-Salazar <i>et al.</i> , 1987
35.10	0.53	2.5	Traeth Melynog	Wales	1986	53	Low Shore	Sanchez-Salazar <i>et al.</i> , 1987
42.45	NA	NA	Traeth Melynog	Wales	1976-1997	53	Intertidal	Richardson <i>et al.</i> , 1980
40.00	0.40	2.4	Wadden Sea	Germany	1994-1995	53	Intertidal	Ramón, 2003
43.24	0.40	2.5	Cork (Cuskinny)	Ireland	2018-2019	51	Intertidal	This Study
40.74	0.47	2.6	Cork (Ringaskiddy)	Ireland	2018-2019	51	Intertidal	This Study
38.40	0.54	2.6	Bay of Saint-Brieuc	France	2001-2006	48	Intertidal	Ponsero <i>et al.</i> , 2009
36.00	0.64	2.7	Arcachon	France	1997-2014	44	Intertidal	Magalhães <i>et al.</i> , 2016
38.40	1.30	3.4	Arcachon	France	2005-2007	44	Intertidal	Gam <i>et al.</i> , 2010
34.29	0.34	2.1	Arcachon	France	2018-2019	44	Intertidal	This Study
31.20	1.43	3.3	Merja Zerga	Morocco	2005-2007	34	Intertidal	Gam <i>et al.</i> , 2010

4. Discussion

This field survey further affirmed the variability of cockle populations, in terms of size and growth, external (temperature, salinity, density) and internal

(trematodes) drivers on the population dynamics of this commercially and ecologically important species. Cockles at the suction dredged fishery (Dundalk) reached largest sizes in the first three years according to the growth curves. This finding is most likely due to a reduced representation of larger cockles in the population caused by local fishing activity. However the historic survey indicated that latitude may potentially impact cockle growth parameters, with cockles reaching larger asymptotic average length (L_{∞}) at northern sites, contradicting a previous study where cockles grew faster at southern latitudes (Iglesias and Navarro, 1990). Differences between these studies may be attributed to climate, with the Atlantic Multidecadal Oscillation shifting to a positive phase (i.e. warmer Atlantic sea surface temperature) in the interim (1980s to present, NOAA, 2019). However further research would be required to confirm this. Furthermore, populations at the same latitude did not always have similar growth rates (e.g. Dundalk vs the Dee). This highlights that local abiotic and biotic drivers influence growth, more so than latitudinal variation, with potentially complex interactions occurring between these variables.

Cockles at Dundalk Bay reached greater than 30 mm earliest supporting a productive fishery here. However, Dundalk also exhibited amongst the lowest growth performance indices. Furthermore, while strictly speaking, cockles at Carlingford (lightly fished) exhibited the highest growth performance, the growth never exceeded that of other sites and cockles here had a small asymptotic average length (L_{∞}). Additionally, cockles at all three

unfished/lightly fished beds (Cuskinny, Ringaskiddy and Carlingford), initially exhibited lower t_0 . The lack of older individuals is a common phenomenon impeding model fitting with a von Bertalanffy growth model, resulting in an attempt to fit a nonlinear function to an erroneously linear model (Ogle, 2015). Therefore, interpretations are only valid for the first stages of the growth curves in this study.

Additionally, prior to examining the role of abiotic factors on cockle growth, it is important to consider that the data in this study originated from oceanographic modelling (Copernicus, 2020). Rather than conducting in situ measurements these data were gathered from satellite data as a cost saving and time efficient measure. Previous data at other sites agree with the measurements (de Montaudouin and Lanceleur, 2011), and as inferences are made relating to low salinity values at Carlingford, it is important to affirm that salinity values within this site are variable and can be influenced by riverine input at low tide (Wilson *et. al.*, 1974; Wilson *et. al.*, 1977). However, due to the large spatial resolution of earth observation data, as well as the potential for environmental variability at a micro level, it would be worthwhile to conduct more comprehensive analysis on the influence of the environment on cockles.

While growth performance was not lowest at Carlingford (lowest salinity), the growth curve demonstrated poor growth after three years. This may demonstrate the role of abiotic drivers on cockle growth. Non-fished cockles at Cork, where salinity was highest, grew larger than all other sites. The negative impact of low salinity in this study supports a previous experiment

demonstrating that reduced salinity causes cockles to close their valves, therefore feeding less and thus resulting in less energy available for growth (Domínguez *et al.*, 2020). As the potential for increased rainfall events (and higher water temperatures) are predicted due to climate change (Beniston *et al.*, 2007), this negative impact of low salinity is a potential threat for the future growth of cockles. This, in combination with the impact of increasing water temperatures is concerning, considering the potential for increased rainfall events and higher water temperatures resulting from changing climate. However, higher water temperatures may also result in increased primary productivity (Gosling, 2015), which is linked with fast growth in cockles, therefore these opposing effects may negate the impact on cockles.

As well as abiotic environmental variables, biotic variables also impacted cockle growth. Considering that reproduction at Carlingford has been shown to be suboptimal (Mahony *et al.*, in review) it is unsurprising that growth curves were also suboptimal, in comparison with the nearby site of Dundalk. Furthermore, although density was not shown to impact the Brody growth rate coefficient (k), at Cork where density was lowest, cockles could attain a large size likely due to decreased competition for space and resources, as well as not being removed by fishing. Finally, while trematode prevalence was not found to significantly impact cockle growth, it was likely that high metacercarial prevalence, potentially in combination with low salinity at Carlingford was detrimental to growth. This is concerning, due to the possibility of increased trematode transmission resulting from warming seawater (de Montaudouin *et*

al., 2016). However, the distribution of trematode species varies across the range of cockles (de Montaudouin *et al.*, 2009), with some species having more of a detrimental impact than others (Longshaw and Malham, 2013). Therefore, further molecular work would be beneficial to determine the species present at these sites. Furthermore, it would also be useful to conduct surveys in these areas to determine the impacts of other pathologies or pollutants. It would also be worthwhile to examine the links between temperature and food availability. As seasonal variation of growth was beyond the scope of this study it was not analysed in the models. However a positive relationship between growth and water temperature has been demonstrated previously in cockles, likely due to food availability (Beukema *et al.*, 2017).

Previous studies have been conducted at Arcachon and Dundalk, allowing for a comparison between current and past growth rates. In Dundalk in 2003-2004, asymptotic average length (L_{∞}) was higher than 2018-2019. However, the earlier study was carried out at intertidal and subtidal locations, the latter of which may have higher growth rates due to increased immersion time and, therefore, increased feeding (de Montaudouin, 1996; Wegeberg and Jensen, 2003). Asymptotic average length (L_{∞}) was lower at Arcachon in this study, compared to previous studies, however this was due to a mass mortality event and the removal of older individuals from the population. Density and microphytobenthos were historically found not to impact growth in cockles at Arcachon Bay (de Montaudouin, 1996), and this was supported by this study. It is also possible that growth at Arcachon is influenced by the allocation of

energy to gametogenesis, rather than somatic growth, with gonad at the “spawning” stage occurring almost year-round at this location (Mahony *et al.*, 2021). However, cockles at Arcachon display a large inter-individual variation in growth rate even in the same environmental conditions (de Montaudouin *et al.*, 2012).

No major conclusions could be drawn on the impact of food source on cockles, which were approximated with the $\delta^{13}\text{C}$ values of cockle flesh. Typically, $\delta^{13}\text{C}$ can be used as a rough guideline as to whether a food source is of marine or terrestrial origin, with the ratio of carbon isotopes barely changing as it moves through the food web. This means the carbon assimilated by filter feeding cockles reflects the primary food source of cockles (DeNiro and Epstein, 1980; Peterson and Fry, 1987). Significantly lower $\delta^{13}\text{C}$ was observed at the Dee Estuary and at Annagassan (Dundalk), indicating a possibly larger contribution of terrestrial food at these sites (Fry and Sherr, 1984). However in this study, $\delta^{13}\text{C}$ was not a significant driver of cockle growth, suggesting that either food source does not influence growth of cockles or the proportion of terrestrial input among sites is not strong enough to impact growth. However, the stable isotopes of local food sources were not measured in this study, therefore the exact food source of cockles at each ecosystem could not be defined. In addition, it is important to recognise that sampling only occurred during one month for stable isotope values, despite variations in food sources for cockles throughout the year. Therefore, it is important to reiterate that these results are not definitive and should be interpreted with caution.

Patterns of cockle growth varied spatially, and much of this variation was likely caused by local environmental factors, in particular sea temperature, salinity and primary productivity: factors that may exert, so far, undetermined effects on cockle growth in the context of climate change. This may be particularly interesting given that cockles reached larger sizes at northern latitudes, which generally exhibit lower temperatures. With the potential for temperatures to increase at higher latitudes, northern cockles may follow similar, reduced growth trajectories as currently experienced at warmer, southern locations. This may consequently disrupt the production of cockles at northern latitudes, damaging fisheries. Finally, due to the local differences, it was evident that growth rate varied greatly among sites, even within close proximity, highlighting the importance of carrying out local and frequent surveys to determine the most suitable minimum capture size, as has occurred in other invertebrate species (Sulardiono *et al.*, 2012). The findings of this study not only bridge a 30-year knowledge gap on latitudinal growth rate variability but highlights the usefulness of local surveys in determining which cockles to choose for aquaculture breeding lines based on fast growth rate.

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Chapter 6: General Discussion

Throughout this thesis cockles *Cerastoderma edule* were analysed in a holistic manner, examining their past and present population dynamics, health and reproduction, with a view to predicting the future threats to this species. This is a novel approach to studying cockles, as it comprehensively details current trends, as well as past trends from multiple sites, which may help support our understanding for the future. A general overview of the key historic and current findings will be discussed. These findings will also be considered in the context of the future, in particular under climate change scenarios.

Summary of findings

Cycles of variability in cockles are normal historically, with cockles renowned for their boom and bust cycles (Morgan *et al.*, 2013). This thesis further supported this variability, with spatial and temporal differences evident in all characteristics examined, and variation of cockle populations occurring even within a single bed, or within a particular year. However, an issue of major concern is the potential for more frequent and extreme changes in cockle populations. Previous literature demonstrated that cockles were variable in the past, but variability is likely to become more frequent in the future due to changing environmental conditions and pathogen induced mortalities.

Importantly, new information is provided on the role of climate on cockle population dynamics, in particular the decrease of cockle abundance in

response to increased sea surface temperatures. While climate was demonstrated as impacting population dynamics at a large scale, at local scales it appeared that extremes are having contrasting impacts, which are not being observed when examining the Atlantic Multidecadal Oscillation (AMO). However, as the AMO is a metric describing the entire Atlantic, it is possible that it is masking local extremes. The global study supported a local study in the Wadden Sea, where cockle recruitment was less successful as a result of severe hot or cold conditions (Beukema and Dekker, 2020). Furthermore in terms of climate, a range of pathogenic parasites may be directly or indirectly impacted by changing climatic conditions. While further sites must be analysed to affirm these results, these findings are concerning, as more frequent weather extremes are predicted as a result of climate change (Beniston *et al.*, 2007), highlighting the importance of managing easily controllable factors, for example fisheries management schemes.

Delving further into the impact of abiotic factors, water temperature and salinity were found to have substantial impacts on cockle populations. Interestingly, spawning was observed year-round at Arcachon, despite recruitment not happening year-round here (de Montaudouin, pers comms.). This occurrence is likely explained by the lower number of cockles spawning, and slight asynchronicities between sexes. However, it is possible that environmental variables also play a role in this phenomenon. First, fertilisation occurs between 10 and 20°C (Kingston, 1974, in laboratory conditions, so this range may be narrower in the wild) so it is possible that fertilisation is not

occurring year-round. Secondly, larvae (compared to adults) are less resistant to low temperature and salinity extremes (Kingston, 1974), which may further result in lack of year-round recruitment. It is also possible that changing hydrodynamics and/or winds are influencing settlement at Arcachon, a phenomenon previously demonstrated by modelling bivalve larvae in the Irish Sea (Young *et al.*, 1998; Coscia *et al.*, 2020). Cockles may not be retained in their natal area at Arcachon and may instead be settling elsewhere. This is a likely scenario considering the lack of cockles observed at the end of the sampling period.

Abiotic factors are also likely to be influencing cockle biology in terms of energy allocation, with higher water temperatures potentially leading to the diversion of energy from growth to gametogenesis. This was experienced in warm locations but may impact productivity of cockles at more northern latitudes in the future. Furthermore, growth trajectories of cockles may be reduced due to lower salinity from climate induced precipitation increases. This is a potential threat to fisheries due to reduced yields and availability of cockle meat.

Biotic factors, such as parasites, were evidently a major influencer of cockle populations. This thesis highlights further the wide range of parasites and commensals that cockles co-exist with, which can vary in prevalence and species richness even at sites of close proximity. This highlights the importance of biosecurity even for non-notifiable diseases. When considering the results of the studies in combination, it became even clearer that the impacts of these

biotic factors are often interlinked. For example, high prevalence of trematodes negatively impacted populations, resulting in reduced spawning and more indeterminate individuals. Growth was also impacted by trematodes, with poor growth occurring at trematode impacted sites, compared to less impacted sites. This was demonstrated in Carlingford, when examining growth curves in later years. Further research examining seasonal variations in growth due to food availability would help to clarify these results.

Valuable information was learned in the methodology of Chapter 3. Von Bertalanffy growth parameters were not as beneficial as was assumed, despite being the growth model typically used in cockle studies. When compared with the corresponding growth curve, differing interpretations were reached. The growth curves provided a more in-depth view of cockle growth through time, and better explained the stresses experienced by cockles at the various sites. For example, at Carlingford, despite growth parameters describing fastest growth, the growth curves did not demonstrate such, indicating that cockles here are diverting energy from growth (likely due to stress from salinity and trematodes). Therefore, future studies may benefit from assessing alternative growth models for cockles to determine a model more suitable than the von Bertalanffy growth model.

Impact of this research

Important recommendations have been derived from this thesis, which will protect cockle populations for commercial use, as well as for their ecosystem services. The overall recommendation is regular, standardised

monitoring. It is important not to generalise a particular region, as it was obvious that cockle populations can vary greatly within a number of kilometres (for example Carlingford and Dundalk). It was found that gaps exist in the literature relating to cockles. This is surprising considering the ecological, economic and social importance of cockles across Europe. Sharing of information is vital, and does not always occur, as demonstrated by difficulties when gathering historical data for this thesis. This highlights the importance of open access, and publishing or publicly reporting all information, not just significant results. Implementing these recommendations is an achievable goal in the protection of cockle fisheries.

Dundalk Bay in Ireland can be viewed as an important case study for cockle fisheries. While not as widely harvested or consumed as historically, Dundalk Bay has become the key source of Irish cockles since 2001, generating important income for locals. While previous studies individually examined growth, density and singular parasite groups at Dundalk Bay, this is the first comprehensive study examining the key features of cockle populations in combination. To protect the productivity of this fishery, it is evident that holistic sampling as conducted in this thesis is highly important. In terms of the population currently, this section of the discussion is a good news story. No notifiable diseases were observed, and cockles at Dundalk appeared generally healthy, exhibiting no neoplasia and relatively low trematode prevalence. Anecdotally, fishers have claimed that Dundalk cockles exhibit rapid growth, and this was proven (at least in the first number of years). This is a site with

good water quality, and while not explicitly monitored, the low prevalence of ciliates may be additional proof of this (Palm and Dobberstein, 1999). Salinity here remains relatively constant year-round, further highlighting that lack of stress may be an important factor for cockle populations. Furthermore, the good communication between fishers and managers at the bay was highlighted, which exemplifies the type of communication that should be occurring on a national and international scale.

In addition to the impact of this research for fisheries, useful information can be used to inform cockle aquaculture. Efforts are being made to create successful aquaculture conditions for cockles (Pronker *et al.*, 2015; Philippart *et al.*, 2020). Breeding programmes for aquaculture are interested in selecting for increased growth rates (Gjedrem and Rye, 2018) to improve yield, so it would therefore be beneficial to detect already fast growing individuals, as well as the conditions they thrive in. However, this thesis provides further support of growth plasticity in cockles (de Montaudouin, 1996). This was shown with the cockles in Dundalk and Carlingford, which are unlikely to be genetically distinct due to close proximity, exhibiting differing growth characteristics. This further highlights the importance of perfecting growing conditions for cockle aquaculture, as well as selecting suitable genetic lines.

Further work

In addition to the potential of future research discussed above, much of the further work identified in this thesis relates to the parasitological survey, primarily regarding study methods. While molecular techniques are fast

becoming the “go-to” practice in pathology, traditional histology remains useful. Molecular techniques typically only target a particular pathogen group due to the specificity of these methods (Verweij and Rune Stensvold, 2014), with histology being particularly valuable in terms of diagnosis of new diseases, as it is less specific. Unfortunately, histology is unable to easily differentiate between trematode species (with the exception of *Parvatrema minutum*). Therefore, it would be interesting to conduct molecular studies to determine which species of metacercariae are occurring at particular sites, with the appropriate molecular tools. It may be possible that more detrimental metacercariae are occurring at Carlingford, impacting health at this site. Furthermore, histology is unable to accurately or fully make an assessment of intensity of infection. Therefore, further research using squash preparations to determine metacercarial species and intensity would be worthwhile. It is possible that cockles at Carlingford have higher intensities of metacercariae, as a result of salinity induced stress, likely resulting in the diversion of energy from reproduction and growth to homeostasis. As trematode transmission is likely to increase (de Montaudouin *et al.*, 2016) and salinity likely to decrease (Beniston *et al.*, 2007) resulting from climate change, the potential impacts at a site and wider scale may be significant.

Another interesting angle for further work is interactions between parasites, and between parasites and the environment. A number of associations were observed between cockles and their parasites. These findings provide a useful starting point for future research, in particular to determine

the specific causes of these interactions, which may also be explained by confounding factors involved due to site specific variables (e.g. environmental variables). Additionally, the presence of other host species was not thoroughly examined. For example at Carlingford, high numbers of barnacles were observed on the shells of cockles. It would be worth determining if these organisms are having negative impacts on cockles, due to impacts on the life cycle of the parasite, difficulties in cockle valve closure, the potential disruption of parasite transmission, or as a potential reservoir for parasites.

Concluding remarks

Cockles in the Atlantic Area have faced numerous challenges historically but remain a well distributed species. While this highlights the resilience of cockles, as well as their ability to exist in challenging conditions, this thesis brings to the fore the issue of climate change. Climate change is likely to be a major threat to the future of cockles, both in terms of wild populations and their fisheries. Due to their economic, ecological and cultural importance, negative impacts on cockle populations will have cascading effects on coastal communities, economies and ecosystems. The obvious answer to protecting cockle fisheries is to prevent climate change. However, smaller changes, such as improved knowledge transfer, streamlined management techniques and future research, will assist in the protection of this emblematic species.

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No thanks are due to the Covid Pandemic, which hit during the final year of my PhD! However, this led me to join the great PhD Forum community. The new friends I gained through online writing groups was an amazing source of motivation and support.

Thank you to my “Homegirls”, Áine, Avril, Emma, Louise, Niamh D and Niamh H. As always, your friendship has kept me going and I am amazed that none of you told me to stop talking about cockles! Of course, I have to thank the “Cooperage Crowd”, past and present, for the countless tea, cake, laughter (and crying) sessions. In particular, I extend heartfelt gratitude to the “Shellfish Health Crew”, Sara Albuixech-Martí, Katie Costello and Gary Kett. It was an honour to make this journey together and I have made best friends for life.

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To the love of my life, Stephen. You always believed in me, supported me during rough patches, and celebrated achievements with me. I’m so lucky to have you.

This work would not have happened without my Dad. While he wasn’t here during my PhD, his curiosity about the natural world is the reason I chose this path. Thanks Dad.

from Squarings, Settings xxiv

Deserted harbour stillness. Every stone
Clarified and dormant under water,
The harbour wall a masonry of silence.

Fullness. Shimmer. Laden high Atlantic
The moorings barely stirred in, very slight
Clucking of the swell against boat boards.

Perfected vision: cockle minarets
Consigned down there with green-slicked bottle glass,
Shell-debris and a reddened bud of sandstone.

Air and ocean known as antecedents
Of each other. In apposition with
Omnipresence, equilibrium, brim.

Seamus Heaney

Appendices

Appendix A: Dissemination

Accepted Publications

Mahony, K. E., Lynch, S. A., Egerton, S., Laffan, R. E., Correia, S., de Montaudouin, X., Mesmer-Dudons, N., Freitas, R., Culloty, S. C. (2021) Latitudinal influence on reproductive health and host-parasite ecology in an ecosystem engineer bivalve model, *Ecology and Evolution* (In Press).

Mahony, K. E., Lynch, S. A., Egerton, S., Cabral, S., de Montaudouin, X., Fitch, A., Magalhães, L., Rocroy, M. and Culloty, S. C. (2020) Mobilisation of data to stakeholder communities. Bridging the research-practice gap using a commercial shellfish species model, *PLoS ONE*, 15(9), e0238446.

Carss, D. N., Brito, A. C., Chainho, P., Ciutat, A., de Montaudouin, X., Fernández Otero, R. M., Filgueira, M. I., Garbutt, A., Goedknecht, M. A., Lynch, S. A., **Mahony, K. E., Maire, O., Malham, S. K., Orvain, F., van der Schatte Olivier, A. and Jones, L. (2020)** Ecosystem services provided by a non-cultured shellfish species: The common cockle *Cerastoderma edule*, *Marine Environmental Research*, 158, 104931.

Submitted Publications

Mahony, K. E., Egerton, S., Lynch, S. A., Blanchet, H., Goedknecht, M. A., Groves, E., Savoye, N., de Montaudouin, X., Malham, S. K., Culloty, S. C. (In Review) Drivers of growth in a keystone fished species along the European Atlantic coast: the common cockle *Cerastoderma edule*, *Journal of Sea Research*.

Lynch, S. A, Egerton, S., Bookelaar, B., Dickerson, B., **Mahony, K. E.**, Culloty, S. C. (Submitted) Deciphering host-pathogen interactions and resource theory in a stressful environment using a bivalve paradigm, *Diseases of Aquatic Organisms*.

Bué, M., Brito, A. C., Cabral, S., Carss, D. N., Carvalho, F., Chainho, P., Ciutat, A., Couñago Sanchez, E., de Montaudouin, X., Fernández Otero, R. M., Incera Filgueira, M., Fitch, A., Garbutt, A., Goedknecht, M. A., Lynch, S. A., **Mahony, K. E.**, Maire, O., Malham, S. K., Orvain, F., Rocroy, M., van der Schatte Olivier, A., Jones, L. (Submitted) Inter-country differences in the cultural ecosystem services provided by cockles, *People and Nature*.

Publications in preparation

Mahony, K. E., Lynch, S. A., de Montaudouin, X., Culloty, S. C. (In Preparation) Host, pathogen and environmental drivers of parasite prevalence and parasite species richness in an ecosystem engineer.

Wang, Q., Egerton, S., **Mahony, K. E.**, Costello, K., Albuixech-Martí, S., Culloty, S. C., Lynch, S. A. (In Preparation) Disseminated neoplasia revisited: an epizootiological assessment of this disease in a cockle *Cerastoderma edule* population forty years after its first detection.

Reports

Mahony, K. E., Lynch, S. A., Egerton, S., Cabral, S., de Montaudouin, X., Fernández Otero, R., Fitch, A., Iglesias, D., Magalhães, L., Rocroy, M., Villalba, A., Culloty, S. C. (2019) *Baseline historical survey of common cockle (Cerastoderma edule) populations in the Atlantic area*. COCKLES Project.

Mahony, K. E., Egerton, S., Lynch, S. A., Culloty, S. C., Groves, E., Malham, S., Goedknecht, A., Blanchet, H., de Montaudouin, X., Orvain, F., Vasconcelos, P., Carvalho, A.N., Pereira, F., Piló, D., Moura, P., Gaspar, M., Cabral, S., Chainho, P., Villalba, A., Iglesias, D., Correia, S., Freitas, R., Incera, M., Couñago, E. (2020). *Field survey of cockle distribution, abundance & population dynamics currently*. COCKLES Project.

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Conferences

Mahony, K. E., Lynch, S. A., Culloty, S. C. (2018, September 3) Understanding the past of the common cockle (*Cerastoderma edule*) to better understand its future [Conference poster and oral presentation]. *British Ecological Society Fishes of the Future Event*, London. tinyurl.com/yy578bhn

Mahony, K. E., Lynch, S. A., Culloty, S. C. (2018, September 11-12) Understanding the past of the common cockle (*Cerastoderma edule*) to better understand its future [Conference oral presentation]. *3rd UK and Ireland EAFP Branch Meeting, Galway*. tinyurl.com/yxqt7wdt

Mahony, K. E., Lynch, S. A., Culloty, S. C. (2019, September 9-12) What the history of the common cockle (*Cerastoderma edule*) can tell us about its potential future [Conference oral presentation]. *European Association of Fish Pathologists, Porto, Portugal*. tinyurl.com/yypt2c4v

Mahony, K. E., Lynch, S. A., Culloty, S. C. (2019, January 9-12) Understanding the past to predict the future: What the history of the common cockle (*Cerastoderma edule*) can tell us about its potential future [Conference poster and flash presentation]. *Ecology and Evolution Ireland, Galway*. tinyurl.com/yxknpboy

Mahony, K. E., Lynch, S. A., Culloty, S. C. (2020, October 20-22) Cockles Molly Malone would be proud of? The growth of Irish cockles (*Cerastoderma edule*) and potential climate impacts [Virtual conference presentation]. *Environ 2020, Online*. tinyurl.com/yyhtmx8r

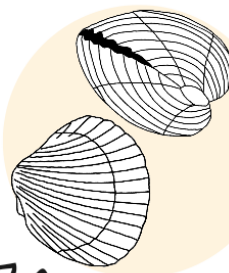
Articles/Manuals/Infographics

1. COCKLES Newsletter 2: Historical survey of cockle distribution, abundance and population dynamics in the Atlantic Area, 2018 [Newsletter]. COCKLES Project. tinyurl.com/y5skxht5
2. COCKLES Newsletter 5: COCKLES field work and trematode identification at Aveiro, In Preparation [Newsletter]. COCKLES project.

THE LIFE & TIMES OF COCKLES

WHAT THE SHELL ARE COCKLES?

COCKLES are shellfish that live in the sand on beaches. They belong to a group of animals called 'Bivalves' because they have two shells. There are over **200** species of COCKLES worldwide.



FUN FACT

You can tell a COCKLE'S age by counting its shell rings, just like a tree!

THE COCKLES PROJECT

In the COCKLES project, scientists looked at **10,000** records of COCKLE history to better understand it



Vikings liked to eat COCKLES too. YUM!

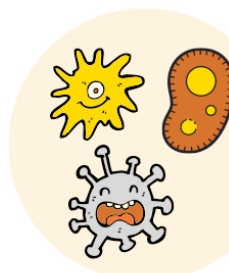


DID YOU KNOW?

COCKLES were around **100 MILLION** years ago during the Age of Dinosaurs! Fossils are proof that COCKLES lived when dinosaurs roamed the earth.

COCKLES GET SICK TOO

More than **50** parasites & bugs live in COCKLES. Parasites might like warmer weather, which means there might be less COCKLES in the future with Climate Change.



www.ckles-project.eu



Created by:
Kate Mahony
Sian Egerton
Sharon Lynch

3. Mahony, K. E., Egerton, S., Lynch, S. A. (2020) The Life and Times of Cockles

[Infographic, translated to French, Portuguese and Spanish]

UNDERSTANDING THE COMMON COCKLE

ECOSYSTEM SERVICES PROVIDED BY COCKLES



Cerastoderma edule,
one of two species
in its genus



Acts as an
ecosystem engineer



Supports the economy
of many coastal
communities in Europe



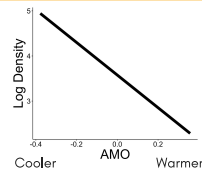
Important source of
food for birds, crabs
and people.



To understand the future of cockles, the past of cockles was examined. This was achieved by gathering historic literature from various sources including from science, fishing, museums, newspapers



Cockle populations vary due to
parasites, legislation, recruitment
and the environment



Overall, lower densities were
found in years with warmer
seawater temperatures

IMPORTANT POINTS



Different
measurements making
standardisation and
comparison difficult



Some areas studied
better than others
(e.g. where fisheries
occur)



Lower densities
might result from
warming seawater
temperatures



More data sharing is
needed to fully
understand cockles

THIS WORK WAS PART OF THE COCKLES PROJECT



[HTTP://WWW.COCKLES-PROJECT.EU/](http://www.cockles-project.eu/)



Created by:
Kate Mahony
Sian Egerton
Sharon Lynch

4. Mahony, K. E., Egerton, S., Lynch, S. A. (2020) Understanding the Common Cockle [Infographic, translated to French, Portuguese and Spanish]

WHAT THE SHELL

IS HISTOLOGY?

A fun and illustrative guide to how scientists look at the tissues of the common cockle



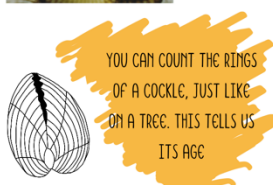
WHAT IS HISTOLOGY?

Scientists use histology to look at animal tissues (groups of cells) under the microscope. In COCKLES project, we want to understand what makes them sick (parasites) and how they reproduce (make baby cockles).



Cockles are a type of shellfish (mollusc) that lives in sandy and muddy shores. People and animals including birds and crabs like to eat them. This is one of the reason why scientists want to understand them.

First, we must go to the beach and collect some cockles.



In the lab, we open the cockles and slice the body down the middle. We place this in a special case called a histocassette and put it in a chemical called Davidson's Solution. This is to "fix" the tissues, so we can keep them for a long time.



After 24 hours, we put the histocassette into a machine called a tissue processor. This machine puts the cockle tissues into different chemicals, including alcohol, to dry out the tissue.



Next, we put tissues in paraffin (like candle wax), to make blocks.

FUN FACT: 5 MICRONS IS ABOUT 20 TIMES SMALLER THAN THE THICKNESS OF A STRAND OF HAIR

We then cut the blocks on a device called a microtome, to very thin sections (5 microns) which we put on a microscope slide.



Later, in the stainer, the paraffin is removed with a chemical called xylene, and the tissues are coloured with stains to allow us to see the cells.

THE FINAL RESULT

Finally, we have a slide that we can look at under the microscope. Here you can see some of the organs found in cockles.



5. Mahony, K. E., Correia, S. (2020) What the shell is histology? A fun and illustrative guide to how scientists look at the tissues of the common cockle. [Manual for COCKLES Project educational pack, translated to French, Portuguese and Spanish]

Media



UCC Scientists call for comprehensive shellfish studies to safeguard cockles

1. UCC Scientists call for comprehensive shellfish studies to safeguard cockles, *EchoLive.ie*, 23/9/2020 [Online: tinyurl.com/yylahtl5]



2. Alive, alive-o? Not now Molly, thanks to climate change, *Irish Daily Mail*, 24/09/2020 [Print]



3. Appeal to help keep cockles alive alive-oh, *Irish Daily Mirror*, 24/09/2020

[Print]



4. Cockles & Mussels Alive-oh But Perhaps Not with Molly Malone, *Afloat.ie*, 24/9/2020 [Online: tinyurl.com/y5vyl7fo]

Cork Scientists Making Sure That Cockles Survive

Though they are more connected with Dublin, certainly in song through “cockles and mussels,” the future survival of cockles depends on a greater consistency in the study of the shellfish and how this research is communicated to the fishing industry, according to scientists at University College Cork.



5. Cork Scientists Making Sure That Cockles Survive. *Marine Times*, 26/09/2020

[Online: tinyurl.com/y3hlfbra]



Alive, alive-o? Not now Molly,
thanks to climate change



By **Sean O'Driscoll** - 04/10/2020



6. Alive, alive-o? Not now Molly, thanks to climate change, *Extra.ie*, 4/10/2020

[Online: tinyurl.com/y2ccdb5h]

Bandon scientist is on a mission to save one of Ireland's iconic shellfish

7. Bandon scientist is on a mission to save one of Ireland's iconic shellfish, *The Opinion*, 21/10/2020 [Print]

8. Éanna Ní Lamhna interviews Kate Mahony about cockles on Mooney Goes Wild, *RTE One Radio*, 2/11/2020 [Radio Interview: <https://tinyurl.com/y5dcetc3>]

Public outreach and engagement events

1. Our Ocean Wealth Summit Trade Show. 28-29th June 2018 [Attendance: 200 people]

2. Seafest Festival. 2018, 29th June-1st July 2018 [Attendance: 100,000 people]

3. UCC Cork Discovers, European Researchers Night, Career Café, 28th September 2018 [Attendance: 200 people]

4. Seafest Festival. June 7-9th 2019 [Attendance: 100,000 people]

5. Field Trip for Brownies Science Badge. 13th April 2019 [Attendance: 30 children]

Other activities



1. Ongoing Twitter updates on my personal twitter account, @kate_mahony

Featured ‘Day in the life of’ : Kate, PhD student researching the common cockle.

AUGUST 28, 2019 · LEAVE A COMMENT

Hi, I’m Kate and I’m a second year PhD student in University College Cork (UCC), Ireland. My work focusses on the common cockle, a type of shellfish found in Europe. I’m trying to understand why cockles have been dying in large numbers, by looking at reproduction, parasites and things like weather. I received an undergraduate degree in Zoology, as well as a MSc in Marine Biology, both from UCC.

2. Blog post (28th August 2019). Featured ‘Day in the life of’: Kate, PhD student researching the common cockle. [tinyurl.com/yylr2ymu]

3. Facilitation of visiting work experience student (25-29th November 2019).
Educating secondary school student on cockles, literature reviews, histology and data analysis.



4. Staying Alive-Oh Game (18th October 2020). Educational game informing of the threats to cockles e.g. predation, parasites, environmental factors.
[tinyurl.com/y549kbz5]

5. Contribution to online GIS viewer of COCKLES Project (2018-2020). This map viewer (in preparation by COCKLES partner CETMAR), will enable dissemination of project outputs to stakeholders.

Appendix B: Supplementary Material to Chapter 2

S1 Table. Classification of topics in each data source in a study of historic populations of *Cerastoderma edule*.

Topic	Content type
Cockles	Relating to the biology of cockles (morphology, reproduction, growth, abundance etc.)
Cultural	Aspects of cockles related to human culture and society (e.g. food, art)
Ecosystem	Dealing with interactions between cockles and other species or the ecosystem (e.g. sediment dynamics, food for birds).
Fishery	Relating to landings, fishing types, legislation
Parasites	Details of parasitology (and lesions, disseminated neoplasia) in cockles

S2 Table. Variables, variable types and factor levels included in the mixed effects model examining density in cockles.

Variable	Variable Type	Factor Levels	Comments
AMO Index	Continuous	-	-
Season	Discrete	All Year Autumn Autumn, Winter Not Stated Spring Spring, Summer Summer Winter	An observation occurred “All Year”, if the density measurement was a result of sampling in three or more seasons. Autumn, Winter/Spring, Summer, indicates that an observation was recorded over two seasons
Sampling Type	Discrete	Intensive Extensive	Levels were chosen to reflect the impact of the sampling gear in a commercial setting. Extensive sampling was obtained by hand gathering (e.g. quadrats, raking, transects). Intensive samples were obtained by dredging, cores and grabs.
Latitude	Continuous	-	-
Age	Discrete	Adult Juvenile Both Not Stated	-

S3 Table. Models examined by linear mixed effects model fit by REML, on the dependent variable, density.

Model	Fixed Effects	Random Effects	AIC
1	AMO, Sampling Type, Season, Latitude, Year, Age	Year Latitude	3794
2	AMO, Sampling Type, Season, Latitude, Year, Age	1 Latitude	3791
3	AMO, Sampling Type, Season, Latitude, Year, Age	1 Year	3813

S4 Table. Summary of available information on harvest and legislation relating to cockles across Europe.

	Denmark	France	Germany	Ireland	The Netherlands	Portugal	Spain (Galicia)	The UK
Maximum Capture (Tonnes)	7,699	40,000	8,133	668	80,000	4,714	21,500	46,615
Year of Max Capture	2015	1913	1983	2007	1989	2017	1968	1991
Number of Key Production Areas	2+	3+	1+	1+	2+	3+	44+	12+
Year of First Legislation	?	1990	1989	2007	1999	1987	ca. 1973	?
Gear Types	Dredging, Hand gathering	Hand gathering, Rakes	Hand gathering	Hydraulic suction dredge, Hand gathering	Hand gathering, Rakes, Hydraulic dredge	Rake, Harvesting knife	Grubber hoe, Hand rake, Bullrake, Hand dredge	Hand rake, Trailed pump scoop dredge
Fisheries in Protected Areas	?	Banc d'Arguin, Bay of Saint Brieuc, Bay of Somme, Bay of Authie	?	Dundalk, Tramore, Castlemaine	?	Ria de Aveiro, Ria Formosa	Ria de Arousa, Ria de Pontevedra, Ria de Vigo	Burry Inlet, Morecambe Bay, Solway Firth, Thames Estuary
TACs	Limfjord	No but quotas per fisher and bed	?	Dundalk	Wadden Sea	No	No but yearly management plans after stock assessment	Burry Inlet, Solway Firth, Thames Estuary
Minimum Capture Size	?	27-30 mm	?	17-22 mm	21 mm	25 mm	25-28 mm	10-23.8 mm

? No data available

S5 Table. Output of the final linear mixed effects models examining variations in cockle density.

Variable	Factor Level	DF	t-value	<i>p</i>
AMO	-	205	-3.972708	0.0001
Season	Autumn	205	-3.410272	0.0008
	Autumn, Winter	141	-0.791095	0.0754
	Not stated	205	0.622367	0.5344
	Spring	205	-2.407012	0.0170
	Spring, Summer	205	-0.785518	0.4331
	Summer	205	-3.523285	0.0005
	Winter	205	-1.735372	0.0842
	Winter, Spring	205	-1.702027	0.0903

Appendix C: Supplementary Material to Chapter 3

S1 Table. Result of Dunn tests with Bonferroni correction to determine if the percentage of indeterminate individuals differed between sites, H_0 rejected when $p < 0.025$.

	Arcachon	Aveiro	Carlingford	Cork
Aveiro	0.999	-		
Carlingford	0.026	0.036	-	-
Cork	0.661	0.939	0.801	-
Dundalk	0.056	0.080	0.999	0.999

S2 Table. Result of Dunn tests with Bonferroni correction to determine if length at spawning differed between sites, H_0 rejected when $p < 0.025$.

	Arcachon	Aveiro	Carlingford	Cork
Aveiro	0.999	-		
Carlingford	<0.001	<0.001	-	-
Cork	<0.001	<0.001	0.999	-
Dundalk	<0.001	<0.001	0.999	0.999

S3 Table. Results of Dunn tests with Bonferroni correction to determine if number of growth rings of spawning individuals differed across sites, H_0 rejected when $p < 0.025$.

	Arcachon	Carlingford	Cork
Carlingford	0.003	-	-
Cork	0.488	0.021	-
Dundalk	0.003	<0.001	<0.001

S4 Table. Results of a chi square test examining if the proportions of individuals infected with metacercariae varied across sites.

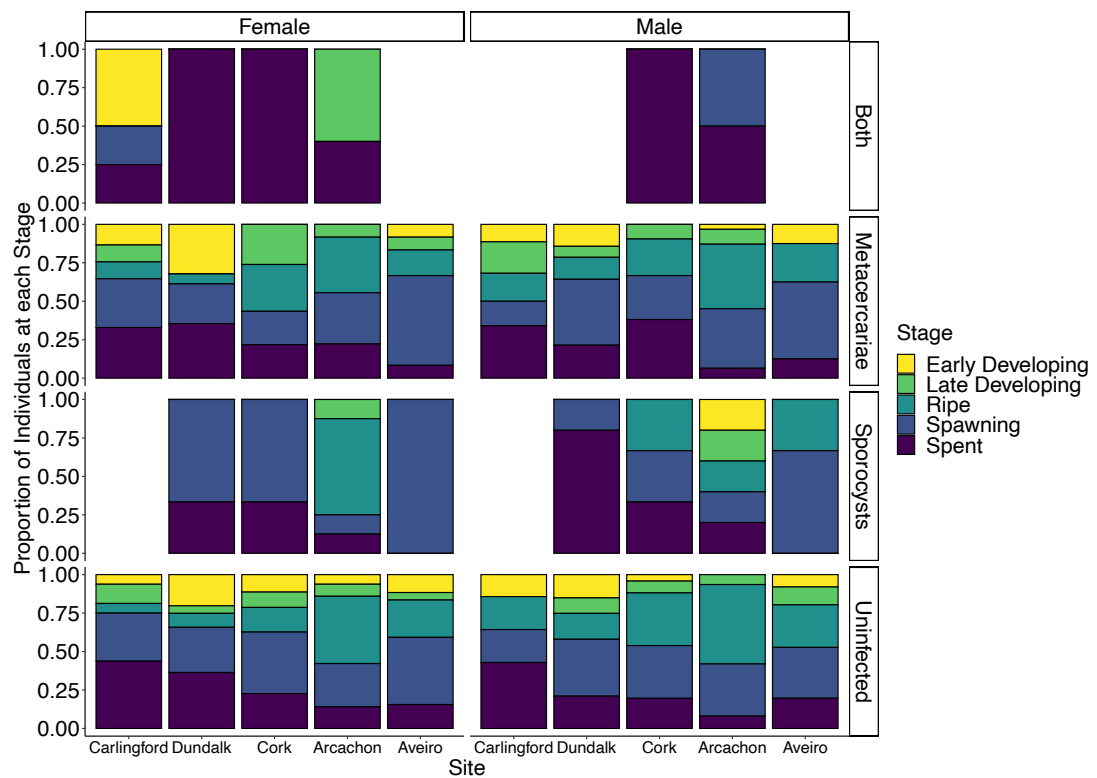
Comparison	Adjusted chi square <i>p</i> value
Arcachon vs Aveiro	<0.001
Arcachon vs Carlingford	<0.001
Arcachon vs Cork	<0.001
Arcachon vs Dundalk	<0.001
Aveiro vs Carlingford	<0.001
Aveiro vs Cork	<0.001
Aveiro vs Dundalk	<0.001
Carlingford vs Cork	<0.001
Carlingford vs Dundalk	<0.001
Cork vs Dundalk	<0.001

S5 Table. Results of chi square test examining if the proportions of metacercaria infected individuals differed at each stage of gametogenesis.

Comparison	Adjusted chi square <i>p</i> value
Indeterminate vs Early Developing	0.3640
Indeterminate vs Late Developing	0.9999
Indeterminate vs Ripe	0.0802
Indeterminate vs Spawning	0.0802
Indeterminate vs Spent	0.6350
Early Developing vs Late Developing	0.5760
Early Developing vs Ripe	0.8550
Early Developing vs Spawning	0.8550
Early Developing vs Spent	0.7940
Late Developing vs Ripe	0.2940
Late Developing vs Spawning	0.2940
Late Developing vs Spent	0.8220
Ripe vs Spawning	0.9999
Ripe vs Spent	0.3120
Spawning vs Spent	0.3120

S6 Table. Results of chi square test examining if the proportions of metacercaria and sporocyst coinfecting individuals differed at each stage of gametogenesis.

Comparison	Adjusted chi square <i>p</i> value
Indeterminate vs Early Developing	0.4680
Indeterminate vs Late Developing	0.8280
Indeterminate vs Ripe	0.0077
Indeterminate vs Spawning	0.0077
Indeterminate vs Spent	0.4680
Early Developing vs Late Developing	0.9220
Early Developing vs Ripe	0.3730
Early Developing vs Spawning	0.7600
Early Developing vs Spent	0.9200
Late Developing vs Ripe	0.1120
Late Developing vs Spawning	0.2650
Late Developing vs Spent	0.9999
Ripe vs Spawning	0.8280
Ripe vs Spent	0.1120
Spawning vs Spent	0.1710



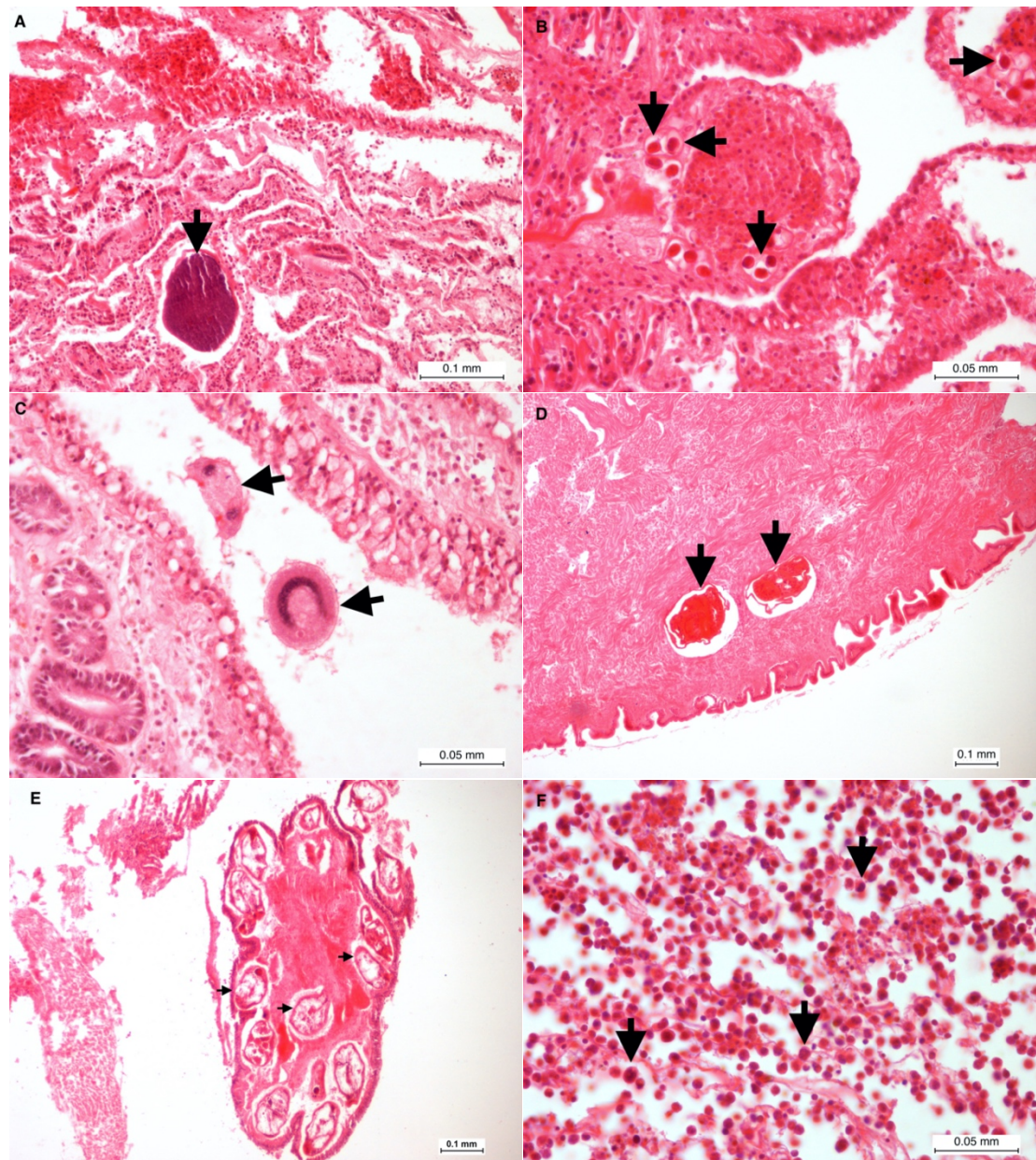
S7 Figure. Proportion of male and female *Cerastoderma edule* at each stage of gametogenesis, for individuals infected and uninfected by sporocysts and metacercariae. Infection state is indicated on the right of the graph, and coinfection indicates that an individual was coinfecting by sporocysts and metacercariae. Indeterminate individuals have been removed from this graph.

Appendix D: Supplementary Material to Chapter 4

S1 Table. Prevalence of key observed species and pathological conditions (lesions) at three sites in Ireland, and one site in France (Arcachon), between April 2018 and October 2019. Additionally, a *Sphenophyra*-like ciliate was detected in one individual in Dundalk and fungus was detected in another individual in Dundalk.

Prokaryotes			Carlingford		Dundalk		Cork		Arcachon	
			Prevalence (%)	CI	Prevalence (%)	CI	Prevalence (%)	CI	Prevalence (%)	CI
Gill			0.00	0.00-0.02	0.33	0.00-0.02	0.74	0.00-0.02	11.72*	0.08-0.16
	Digestive Gland		4.80*	0.02-0.08	0	0.00-0.01	1.23	0-0.03	1.26	0.00-0.04
Protozoa	Apicomplexa	Coccidia	7.42*	0.04-0.12	0.84	0.00-0.02	0.98	0-0.02	2.09	0.01-0.05
		Gregarina	87.34*	0.82-0.91	64.02	0.60-0.68	33.42	0.29-0.38	45.61	0.39-0.52
	Ciliates	Trichodina	3.49	0.02-0.07	4.18	0.03-0.06	12.29*	0.09-0.16	1.26	0.00-0.04
		Rhynchodida	6.99	0.04-0.11	4.18	0.03-0.06	11.79*	0.09-0.15	2.51	0.01-0.05
	Haplosporidia		6.99*	0.04-0.11	3.56	0.02-0.06	4.18	0.02-0.07	0.00	0.00-0.02
Metazoa	Trematode	Metacercariae	82.53*	0.77-0.87	1.05	0.00-0.02	12.53	0.09-0.16	20.08	0.15-0.26
		Sporocyst	4.80	0.02-0.08	4.80	0.02-0.08	2.95	0.02-0.05	12.13*	0.08-0.17
		<i>Parvatrema</i>	15.72	0.11-0.21	17.57	0.14-0.21	1.97	0.01-0.04	18.83*	0.14-0.24
	Crustacea	Unidentified	0.44*	0-0.02	0.42	0.00-0.02	0.25	0-0.01	0.00	0.00-0.02
	Turbellaria	<i>Paravortex</i>	10.04	0.06-0.15	2.93	0.02-0.05	3.19	0.02-0.05	27.62*	0.22-0.34
Total Species Richness			11		14		12		10	
Sample Size			229		478		407		239	
Mean Individual Species Richness (± 1 SD)			3.24 $\pm$ 1.28		1.54 $\pm$ 1.1		1.52 $\pm$ 1.27		1.93 $\pm$ 1.39	
Lesions	Infiltration		23.58*	0.18-0.30	13.6	0.11-0.17	8.35	0.06-0.11	13.81	0.10-0.19
	Granuloma		67.25*	0.61-0.73	32.22	0.28-0.37	36.36	0.32-0.41	29.29	0.24-0.36
	Necrosis		2.18	0.01-0.05	3.94*	0.02-0.06	3.19	0.02-0.05	0.00	0.0-0.02
	Neoplasia		0.44	0.00-0.01	0	0.00-0.01	18.43*	0.15-0.23	6.7	0.04-0.11

For each sample site the parasite species with the highest % prevalence is denoted in bold font, * denotes the highest % prevalence for each parasite species or pathological condition.



S2 Figure. Examples of pathogens and pathologies (arrows) observed in *Cerastoderma edule* from Ireland and France, between April 2018 and October 2019. Slides were prepared using histological techniques and stained with Haematoxylin and Eosin. (A) *Rickettsiae*-like infection in the gill (B) Gregarines within a granuloma (C) *Trichodina* ciliate external to the gill (D) Trematode metacercariae in the foot (E) *Parvatrema minutum* in the hinge tissue (F) Disseminated neoplasia in the connective tissue.

S3 Table. Results of a Dunn test comparing individual parasite species richness by bed.

	Annagassan	Arcachon	Carlingford	Riverstown	Cuskinny
Arcachon	0.0425				
Carlingford	<0.001	<0.0001			
Riverstown	0.9999	0.0514	<0.0001		
Cu skinny	0.4859	0.9999	<0.0001	0.5581	
Ringaskiddy	0.0179	<0.0001	<0.0001	0.0148	<0.0001

S4 Table. Results of a Dunn test comparing salinity by bed.

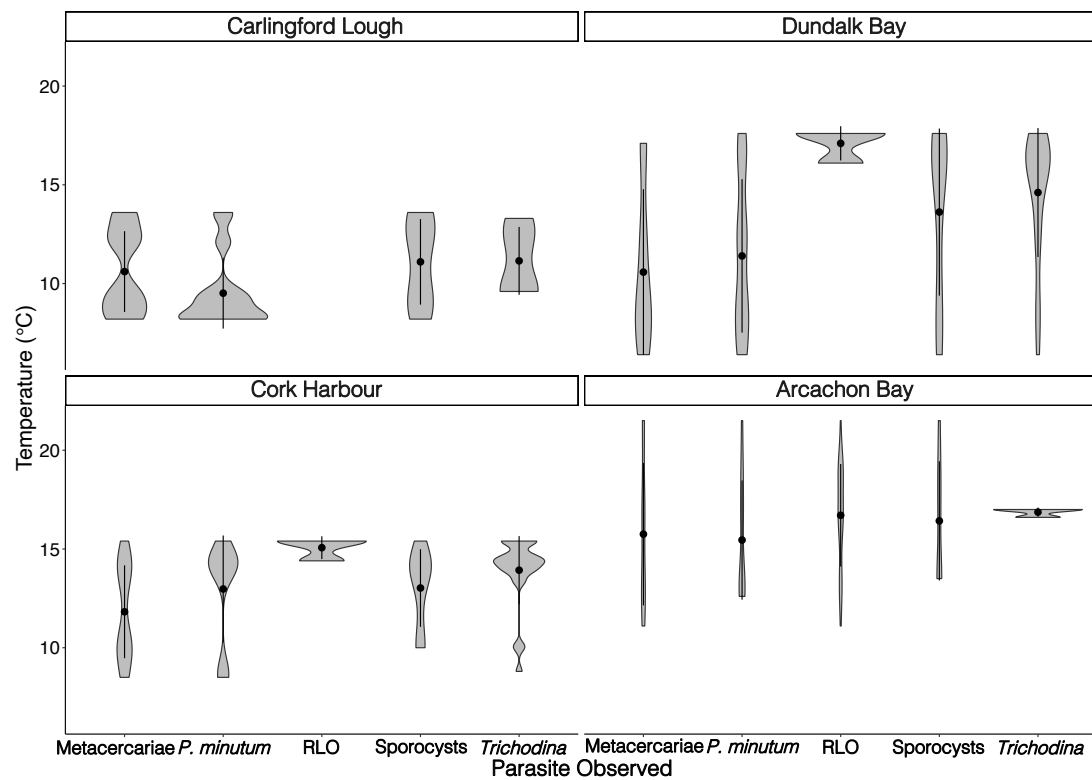
	Annagassan	Arcachon	Carlingford	Riverstown	Cuskinny
Arcachon	0.0031				
Carlingford	0.9999	0.0041			
Riverstown	0.9999	0.0031	0.9999		
Cu skinny	<0.0001	0.6947	<0.0001	<0.001	
Ringaskiddy	<0.0001	0.9057	<0.0001	<0.001	0.9999

S5 Table. Results of a Dunn test comparing seawater temperature by bed.

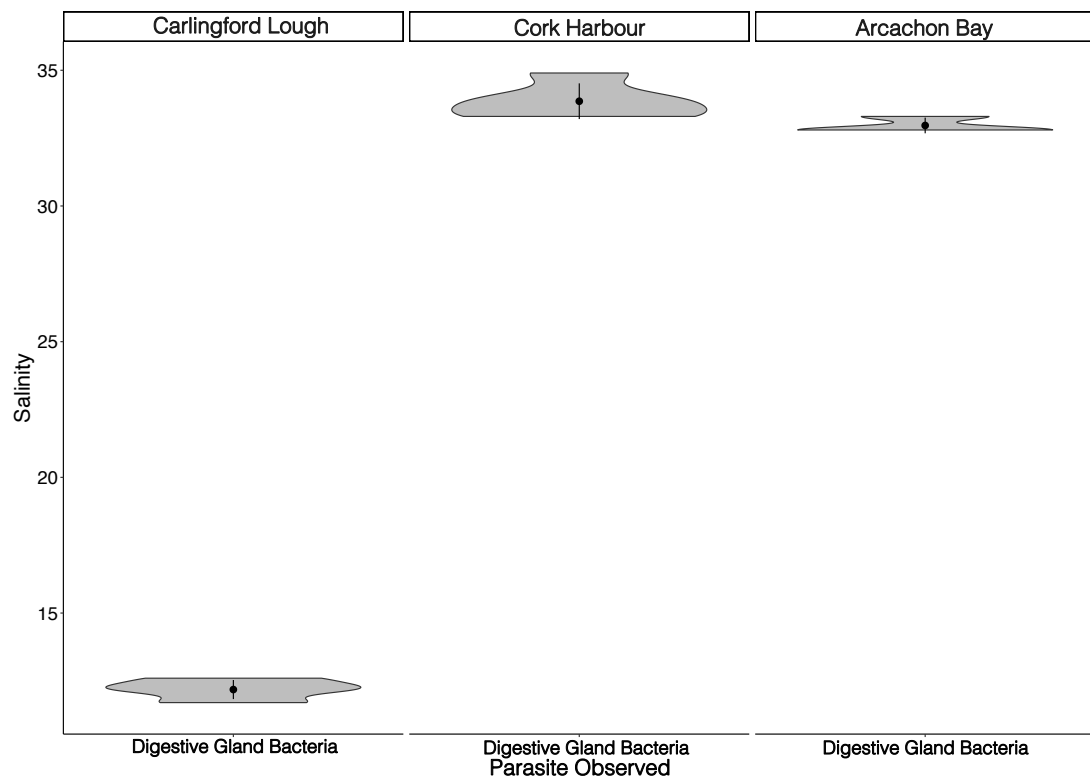
	Annagassan	Arcachon	Carlingford	Riverstown	Cuskinny
Arcachon	0.0120				
Carlingford	0.9999	0.0009			
Riverstown	0.9999	0.0058	0.9999		
Cu skinny	0.9999	0.0281	0.9999	0.9999	
Ringaskiddy	0.9999	0.0178	0.9999	0.9999	0.9999

S6 Table. Results of a Dunn test comparing oxygen by bed.

	Annagassan	Arcachon	Carlingford	Riverstown	Cuskinny
Arcachon	<0.0001				
Carlingford	0.9999	<0.0001			
Riverstown	0.9999	<0.0001	0.9999		
Cu skinny	0.9999	0.0140	0.8629	0.1468	
Ringaskiddy	0.9999	0.0137	0.8757	0.1497	0.9999



S7 Figure. Violin plots (visualising the kernel probability density), demonstrating the relationship between the presence of pathogens and seawater temperature, at each of the sites. Mean $\pm$ 1 SD of temperature is represented by the vertical line and point within the violin plots.

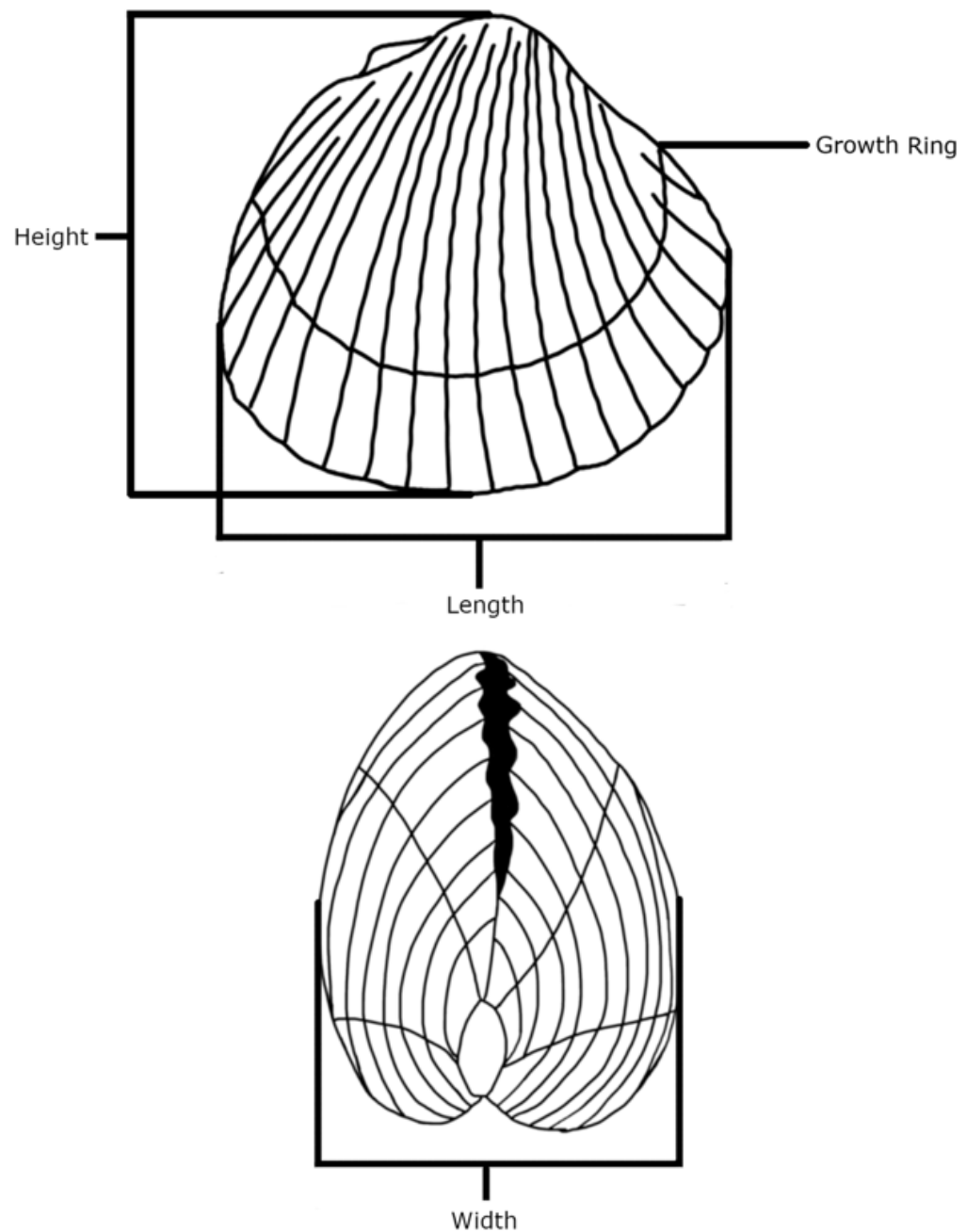


S8 Figure. Violin plots (visualising the kernel probability density), demonstrating the relationship between the presence of pathogens and salinity, at each of the sites. Mean $\pm$ 1 SD of salinity is represented by the vertical line and point within the violin plots.

S9 Table. Results of significant contrasts examined within a binary generalised linear model, examining the impact of intrinsic and extrinsic variables on prevalence of parasites in *C. edule*. Four sites were included as factors, with Dundalk Bay, Cork Harbour and Arcachon compared with Carlingford Lough, for each parasite or parasite group.

Parasite	Site	z	p
Coccidia	Dundalk	-4.008	<0.001
	Cork	-3.717	<0.001
	Arcachon	-2.556	0.016
Gregarina	Dundalk	-6.010	<0.001
	Cork	-11.582	<0.001
	Arcachon	-8.139	<0.001
Metacercariae	Dundalk	-12.445	<0.001
	Cork	-14.588	<0.001
	Arcachon	-8.134	<0.001
Sporocysts	Arcachon	2.048	0.040
<i>Paravortex</i>	Dundalk	-3.451	<0.001
	Cork	-3.109	0.002
	Arcachon	5.183	<0.001
<i>P. minutum</i>	Cork	-5.226	<0.001
	Arcachon	2.865	0.004
<i>Trichodina</i>	Cork	2.377	0.017
	Arcachon	-3.368	<0.001
<i>Rhynchodida</i>	Arcachon	-2.194	<0.001

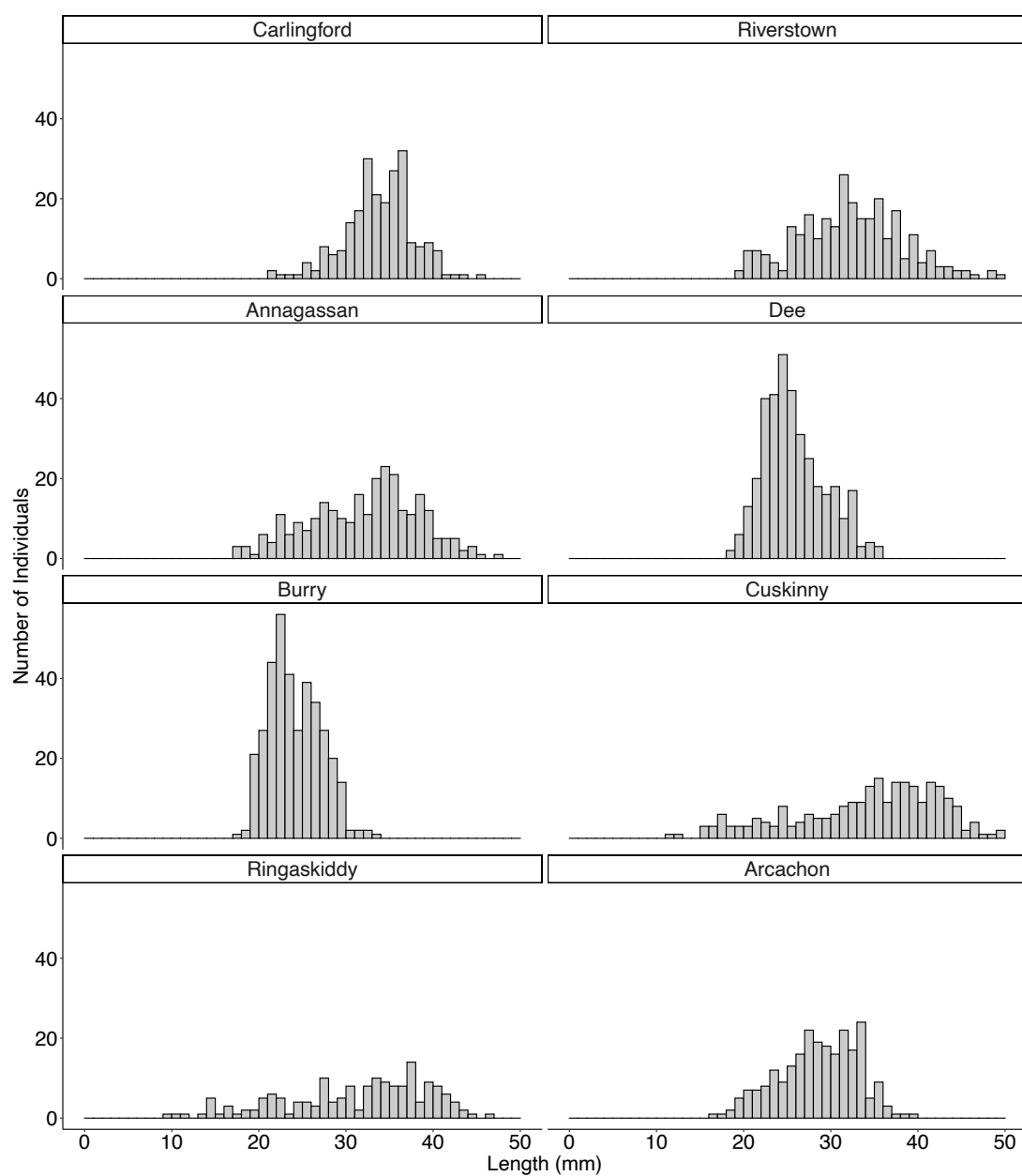
Appendix E: Supplementary Material to Chapter 5



S1 Figure. Morphometric measurements obtained in this study.

S2 Table. Result of Dunn tests (p values) with Bonferroni correction to determine if median length of cockles differed between sites. Results are significant where $p=0.025$.

	Annagassan	Arcachon	Burry	Carlingford	Riverstown	Cuskinny	Dee
Arcachon	<0.001	-	-	-	-	-	-
Burry	<0.001	<0.001	-	-	-	-	-
Carlingford	0.005	<0.001	<0.001	-	-	-	-
Riverstown	0.999	<0.001	<0.001	0.009	-	-	-
Cu skinny	0.147	<0.001	<0.001	<0.001	0.254	-	-
Dee	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	-
Ring skiddy	0.999	0.001	<0.001	<0.001	0.999	0.013	<0.001



S3 Figure. Length frequency distributions of cockles *Cerastoderma edule* studied over 19 months at Irish, Welsh and French sites.

S4 Table. Result of Dunn tests (*p* values) with Bonferroni correction to determine if wet weight of cockles differed between sites. Results are significant where *p*=0.025.

	Annagassan	Arcachon	Burry	Carlingford	Riverstown	Cuskinny	Dee
Arcachon	<0.001	-	-	-	-	-	-
Burry	<0.001	<0.001	-	-	-	-	-
Carlingford	0.001	<0.001	<0.001	-	-	-	-
Riverstown	0.999	<0.001	<0.001	0.003	-	-	-
Cu skinny	0.041	<0.001	<0.001	0.999	0.070	-	-
Dee	<0.001	<0.001	0.017	<0.001	<0.001	<0.001	-
Ringaskiddy	0.999	<0.001	<0.001	0.002	0.999	0.078	<0.001

S5 Table. Result of Tukey's Tests (*p* values) to determine if $\delta^{13}\text{C}$ of cockle tissue differed between sites.

Comparison	<i>p</i> value
Arcachon-Annagassan	<0.001
Burry-Annagassan	<0.001
Riverstown-Annagassan	0.02
Cuskinny-Annagassan	0.04
Dee-Annagassan	0.01
Burry-Arcachon	0.97
Riverstown-Arcachon	0.08
Cuskinny-Arcachon	0.03
Dee-Arcachon	<0.001
Riverstown-Burry	0.02
Cuskinny-Burry	0.01
Dee-Burry	<0.001
Cuskinny-Riverstown	0.99
Dee-Riverstown	<0.001
Dee-Cuskinny	<0.001

S6 Text. Process and results of analysis of multiple nonlinear von Bertalanffy growth models, following Ogle *et al.* (2015). Differences were examined between the simplest model and the most complex, where all parameters differed between beds.

First, the simplest model was tested, where no growth parameters differed ($E[L|t] = L_{\infty}(1 - e^{-K(t-t_0)})$). This model was compared with the most complex model, where all parameters differed ($E[L|t] = L_{\infty}[bed](1 - e^{-K[bed](t-t_0[bed])})$). The likelihood ratio ($\chi^2=308.29$, $p<0.001$) and extra sum-of-squares test ($F=18.58$, $p<0.001$) suggested evidence of a difference in the VGBF parameters between the beds.

Subsequently, three nested models were fit, as follows:

- a) $E[L|t] = L_{\infty}[site](1 - e^{-K[site](t-t_0)})$
- b) $E[L|t] = L_{\infty}[site](1 - e^{-K(t-t_0[site])})$
- c) $E[L|t] = L_{\infty}(1 - e^{-K[site](t-t_0[site])})$

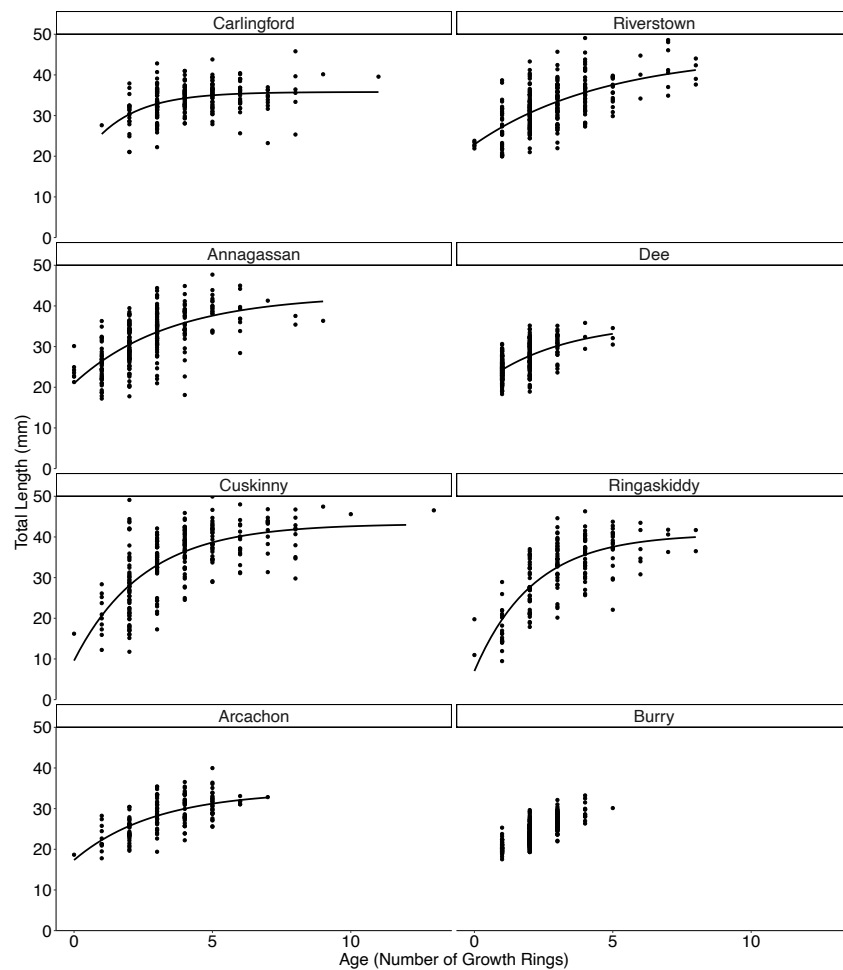
Models a, b and c were then compared to the most complex model using a likelihood ratio test. There was evidence that models b ($p>0.05$) and c ($p>0.05$) fit the data as well as the most complex model. Of the tested models, the log-likelihood value of model c was the lowest (-4.62) and therefore was used for further model reduction.

Finally, two further models were fitted as follows, comparing models with just the parameters K and t_0 , with model c:

$$d) E[L|t] = L_{\infty}(1 - e^{-K[\text{site}](t-t_0)})$$

$$e) E[L|t] = L_{\infty}(1 - e^{-K(t-t_0[\text{site}])})$$

Neither model d nor e ($p < 0.001$ for each) fit as well as model c, therefore model c was deemed to most suitable model and further model reduction was not necessary.



S7 Figure. Estimated von Bertalanffy growth curves for five Irish beds, one Welsh bed and one French bed. Underlying length and weight data for each bed are presented by points. A curve could not be fitted for the Burry in Wales due to a lack of older cockles.

S8 Table. Result of Dunn tests (p values) with Bonferroni correction to determine if median primary productivity differed between sites. Results are significant where $p=0.025$.

	Annagassan	Arcachon	Burry	Carlingford	Riverstown	Cuskinny	Dee
Arcachon	0.028	-	-	-	-	-	-
Burry	0.1172	<0.001	-	-	-	-	-
Carlingford	0.012	0.999	<0.001	-	-	-	-
Riverstown	0.999	0.579	0.003	0.316	-	-	-
Cuskinny	0.999	0.097	0.035	0.046	0.999	-	-
Dee	0.207	<0.001	0.999	<0.001	0.007	0.067	-
Ringaskiddy	0.999	0.081	0.042	0.038	0.999	0.999	0.079

S9 Table. Result of Dunn tests (p values) with Bonferroni correction to determine if median salinity differed between sites. Results are significant where $p=0.025$.

	Annagassan	Arcachon	Burry	Carlingford	Riverstown	Cuskinny	Dee
Arcachon	0.008	-	-	-	-	-	-
Burry	0.110	<0.001	-	-	-	-	-
Carlingford	0.999	<0.001	0.999	-	-	-	-
Riverstown	0.999	0.082	0.106	0.999	-	-	-
Cuskinny	<0.001	0.999	<0.001	<0.001	<0.001	-	-
Dee	0.320	<0.001	0.999	0.9999	0.308	<0.001	-
Ringaskiddy	0.001	0.999	<0.001	<0.001	0.001	0.999	<0.001

S10 Table. Result of Dunn tests (p values) with Bonferroni correction to determine if median sea temperature differed between sites. Results are significant where $p=0.025$.

	Annagassan	Arcachon	Burry	Carlingford	Riverstown	Cuskinny	Dee
Arcachon	0.037	-	-	-	-	-	-
Burry	0.999	0.611	-	-	-	-	-
Carlingford	0.999	0.004	0.999	-	-	-	-
Riverstown	0.999	0.020	0.999	0.999	-	-	-
Cuskinny	0.999	0.075	0.999	0.999	0.999	-	-
Dee	0.999	0.520	0.999	0.9999	0.999	0.999	-
Ringaskiddy	0.999	0.054	0.999	0.999	0.999	0.999	0.999

