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Deliverable 4.2

Field survey of cockle distribution, abundance & population dynamics currently

Lead Partner for Output	University College Cork (UCC)
Contributors	Kate Mahony, Sian Egerton, Sharon Lynch, Sarah Culloty (UCC); Emily Groves, Shelagh Malham (BU); Anouk Goedknegt, Hugues Blanchet, Xavier de Montaudouin (UBX); Francis Orvain (UNCAEN) Paulo Vasconcelos, André N. Carvalho, Fábio Pereira, David Piló, Paula Moura, Miguel Gaspar (IPMA); Sara Cabral, Paula Chainho (MARE), Antonio Villalba, David Iglesias (CIMA), Simão Correia, Rosa Freitas (UA), Mónica Incera, Elena Couñago (CETMAR)
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Contents

1. EXECUTIVE SUMMARY

The edible cockle, *Cerastoderma edule,* is a keystone species found in coastal habitats throughout the Atlantic Area (AA) of Europe, and further afield. While cockles are tolerant of a broad range of environmental conditions, populations of this species also regularly experience boom and bust cycles. Reports of such cycles appear to be increasing in frequency and some research suggests that climate change and an increase in pathogens are important drivers. Although many *C. edule* populations are within Special Areas of Conservation (SACs), and thus receive a general protection while also being exploited in a sustainable way, there are no European-wide regulations for their exploitation, and capacity for site-specific management schemes are often lacking. With many cockle populations under threat in the AA it is conceivable that greater levels of management will be required to maintain future sustainable fisheries. Effective fisheries regulation and management is founded in scientific data. However, knowledge of cockle population characteristics and dynamics and their interaction with environmental drivers, to date, has been mostly derived from experiments and local-scale studies. This comprehensive baseline study aimed to build on these surveys, to understand the wide-scale impacts of environmental factors on cockle populations at both a local and regional scale as well as throughout the Western European AA. Such information is vital given the current trend of changing environmental parameters associated with climate change and anthropogenic activities.

The study comprised four investigations: **Investigation 1** assessed the global distribution of *C. edule*, creating maps using data from previously published literature combined with new data collected by COCKLES partners (BU, CIMA, IPMA, MARE, UBX, UCC) from AA locations in five countries (Wales, Spain, Portugal, France and Ireland) between 2018 and 2020; **Investigation 2** recorded cockle density at 16 bays, estuaries and lagoons across Europe (Ireland (2), Wales (2), France (5), Spain (2), Portugal (5)); **Investigation 3** examined population structure (cockle size and age) with data collected from 14 cockle beds (Ireland (5), Wales (2), France (1), Spain (2) and Portugal (4)). Length frequency was also, separately, calculated for the Ria Formosa, Portugal, for this investigation; **Investigation 4** focussed on cockle growth, analysing data from all beds in **Investigation 3**, based on shell growth rings. Data on environmental parameters (seawater temperature, salinity and primary productivity) for the AA were downloaded from Copernicus (https://resources.marine.copernicus.eu) and used to investigate the impact of environmental factors on cockle populations. Statistical and data analyses were completed using R software to compare density and population dynamics across AA sites and investigate relationships or correlations with local environmental parameters.

The key findings of **Deliverable 4.2** are illustrated in **Figure 1** and are summarised as follows:

- In general, the distribution maps produced in this study show that *C. edule* exhibits an extensive range (at least 15°N to 71°N). This observation highlights AA *C. edule* population resilience considering the many challenges (abiotic, biotic, anthropogenic, meteorological etc.) that the species and European populations have had to overcome and currently experience. Optimal management strategies in the future will support sustainable harvests and abundance levels (**Investigation 1**).
- The densest populations are located in Wales and northern France. Similar high densities in these regions were also noted in COCKLES **Deliverable 4.1** – 'Baseline historical survey of common cockle (*Cerastoderma edule*) populations in the Atlantic area', throughout the 1990s to 2010s. However, density did not always remain consistent temporally, for example *C. edule* densities recorded at Galicia, Spain, were much higher in the 1980s and 2000's compared to the current survey. The pathogen *Marteilia cochillia* (disease agent of marteliosis) first detected in Galicia in 2012 is considered to be the main driver of cockle population dynamics in those beds affected by the disease. Similarly, density at Arcachon has decreased, likely due to climate (positive North Atlantic Oscillation leading to cooler, drier conditions), disease (trematodes and neoplasia) and predation (birds). The population dynamics of cockles experiencing biological stressors such as high levels of known and emerging parasites and pathogens can change, and these drivers can have compounding effects (e.g. low salinity and high parasite prevalence). These results support previous studies, which have also indicated that climate change and an increase in pathogens are driving declines in certain cockle populations. However, work is underway to support cockle populations through selective breeding against marteliosis (COCKLES **Deliverable 7 – '**Procedures for developing cockle culture, supporting genetic breeding programs for resistance to marteliosis'; **Investigation 2**).
- Variability between AA cockle populations in terms of population structures, growth rates and densities, as well as temperature, salinity and food availability was observed in this study. Environmental parameters (salinity, sea temperature and primary productivity) varied significantly between AA sites, confirming that *C. edule* populations adapt and proliferate in coastal environments that experience a wide range of conditions, both locally and globally. For example, at the sites investigated in this report, mean temperature ranged from 10.8°C to

15.6°C, and mean salinity ranged from 20.5 to 35.6. The physiological ability of *C. edule* to tolerate and adapt to a broad range of environmental parameters i.e. be eurytopic, including daily fluctuating conditions commonly experienced at near shore coastal habitats, may be advantageous to the future of AA populations as environmental conditions move further from the optimum (**Investigations 2 and 3**).

- Significant variation in the length, wet weight and age of cockles at different sites was also observed. Average length and weight tended to decrease towards southern latitudes. However, no latitudinal relationship was noted in the age profile of cockle populations. These results align with those from COCKLES **Deliverable 4.3** (Cockle reproductive health) and suggest that increased energy may go towards reproduction rather than growth at low (southern) latitude populations. Such findings highlight the importance of regional or even site-specific knowledge to guide appropriate management, for example taking into account the size/age profile of reproducing individuals to ensure sufficient broodstock remain at a site to better secure the future fecundity and self-recruitment of cockle populations (**Investigation 3**).
- Primary productivity was not a major influencer of cockle growth, as was expected, with cockles at the most productive sites in Wales not achieving large sizes. Instead, it is more likely that high density is driving smaller sizes (**Investigation 4**).
- Correlations detected in this study indicate that *C. edule* experiencing environmental stressors such as low salinity levels may be slower growing. Heavy precipitation events increase freshwater loading and flooding in bays and estuaries, resulting in a reduction in salinity. This will have implications for cockle populations, as an increasing trend in the frequency and intensity of precipitation events has been observed and is expected to continue under future projections (**Investigation 4**).

The findings of this study are valuable due to the large scale they cover, especially considering cockles are rarely studied beyond a national scale. The results highlight that local factors influence cockle populations more so than geographic trends. However, environmental factors clearly exert an effect on population dynamics and future climate scenarios (potential for temperatures to increase at higher latitudes) may see northern cockle populations following similar trends to those at southern sites. The data provided can be used by a wide range of stakeholder groups, particularly fisheries management. Data presented here can inform suitable site-specific capture sizes and local total allowable catch (TAC) levels. It also highlights important environmental drivers, which should be monitored alongside yearly fine-scale surveys of cockle populations. Finally, this study emphasises the need for future surveys to follow a European-wide standard protocol and to have systems in place for open access data sharing to facilitate communication, knowledge sharing and regional comparisons for a holistic overview of European cockle population dynamics and best management practices. Such a knowledge sharing platform would facilitate engagement and interaction between key stakeholders. This exchange of information would be beneficial in instances for example where stakeholders at certain sites are tackling particular issues that have been overcome by other fisheries/sites elsewhere. Such advances will significantly benefit cockle protection and sustainable exploitation into the future.

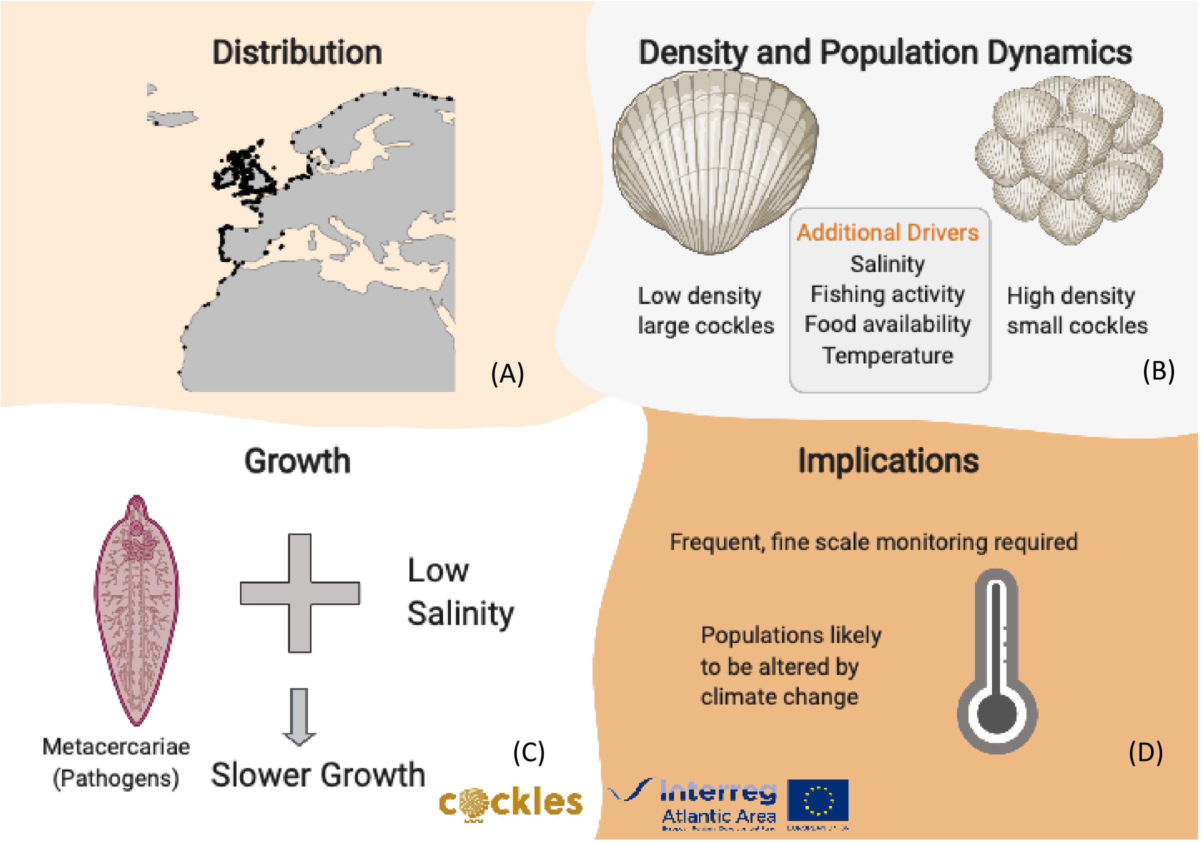


Figure 1. Graphical summary of the key findings of abundance and population dynamics at all sites studied for this report (COCKLES **Deliverable 4.2**). Global distribution of *Cerastoderma edule* based on data from **Investigation 1** and **Deliverable 4.1 (A)**. A negative correlation between cockle density and size and other drivers influencing these parameters **(B)**. Trematode prevalence and salinity levels significantly influenced cockle growth **(C)**. Temporal and geographical changes in cockle populations highlighted the need for more frequent and fine scale monitoring **(D)**.

2. INTRODUCTION

The common cockle (*Cerastoderma edule*, Cardiidae) is an important ecosystem engineer, which influences surrounding sediment (bioturbation and stabilization) and local hydrodynamics (reducing current velocity near cockle beds; Ciutat et al., 2007) along the Atlantic coasts of Europe and northwest Africa (Hayward and Ryland, 1995). They are considered a keystone species because they are important prey items for many birds, fish, crustaceans and echinoderms (Magalhães et al., 2016), they modify and maintain habitat for other species (Philippart et al., 2007) and are foundation species, providing settlement substrate for other sessile invertebrates (Yakovis and Artemieva, 2017). Their status has been recognised across Europe in the designation of numerous Special Areas of Conservation (SACs) in areas that incorporate mud and sandflats which C. *edule* populations inhabit (McLaughlin et al., 2007). This conservation status provided to them under the EU Habitat's Directive (European Council Directive 92/43/EEC, 1992) allows for fishing if the favourable conservation status of the SAC is not threatened. Indeed, cockles are an important species commercially, with the potential to provide €11.3M a year to European coastal communities from the sale of their meat and by-products (Carss et al., 2020). However, current management strategies of cockle fisheries have recently gained attention in light of the increasingly frequent boom and bust cycles impacting the species (Morgan et al., 2013; Burdon et al., 2014). Research is still fully deducing the drivers of these changes but there has been some evidence to suggest climate change (e.g. extreme temperatures, increased precipitation, variability in water quality) and parasitism (Burdon et al., 2014) are playing important roles. This variability in cockle production is a major threat to the many European coastal communities relying on cockles for their economy, as well as culture, biodiversity and ecosystem health (Carss et al., 2020).

Cerastoderma edule population dynamics vary considerably, affected by local abiotic and biotic factors. In some locations they can reach 50 mm in length (Hayward and Ryland, 1995) but their final size is influenced by immersion time (de Montaudouin, 1996; Wegeberg and Jensen, 2003) and local salinity levels (Domínguez et al., 2020). It has been shown that growth in cockles is reduced as a result of metal contamination (copper, lead, nickel, iron, cadmium and zinc in England; Savari et al., 1991), and potentially by acidification and temperature increases, which cause additional demands on energy allocation, as reported in a Dutch meiobenthic community study which included *C. edule* (Mevenkamp et al., 2018). It is therefore important to consider the effects that future scenarios may have on cockle populations, including aspects of the environment that are changing as a result of anthropogenic influence (e.g. pollution, eutrophication, habitat degradation, manipulation of food webs via exploitation).

Biotic factors, including drivers such as density (intraspecific competition), predation (birds, crabs, fish, echinoderms; de Fouw et al., 2020), parasites (de Montaudouin et al., 2012) and food availability (Beukema and Dekker, 2015; Iglesias and Navarro, 1990; Wijsman and Smaal, 2011), also impact cockle population dynamics (e.g. size classes) and growth. Digenean trematodes are a dominant macroparasite taxa in cockles, infecting as both primary (sporocysts) and secondary (metacercariae) intermediate hosts (de Montaudouin et al., 2009). These parasites can have negative impacts on cockle health (Longshaw and Malham, 2013), particularly when coupled with environmental factors (Gam et al., 2009), potentially impacting scope for growth (see COCKLES **Deliverable 4.3 Report**). Cockle growth can also be limited at high densities, due to inter- and intraspecific competition (Beukema and Dekker, 2015; de Fouw et al., 2020; Masski and Guillou, 1999).

All European Atlantic Area (AA) countries permit hand gathering of cockles, while in some, various forms of dredging are also permitted (see COCKLES **Deliverable 4.1 Report**). The main European cockle fisheries occur in the British Isles and France, using bottom trawls and dredges (FAO, 2020). Cockle fishery management schemes vary considerably across regions. There is urgent need to review management strategies to help improve the sustainability of cockle fisheries. Typically, they set minimum capture sizes, however; it has been noted that growth rates of cockles vary both spatially and temporally and can differ even within a single site due to variations in abiotic factors (Mahony et al., *in review*). Thus, while regional standardisation should be sought, broad-scale regulations should be considered with caution and local cockle population dynamics and health should be monitored and used to guide appropriate management.

COCKLES **Deliverable 4.2** aims to investigate the current status of cockle distribution, abundance and population dynamics, across the AA. Differences in these characteristics were examined across sites that varied in terms of exploitation, as well as environmental characteristics (salinity, temperature, primary productivity). As part of this deliverable, four investigations were undertaken with stakeholder contribution, examining 1.) cockle distribution, 2.) abundance, 3.) population structure, and 4.) growth. For cockle distribution, data from current Investigations outlined below were combined with data from COCKLES **Deliverable 4.1** to provide a comprehensive global distribution of *C. edule* populations. Data from recent surveys were used to compare von Bertalanffy growth parameters (i.e. a modelling method to determine mean length at a particular age), length frequencies and age distributions, as well as to create a series of maps detailing cockle distribution and current cockle densities. The von Bertalanffy growth function has been successfully employed in many other cockle studies (e.g. Cardoso, 2007; Ponsero et al., 2009; Gam et al. 2010), and was therefore deemed appropriate for use in this study.

The results of this study build on current knowledge of the influence of environmental drivers on cockle population characteristics and dynamics, derived from previous experiments and local-scale studies (e.g. low salinity; Domínguez et al., 2020, and parasites; Villalba et al., 2014). While previous studies generally only focussed on specific bays and estuaries, this study will demonstrate the wide-scale impacts of environmental factors on cockle populations. It is vital to understand these impacts at a larger scale given the current trend of changing environmental parameters associated with climate change, among other factors. The findings of this deliverable will be valuable to a wide range of stakeholder groups, particularly for fisheries managers and regulation authorities. By comparing this current data with the historic results of COCKLES **Deliverable 4.1**, it will be possible to assess trends and drivers of fluctuations in cockle populations, further helping to inform management of suitable site-specific actions required and providing data with which predictions about future cockle populations and fisheries can be based.

3. MATERIALS AND METHODS

Distribution, density, size and age, and growth of *C. edule* cockle populations in the AA were investigated. For the distribution analysis, data from previously published literature was combined with new data collected from the locations in this survey between 2018 and 2020 (**Investigation 1**). Subsequently, cockle density (**Investigation 2**) was examined at 16 ecosystems across Europe (Ireland (2), Wales (2), France (5), Spain (2), Portugal (5)). To examine population structure (morphometrics; **Investigation 3**), data was collected from 14 cockle beds (Ireland (5), Wales (2), France (1), Spain (2) and Portugal (4)). Additionally, for this investigation, length frequency was calculated, separately, for the Ria Formosa, Portugal. Finally, for **Investigation 4** (cockle growth), all beds from **Investigation 3**, which recorded growth rings, were included.

3.1 Investigation 1: Distribution of *Cerastoderma edule*

A map was created using ArcGIS 10.4 (Esri, 2015) detailing the current distribution of *Cerastoderma edule*. Data obtained from COCKLES **Deliverable 4.1** (Baseline historical survey of common cockle (*Cerastoderma edule*) populations in the Atlantic Area) detailing the distribution of cockles were included in the map. Additional records from published literature, published between 2018 and 2020, were also included in this mapping exercise. Finally, new distribution data was collected in this study, from various AA locations (Ireland, Wales, France, Spain and Portugal), to augment the dataset. In total, an additional 73 records were included in the distribution dataset, compared to those gathered from COCKLES **Deliverable 4.1**. Distribution data used, collected from all sources, spanned the years 1893 to 2020.

3.2 Investigation 2: Cockle abundance (UBX, IPMA, MARE, CIMA, UNCAEN)

The main purpose of Investigation 2 was to create an overview of current cockle densities across the AA. Multiple density measurement schemes were conducted, which varied in methodology. In a wide-scale Investigation led by University of Bordeaux (UBx), density data (number of cockles per square metre) were gathered from a total of 11 ecosystems across the AA. Two sites were analysed within each ecosystem (**Table 1**). These ecosystems were included in the sampling strategy of **COCKLES Deliverable 6.4** (Modelling of carrying capacities, trophic cascades, and population growth). The two sites represented high and low cockle density sites, which were selected based on the knowledge of technical assistants from fishing associations and local partners in the **COCKLES project**. Sampling was conducted between October 2018 and May 2019. At each site the density was estimated using 10 x 0.25 m^2 quadrats (**Figure 2A**).

Table 1. Ecosystems analysed for density estimates of *Cerastoderma edule* across the AA, arranged in decreasing latitudinal coordinates. Data obtained from UBx relate to **COCKLES Deliverable 6.4**. Multiple sites per ecosystem were examined. In the case of the UBx surveys, two sites were sampled per ecosystem: one with relatively high cockle density and one with low cockle density except for Bay of Somme, Cork Harbour and Ria de Arousa.

Country	Ecosystem	Dates	Coordinates	Study Leader
Wales	Dee Estuary	February 2019	53°20'N 3°10'''W	UBx
Ireland	Cork Harbour	February 2019	51°51'N 8°15'W	UBx
Ireland	Dundalk Bay	July 2019	53°56'N 6°19'W	UCC (MI & BIM)
Wales	Burry Inlet	February 2019	51°40'N 4°12'W	UBx
France	Bay of Somme	Apr 2019	50°14'N 1°33'W	UBx
France	Seine Estuary	2017-2018	49°28'N 0°04'W	UnCaen
France	Baie des Veys	2017	49°21'N 1°07'W	UnCaen
France	Roscoff Bay	May 2019	48°43'N 3°59'W	UBx
France	Arcachon Bay	Nov 2018	44°39'N 1°08'W	UBx
Spain	Baiona Inlet	Jan 2019	42°07'N 8°49'W	UBx
Spain	Ria de Arousa	Apr & Sep 2017 -2019	42°30'N, 8°50'W	CIMA
Portugal	Óbidos Lagoon	Jul 2019	39°24'N 9°12'W	MARE
Portugal	Tagus Estuary	Apr 2018 & May 2019	38°49'N 9°03'W	MARE
Portugal	Sado Estuary	May 2018	38°24'N 8°37'W	MARE
Portugal	Ria de Aveiro	Jan 2019	40°38'N 8°44'W	UBx
Portugal	Tagus Estuary	Jan 2019	38°38'N 9°06'W	UBx
Portugal	Sado Estuary	Jan 2019	38°27'N 8°43'W	UBx
Portugal	Ria Formosa	Jan 2019	37°01'N 7°48'W	UBx
Portugal	Ria Formosa	Jan 2018, Nov, Dec 2019	37°01'N 7°48'W	IPMA

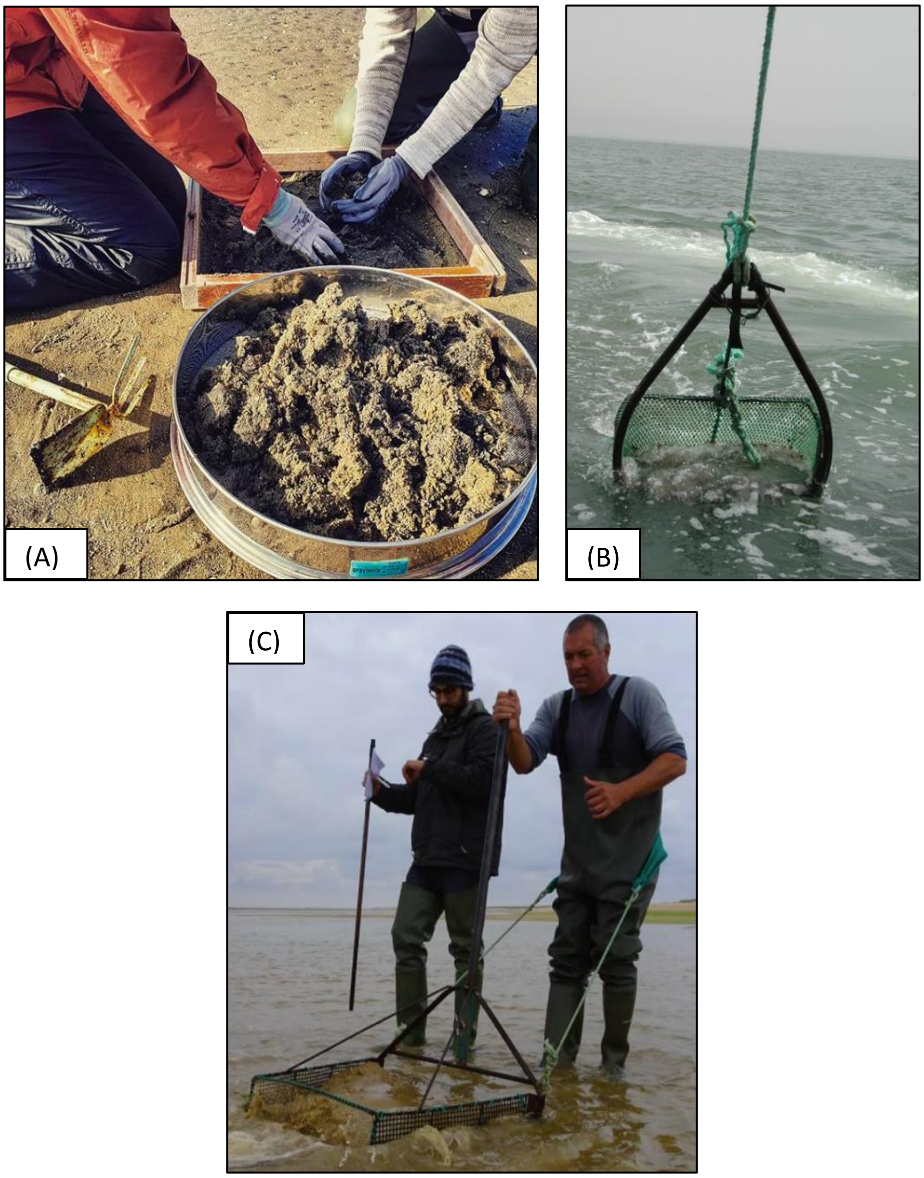


Figure 2. Cockle density being estimated using a 0.5 m^2 quadrat at Ria de Aveiro. This was repeated 10 times at each site per sampling occasion (**A**). Clam dredge used at the Tagus and Sado estuaries and Óbidos lagoon to collect cockles. The dredge was towed once for 30 seconds at a mean speed of 1.5 knots in every sampling station, on board of a professional fishing vessel (**B**). Hand dredge used to estimate cockle density at Olhão (21/11/2018), Faro (11/12/2018) and Fuseta (29/01/2018) in Ria Formosa. Dredges were performed in triplicate, with three 30 second tows conducted at each bed **(C)**.

Additionally, University College Cork (UCC) obtained data from Dundalk from an external dataset (The Marine Institute (MI) and Bord Iascaigh Mhara (BIM), 2019), and the average density was calculated from records collected within a 1 km radius of the beds studied in **Investigation 1** (Annagassan and Cooley). Cockle density was also gathered by University of Caen (UnCaen) team for two sites in Normandie, Baie des Veys and the Seine Estuary (**Table 1**).

In Sarrido, Ria de Arousa, Galicia, Spain density data was gathered through a program to analyse the population dynamics of the exploited shellfish species. This program was performed, uninterrupted, since 2005 (with the exception of April 2006, April 2013 and April 2019) and involves regular sampling at 50 stations, where two samples are taken using a dredge (0.10 m^2 sampling surface), operated by hand during low tides, when the bed is covered by only several centimetres of water. Two sampling campaigns are performed each year (one in April –to evaluate the reproductive stock coinciding with the onset of the spawning season, and another in September –accounting for recruitment that has been incorporated to the population) to estimate density, abundance and spatial distribution of the main bivalve commercial species, including cockles, *C. edule*. All live cockles retained in the net (5 mm mesh) used to sieve the collected materials were carried to the lab to be counted and measured. The estimation of density was performed with standard statistics using the software tool ARouSA (https://sites.google.com/site/arousa09/). The data collection was completed with the technical assistance of Cambados Confraría and is used to assist shellfishery management.

Aside from the data collected by UBx, further density estimates were conducted in Portugal by MARE. At Tagus Estuary (38°49'N 9°03'W), Sado Estuary (38°24'N 8°37'W) and Óbidos Lagoon (39°24'N 9°12'W) density was gathered by towing a clam dredge (**Figure 2B**; **Table 2**) once in every sampling station, for 30 seconds at a mean speed of 1.5 knots, on board of a professional fishing vessel. The dredged area of the towed transect was determined by multiplying the dredge width by the transect recorded with a GPS and the density was represented as individuals/m^2. Due to the size-selectivity of the fishing gear (targeting invertebrate organisms > 2 cm), sampling may be biased towards larger cockles. At the Tagus Estuary, density was measured in both April 2018 and May 2019. At the Sado Estuary, density was measured in May 2018. Finally, at Óbidos Lagoon, density was measured in July 2019.

Additional density data was obtained by IPMA from three of the most important harvesting areas in the Ria Formosa, Portugal (Olhão (21/11/2018), Faro (11/12/2018) and Fuseta (29/01/2018)). Within these areas, several beds were examined (**Table 3**). Density estimates were conducted by a professional harvester using a hand dredge, which consisted of a metallic sorting grid and collection net (**Figure 2C**). The mouth of the dredge measured 75 cm and the net mesh was approximately 12 mm. Dredges were conducted in triplicate, with three 30 second tows conducted at each bed. The dredged area was calculated as the dredge mouth width multiplied by the dredge path length. Density was presented as kg/m^2, which corresponds to the catch per unit effort (CPUE) in weight, standardised for an area of 1m^2. Due to the size-selectivity of the fishing gear, sampling was biased towards larger cockles.

Table 2. The major characteristics of the clam dredge used by MARE to collect density data at Tagus Estuary, Sado Estuary and Óbidos Lagoon, Portugal, in 2018 and 2019.

Gear specifications	Dimensions (cm)
Shaft	
Diameter	80.0
Width	60.0
Height	30.0
Tooth bar	
Number of teeth	13.0
Tooth spacing	1.5
Tooth thickness	1.0
Tooth length	12.0
Net bag	
Length	230.0
Width	70.0
Mesh size	3.0

Table 3. Beds surveyed by IPMA within different areas of the Ria Formosa, for calculation of cockle density.

Area	Bed	Date sampled	Coordinates
Olhão	Cabeço do Zé Bruto	21/11/2018	36°59'N, 7°50'W
	Cabeço do Berbigão		36°59'N, 7°51'W
	Areais		37°00'N, 7°50'W
	Fortaleza		37°00'N, 7°49'W
Faro	Esteiro do Ramalhete	11/12/2018	37°00'N,7°58'W
	Cabeço do Arnaldo		36°59'N, 7°58'W
	Ilhote das Cobras		36°59'N, 7°57'W
Fuseta	Cidade sem Lei (sul)	29/01/2018	37°03'N, 7°43'W
	Cidade sem Lei (norte)		37°03'N, 7°43'W

3.3 Investigation 3: Population dynamics: cockle population structure

3.3.1 Morphometrics

In total, population structure (cockles' size and age) were studied at 12 sites in the AA (**Table 4**). The general aim was to collect at least 30 cockles per site per sampling occasion. However, variations in sampling regimes occurred due to differences between monitoring schemes in regions (**Table 4**), resulting in up to 2,843 individuals recorded in a single month at the Tagus Estuary (Portugal). At Dundalk (Ireland) and Noia (Spain) only, a distinction was made between surfaced and buried cockles. Cockles at Sarrido were collected within the scope of **COCKLES Deliverable 5.1** (Pathogens census along Atlantic Area), which were selected based on size (juvenile and adult) and burial (buried, surfaced), creating bias in these data.

Growth rings (**Figure 3**) were counted as an estimation of age in Ireland, Wales and France. Age was not determined at the Spanish and Portuguese areas. Whole wet weight (g), using an electronic balance scale, and length (mm), width (mm) and height (mm), using a Vernier calliper, were also measured (**Figure 3**). Whole wet weight was not obtained at three of the Portuguese sites: Óbidos, Tagus or Sado, but it was measured at all other sites.

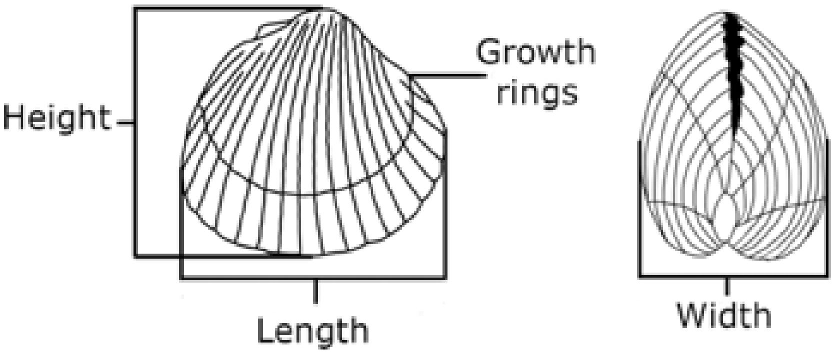


Figure 3. Measurements taken for cockle morphometrics and age.

Table 4. Description of the sites and beds examined for morphometrics (**Investigation 3**), across the Atlantic Area. MCS = Minimum capture size.

Area	Bed	Sampling frequency	Sampling duration	n	Coordinates	Fishery	MCS	Activities	Conservation designation
Carlingford	Oyster Farm	Bimonthly	April 2018-October 2019	229	54°01'N, 6°09'W	Occasional light hand-harvesting	17mm	Shipping, aquaculture, farming	SAC, SPA. Ramsar Site
Dundalk	Annagassan	Bimonthly	July 2018-October 2019	269	53°52'N, 6°20'W	Suction dredge	22mm	Razor clam fishery	SAC
	Cooley			269	54°00'N, 6°17'W				
Dee	-	Seasonal	July 2018-September 2019	360	53°20'N 3°10'W	Hand raking and sieving	20mm	Agriculture, industry	SPA, SAC
Burry	-	Seasonal	July 2018-September 2019	360	51°40'N 4°11'W	Hand raking and sieving	Variable	Agriculture, industry	SAC, SPA, Ramsar Site
Cork	Cuskinny	Bimonthly	April 2018-October 2019	240	51°51'N, 8°15'W	Unfished	17mm	Industry, shipping	SPA
	Ringaskiddy			167	51°49'N, 8°18'W				
Arcachon	Banc d'Arguin	Bimonthly	April 2018-June 2019	239	44°35'N, 1°13'W	Hand raking	27mm	Recreational boating	National Reserve
Ria de Muros e Noia	Noia	Monthly	February 2018-January 2020	910	42°47'N, 8°55'W	Hand operated hoes, rakes and dredges	28 mm	Shellfishery, mollusk aquaculture	SAC

Table 4 continued. Description of the sites and beds examined for morphometrics (**Investigation 3**), across the Atlantic Area. MCS = Minimum capture size. Only size classes were calculated for sites in italics and were only included in calculations of length frequency distributions.

Area	Bed	Sampling frequency	Sampling duration	n	Coordinates	Fishery	MCS	Activities	Conservation designation
Ria de Arousa	Sarrido	Once	February 2018	60	42°30'N, 8°50'W	Hand operated hoes and rakes	25 mm	Shellfishery, mollusk aquaculture, fishing, agriculture	SAC, SPA, RAMSAR site
Aveiro	Aveiro Lagoon	Bimonthly	April 2018-October 2019	300	40°38'N, 8°44'W	Hand rake	25 mm	Aquaculture, agriculture, fishing, industry	Marine Reserve, SPA
Óbidos	-	Once	July 2019	129	39°24'N, 9°13'W	Hand operated hoes, rakes, dredges, harvesting knife and freediving	25 mm	Agriculture, industry	CORINE Biotope
Tagus	-	Annual	April 2018-May 2019	4542	38°49'N, 9°01'W	Hand operated hoes, rakes, dredges, harvesting knife and freediving*	25 mm	Urban Centre, industry, fishing, agriculture	SPA, SCI, Natural Reserve, RAMSAR site
Sado	-	Annual	May 2018-May 2019	215	38°24'N, 8°37'W	Hand operated hoes, rakes, dredges, harvesting knife and freediving	25mm	Urban Centre, industry, fishing, aquaculture	SPA, SCI, Natural Reserve, RAMSAR site, CORINE biotope

*Illegal fishing also occurs via vessel dredging and scuba diving

3.3.2 Environmental parameters

Productivity (net primary production of carbon), salinity and seawater temperature were obtained from the Atlantic-Iberian Bay Irish-Ocean Physics Analysis and Forecast for the 12 sites in **Table 4** (Copernicus, 2020: https://resources.marine.copernicus.eu/documents/PUM/CMEMS-GLO-PUM-001-024.pdf). Due to the heterogenous nature of the data, Kruskal-Wallis tests followed by post-hoc Dunn Tests were employed to determine if median environmental variables (temperature, salinity, primary productivity) differed between sites.

3.3.3 Weight, length & length frequency distributions

Kruskal-Wallis tests were employed to determine if the length or weight of cockles differed among sites. Additionally, a Kruskal-Wallis test was used to determine whether length or weight differed depending on whether cockles were surfaced or buried. Length frequency distributions were composed from the 12 sites examined for morphometrics (**Table 4**) in addition to the sites at Formosa, which were examined for density and morphometrics (**Investigation 2, Table 3**).

3.4 Investigation 4: Population dynamics: cockle growth

Growth analysis was conducted at all sites from **Investigation 3** which collected data on growth rings. These were the sites located in Ireland, Wales and France only (**Table 4**).

3.4.1 von Bertalanffy growth models

Growth was examined using the von Bertalanffy growth model, which is represented by:

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

where L_t is the expected length at age t, L_∞ is the asymptotic average length (i.e. the maximum mean length reached) and k is the Brody growth rate coefficient, which refers to how quickly L_∞ is approached. Finally, t_0 is not biologically meaningful and is only necessary for model fitting (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). Nonlinear least squares models are used to estimate parameters of a nonlinear (i.e. curved) relationship (Crawley et al., 2015). Differences in growth models were then compared using the 'fishmethods' package (Nelson, 2019), in order to determine if L_∞, k or t_0 all differed between sites, or if a simpler model was more appropriate. A general model and four sub-models 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 sub-model - 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

$$\phi' = 2 \times \log10(L\infty) + \log10(k) \quad \text{(Pauly and Munro, 1984)}$$

This calculation was necessary because a negative correlation between L_∞ and k can invalidate bivalve models based on individual parameters (Pauly and Munro, 1984, Magalhães et al., 2016)

3.4.2 Growth relationships

Linear and polynomial regression were compared with Akaike's Information Criterion values to determine which model fitted the observed length and weight data best. These models were used to determine if cockle growth followed a linear relationship (increase in length correlates with an increase in age, **Figure 4A**) or a curved relationship (the relationship between length and age varies at different time points, **Figure 4B**).

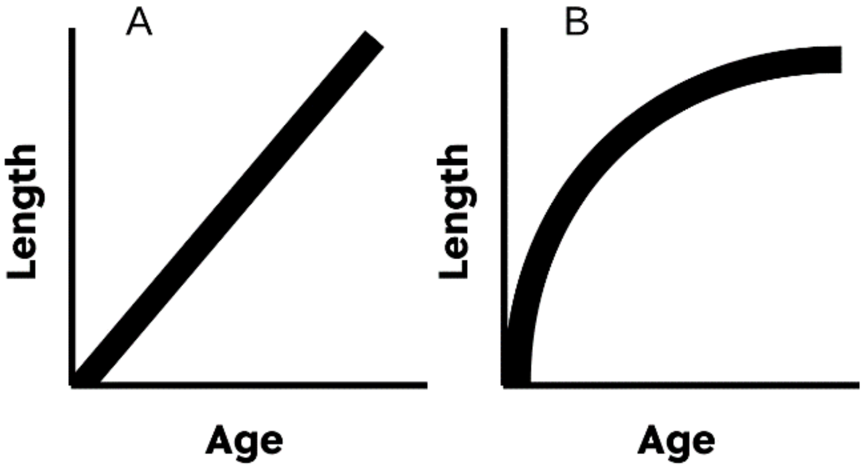


Figure 4. Theoretical linear **(A)** and curved **(B)** relationships between cockle length and age.

3.4.3 Relationship between biotic (environmental) and biotic parameters, and cockle growth

Mixed effects models were examined to determine the impact of spatially varying factors (primary productivity, sea temperature, salinity, trematodes (metacercariae and sporocysts), and density) on the cockle growth performance index (ϕ'). Data regarding trematode prevalence, attained by histology, was obtained from WP4.3 (**Appendix 1**). Two sub-models were first fitted to determine the most important environmental and biotic variables to be included, and those where $p < 0.2$ (Heinze and Dunkler 2017) were included in the final model. Environmental data included in this model were obtained from the Atlantic-Iberian Bay Irish-Ocean Physics Analysis and Forecast, from 2018 to 2019 (Copernicus, 2020). A separate sub-model was employed to examine the impact of cockle density on growth, due to the lack of availability of data from certain beds (Carlingford and Ringaskiddy, Ireland).

3.5. Analysis

All analyses were conducted in R (R Core Team, 2019). All maps were created using ArcGIS 10.4 (Esri, 2015).

3.6. Stakeholder Engagement

Local shellfish farmers, fishers and technical assistants of fisheries associations assisted with sample collection, as well as providing information regarding the sites being surveyed (**Table 5**).

Table 5. Details of stakeholder involvement in the Investigations of COCKLES **Deliverable 4.2**.

Research Institute	Investigation	Stakeholder	Contribution
UCC	3,4	Martin Hoey (Dundalk Cockle Fishery)	Assistance with sample collection, provision of site information
UCC	3,4	Brian McGill (Carlingford Oyster Company)	Assistance with sample collection, provision of site information
BU	3,4	Stuart Thomas, Timothy Ellis, Rhys Griffiths (Natural Resources Wales)	Collection of samples from Burry Inlet and Dee, provision of site information
IPMA	2,3	Ricardo Raimundo (Cooperativa Formosa - Cooperativa de Viveiristas da Ria Formosa)	Collection of samples
MARE	2,3	Miguel Letra (Sindicato Livre dos Pescadores), Carlos Silva (ICNF)	Assistance with sample collection, provision of site information
CETMAR	2	José Antonio Santiago Amoedo, technical assistant Confraría de Baiona	Assistance with sample collection, provision of site information
CIMA	2, 3	Dr Carlos Mariño Balsa, technical assistant Confraría de Cambados	Assistance with sample collection, provision of site information and density values derived from their own cockle stocks assessment

4. RESULTS

4.1. Investigation 1: Distribution of *Cerastoderma edule*

Cockle distribution from COCKLES **Deliverable 4.1** was combined with the locations of current cockle populations surveyed in this deliverable. In total, 8,191 records of *Cerastoderma edule* were obtained, ranging from 1893 to 2020. The northernmost records of cockles were in Russia (Genelt-Yanovskiy et al., 2010; Nazarova et al., 2015), and the southernmost was in Mauritania, Africa (Honkoop et al., 2008). Reports of *C. edule* were recorded on the Mediterranean coast of Spain, as well as the Balearic Islands (Nunn and Holmes, 2008; Carrasco et al., 2011). The western-most report of *C. edule* was from Iceland (Ingólfsson, 1999), with the most eastern record from western Russia (Genelt Yanovskiy et al., 2010; **Figure 5**).

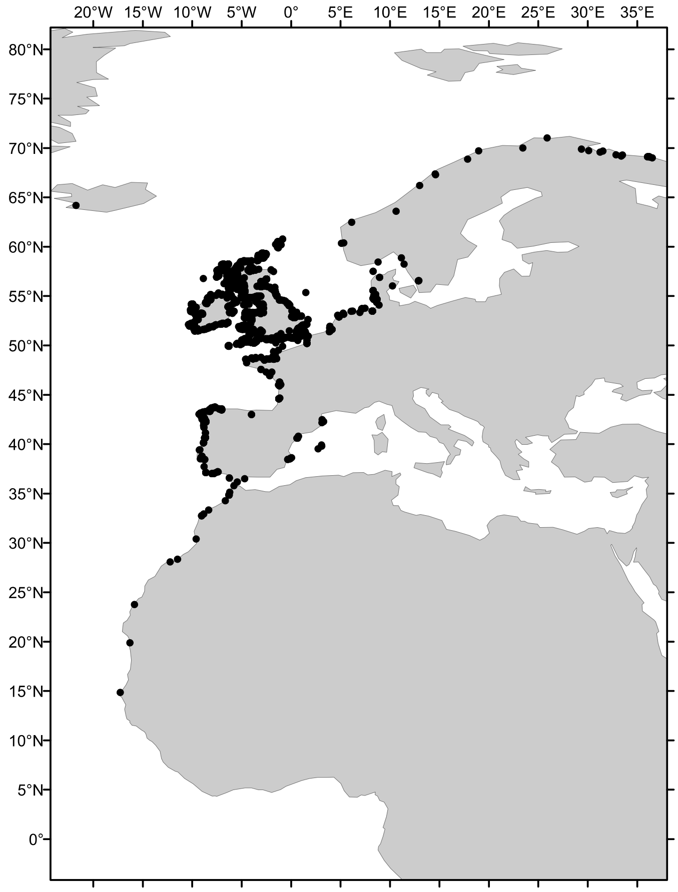


Figure 5. Distribution of *Cerastoderma edule* according to records from COCKLES **Deliverable 4.1, 4.2** and studies published in the interim between these reports (1893 to 2020).

4.2. Investigation 2: Cockle abundance

For the UBx density survey (COCKLES **Deliverable 6.4)**, cockle density was estimated for 11 ecosystems located in Ireland, Wales, France, Spain and Portugal. Large variations in density were evident at these beds, with low densities observed at one of the Roscoff sites (Roscoff Low, 2.8 individuals/ m^2). In contrast, density at the Burry (Burry 1) reached 3,525 individuals/ m^2. In the survey carried out by the UnCaen team, densities also varied significantly in northern France - from 1126.07 individuals/ m^2 in the Baie des Veys in 2017 to lower numbers in the Seine Estuary (247.27 individuals/ m^2 in 2017 and 234.92 individuals/ m^2 in 2018; **Figure** 6). These variations in density were apparent on a macro-scale (i.e. across ecosystems, **Figure 6**) as well as at a micro-scale (within ecosystems, **Figure 7**). For example, at the Burry Inlet, cockles at two nearby sites ranged from 3,525 to 338 individuals/ m^2. Similar findings were observed from the externally gathered Dundalk data (The Marine Institute and Bord Iascaigh Mhara, 2019), ranging from 31 individuals/ m^2 at Cooley to 94 individuals/ m^2 at Annagassan. However, differences observed must be considered with caution because sampling date and local fishing regimes varied significantly between sites. Not all ecosystems demonstrated large differences between sites, particularly where density was low all-round, e.g. mean density at the two sites at Roscoff ranged from 3 to 13 individuals/ m^2. Cockle density, when measured with the hand dredge, within the Ria Formosa was patchy. It ranged from 0.03 kg/ m^2 at Cidade sem lei (norte, Fuseta) to 3.3 kg/ m^2 at Cabeço do Zé Bruto (Olhão; **Table 6**).

Stock assessments performed in Sarrido, Ria de Arousa, Galicia, showed quite large variations in cockle densities (range: 35-359 individuals/ m^2) between years and between sampling seasons within the same year (**Figure 8**). Sarrido is heavily affected by the protistan parasite *Marteilia cochillia*, responsible for the disease called marteiliosis. Heavy mortalities associated to disease outbreaks detected in winter months caused high reductions in cockle density from September 2017 to April 2018 and from September 2018 to September 2019 (**Figure 8**).

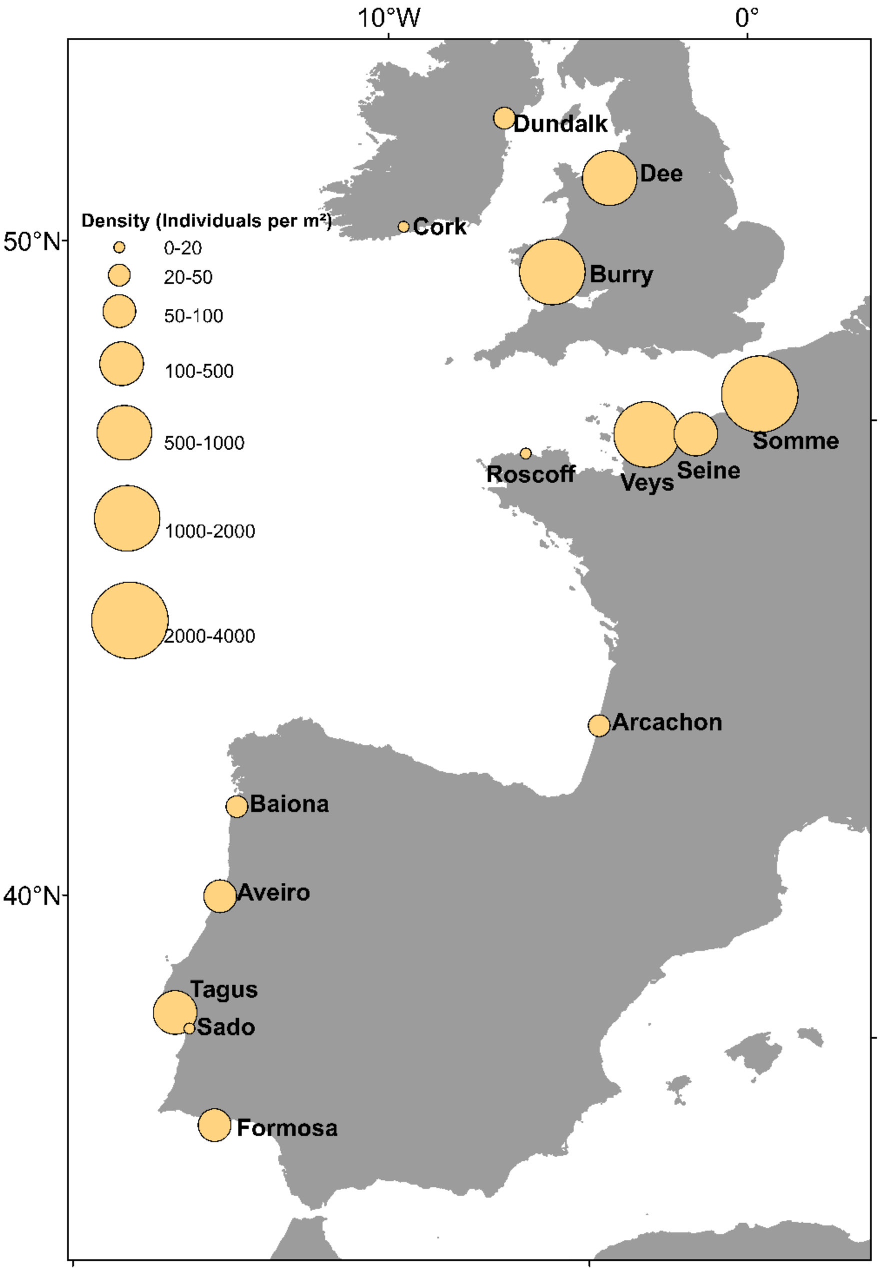


Figure 6. Average density at each of the 11 ecosystems sampled by UBx, and externally gathered data from Dundalk Bay (The Marine Institute and Bord Iascaigh Mhara, 2018) studied between 2018 and 2020. Density data for Baie des Veys (2017) and the Seine Estuary (Average of 2017 and 2018) were gathered by UnCaen. Note that Dundalk and UnCaen measurements were obtained using different methodology to the UBx survey.

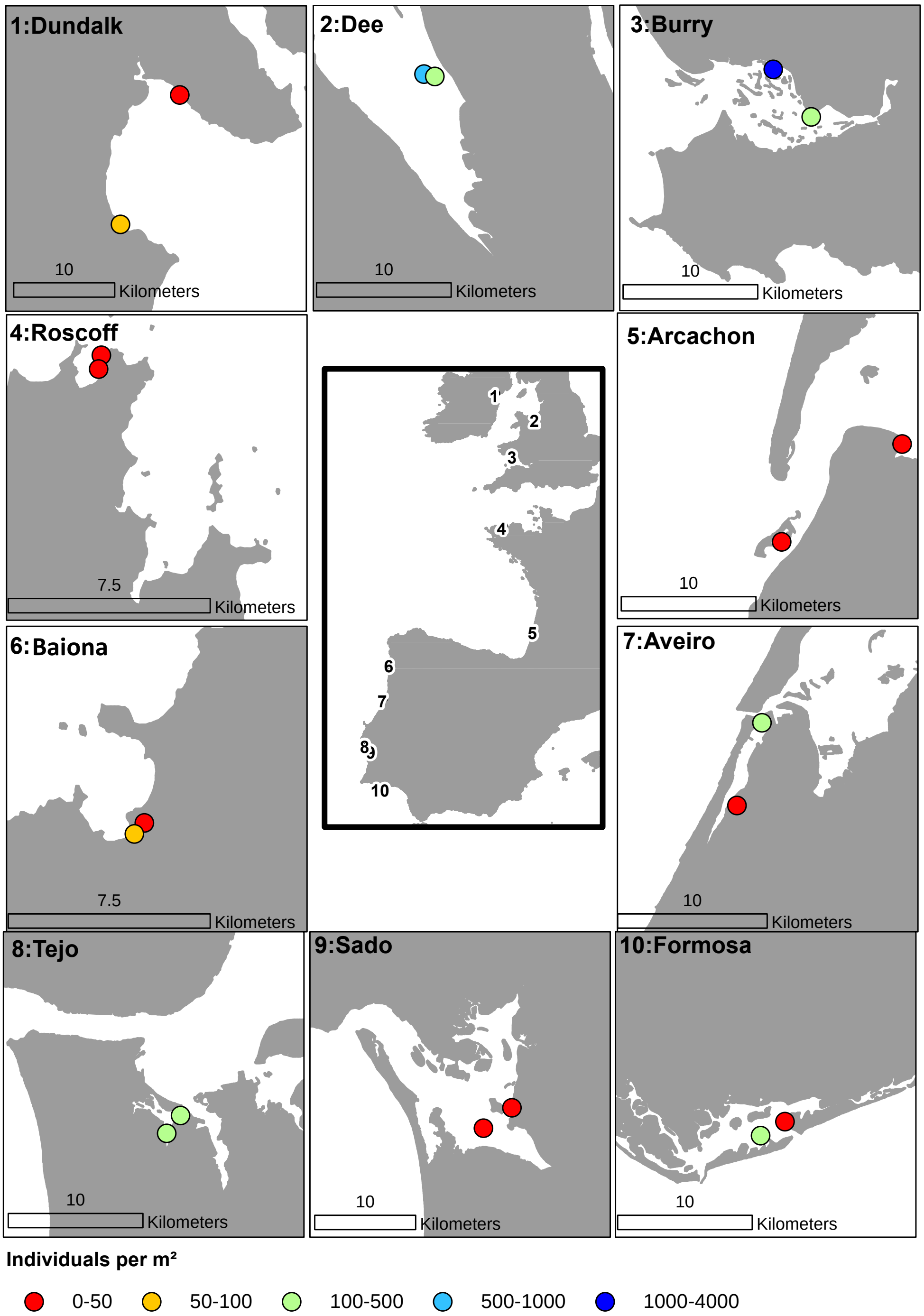


Figure 7. Density (Individuals/ m^2) measured at 18 sites in 9 AA ecosystems by UBx, and externally gathered data from Dundalk Bay (The Marine Institute and Bord Iascaigh Mhara, 2019) between 2018 and 2019. Note: ecosystems were excluded from this map if only one site was measured.

Table 6. Cockle densities measured in the Ria Formosa in 2018.

Area	Bed	Density (kg/ m²)
Olhão	Cabeço do Zé Bruto	3.3
	Cabeço do Berbigão	0.7
	Areais	0.8
	Fortaleza	1.0
Faro	Esteiro do Ramalhete	0.1
	Cabeço do Arnaldo	1.1
	Ilhote das Cobras	1.5
Fuseta	Cidade sem Lei (sul)	0.04
	Cidade sem Lei (norte)	0.03

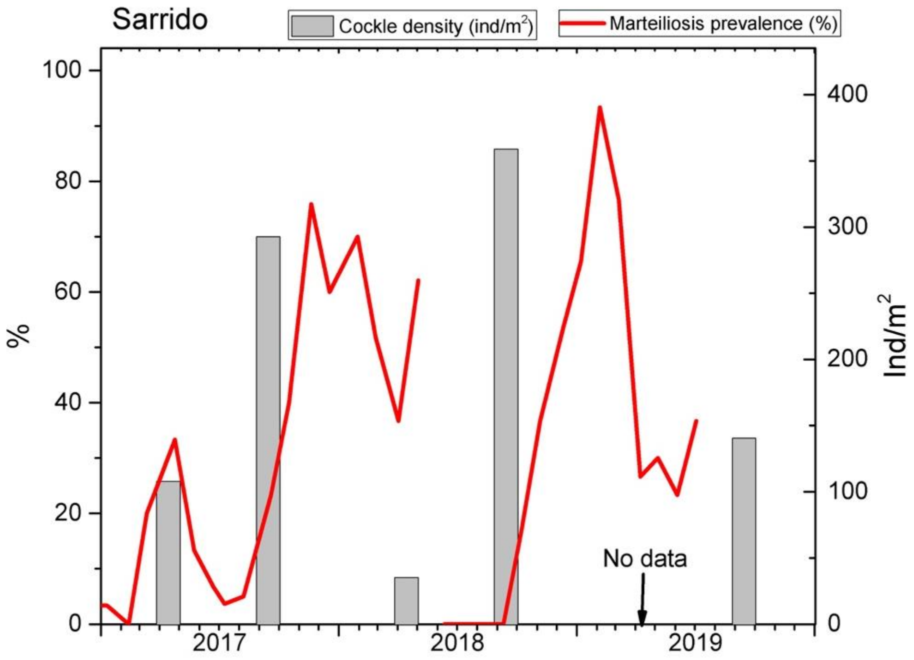


Figure 8. Cockle density (Individuals/ m^2) and prevalence of *Marteilia cochillia* infections at Sarrido, Galicia between 2017 and 2019.

In addition to the Portuguese data gathered by UBx and IPMA, detailed surveys were carried out by MARE. Density was most heterogenous at the Tagus Estuary, ranging from 0.06 to 58.55 individuals/ m^2 (**Figure 9**). Average density at the Sado Estuary was 0.64 individuals/ m^2, the lowest average density observed by any partner institute. Average density at the Óbidos Lagoon and the Tagus Estuary were both relatively low, 1.35 and 7.12 individuals/ m^2 respectively.

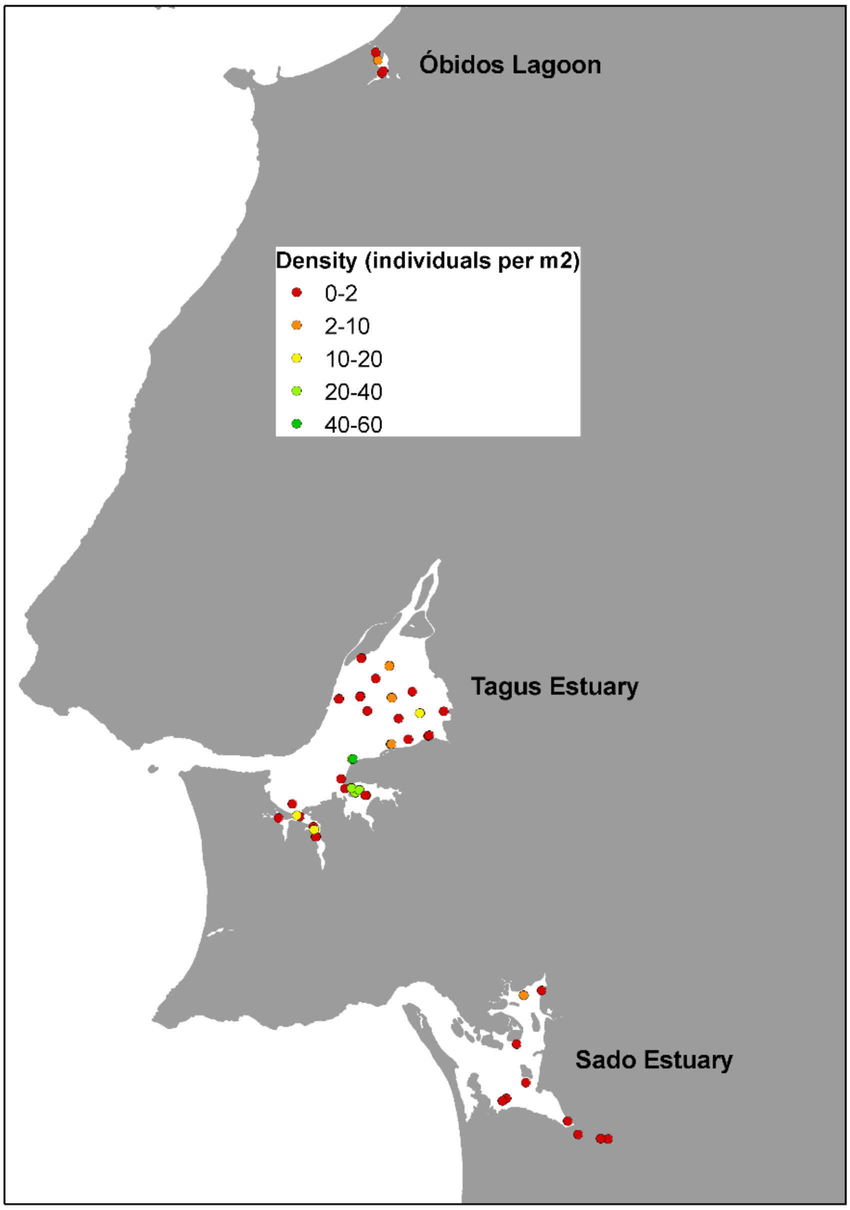


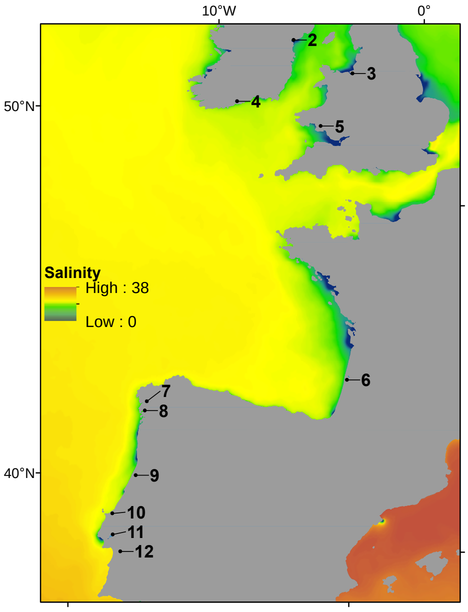
Figure 9. Density (Individuals/ m^2) measured by MARE at the Tagus and Sado Estuaries, and Óbidos Lagoon. Sampling was conducted between 2018 and 2019 using a vessel-operated clam dredge.

4.3. Environmental variables for Investigation 3

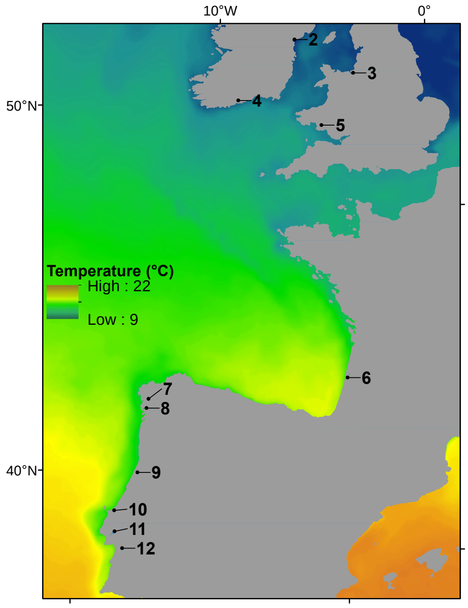
Salinity differed significantly across sites (H=282.4, df=13, p<0.001; **Figure 10A**). Salinity was significantly lower at Carlingford compared with all other sites, except for the Dee Estuary, Tagus, Cooley, Annagassan and Arcachon. While median salinity was not found to be statistically significantly lower than the two nearby sites at Dundalk, mean salinity did appear to be much lower at Carlingford (**Table 6**). The lack of statistical significance was due to the large variance at Carlingford but not at the Dundalk beds. Salinity at Sado was significantly higher than most other sites but was similar to some of the other southern sites: Aveiro, Noia, Arousa and Óbidos.

A large seawater temperature range was observed across the sampled sites (**Figure 10B**), and it was found to differ significantly between these sites (H= 91.467, df=13, p<0.001). Sea temperatures were highest at Sado, followed by Arcachon. Sea temperatures at Arcachon were only significantly higher than those recorded at the Dundalk beds. Sea temperature at Carlingford, Annagassan and Cooley were significantly lower than all the French and Portuguese sites. Sea temperature at the Spanish sites (Noia and Arousa) were significantly higher than Carlingford and Cooley but no differences were found statistically between Annagassan and these sites (**Table 7**).

Large variations were also observed in primary productivity (**Figure 10C**), which differed significantly between beds (H=100.43, df=13, p<0.001). Primary productivity was lowest at Carlingford, and significantly less so than all sites, except for Cooley, Óbidos, Sado, Arcachon and Aveiro. Primary productivity was highest at the Welsh sites. At the Dee Estuary it was significantly higher than Sado, Arousa, Arcachon, Aveiro and Carlingford. Primary productivity at Burry was significantly higher than Arcachon, Aveiro, Carlingford, Cooley, Óbidos and Sado. Although not statistically significant, primary productivity appeared to differ between the two beds at Dundalk Bay, whereas primary productivity between the two Cork Harbour sites was similar. While mean primary productivity of all sites was relatively high, it varied largely over the sampling period (**Table 7**).



(A)



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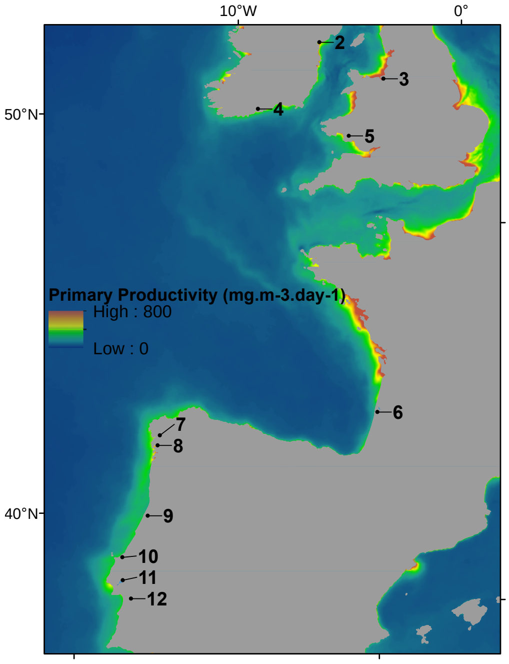

(C)

Figure 10. Mean salinity **(A)**, sea temperature **(B)** and primary productivity **(C)**, over the range of the studied sites for population dynamics, from January 2018 to January 2020. 1=Carlingford Lough (not visible due to map scale, approx. 10km north of Dundalk Bay), 2=Dundalk Bay, 3=Dee Estuary, 4=Cork Harbour, 5=Burry Inlet, 6=Arcachon Bay, 7=Ria de Noia, 8=Ría de Arousa, 9=Ria de Aveiro, 10=Óbidos, 11=Sado, 12=Tagus.

Table 7. Summary statistics (Mean (Median) ± SD) of key environmental variables (salinity, sea water temperature (°C) and productivity (mg C/ m^3/ day)) at all sites (in descending order latitudinally) from **Investigation 3** (Population dynamics), from January 2018 to January 2019. Data was obtained from Copernicus, 2020. The minimum value for each parameter is in italics and the maximum is in bold.

Country	Location	Bed	Salinity	Seawater temperature	Productivity
Ireland	Carlingford	Oyster Farm	*20.5* (12.4) ± 10.6	*10.8* (10.4) ± 2.5	*24.0 (15.0)* ± 28.1
Ireland	Dundalk	Annagassan	30.3 (30.3) ± 1.0	10.9 (10.1) ± 3.9	80.4 (70.0) ± 6.40
		Cooley	30.3 (30.3) ± 0.9	*10.8* (10.6) ± 3.5	56.1 (45.0) ± 42.9
Ireland	Cork Harbour	Cuskinny	33.9 (34.0) ± 0.7	11.6 (10.9) ± 2.6	68.6 (53.0) ± 48.8
		Ringaskiddy	33.9 (33.9) ± 0.7	11.6 (11.3) ± 2.6	68.9 (60.0) ± 49.6
Wales	Dee Estuary	Dee	26.7 (26.3) ± 2.5	11.2 (10.2) ± 6.3	247.8 (164.0) ± 224.1
Wales	Burry Inlet	Burry	27.0 (27.2) ± 1.5	12.0 (10.2) ± 5.0	**258.1 (150.0)** ± 236.4
France	Arcachon	Banc d'Arguin	33.3 (33.3) ± 0.5	15.5 (14.2) ± 5.3	27.2 (18.0) ± 21.2
Spain	Ría de Muros y Noia	Noia	34.3 (34.6) ± 1.0	14.3 (13.9) ± 1.8	63.2 (52.0) ± 38.1
Spain	Ría de Arousa	Sarrido	34.3 (34.5) ± 1.0	14.8 (14.4) ± 2.3	86.4 (91.0) ± 41.2
Portugal	Ria de Aveiro	Aveiro Lagoon	34.2 (34.4) ± 1.0	14.8 (14.8) ± 1.7	38.6 (25.0) ± 34.2
Portugal	Óbidos	Óbidos	35.0 (35.1) ± 0.3	15.1 (14.7) ± 1.6	44.6 (28.0) ± 30.0
Portugal	Tagus	Tagus	28.2 (29.3) ± 2.6	15.2 (15.1) ± 1.5	71.8 (47.0) ± 53.8
Portugal	Sado	Sado	**35.6 (35.6)** ± 0.2	**15.6 (15.2)** ± 1.8	40.9 (31.0) ± 31.0

4.4. Investigation 3: Population dynamics - cockle population structure

Median length of cockles differed significantly between sites (H=4749.5, df=11, p<0.001, **Figure 11A**). Cockles at Óbidos (mean= 15.67 mm) were significantly smaller than at all other sites and had a narrow length frequency distribution (**Figure 12**). Cockles at Cork were significantly larger than all other sites (mean= 32.87 mm), except for Arcachon (mean=28.59 mm), Dundalk (mean=32.14 mm) and Noia (mean=29.14 mm). Cork also demonstrated the broadest length frequency distribution. At Arousa (Sarrido bed), two peaks were evident in the length frequency distribution (**Figure 12**) but this distribution reflects the bias associated to the selection of the sample (juveniles and adults) as reported in section 3.3.1.

Median wet weight also differed significantly between sites (H=1253.8, df=8. p<0.001, **Figure 11B**). Weight differed for all pairwise comparisons, with the exception of Sarrido (mean= 4.47 g) vs Burry (mean= 5.25 g), Noia (mean= 7.83 g) vs Arcachon (mean= 8.49 g), Aveiro (mean= 6.25 g) vs Dee (mean= 6.43 g), and Cork (mean= 17.11 g) vs Dundalk (mean= 14.66 g). Greatest weight was observed at the Irish sites and the cockles with the lowest weight were observed at Sarrido (mean= 4.47 g). Length and weight followed a quadratic relationship ($\text{Weight} = \beta 1 + \beta 2(\text{Length}^2) + \epsilon$, *where* $\beta 1$ is the intercept and $\beta 2$ is the slope), where $R^2=0.9$. Furthermore, the length and weight of surfaced and buried cockles were found to not differ significantly (H=1.87, df=1, p=0.2 and H=3.5168, df=1, p=0.06), however there was a trend for buried cockles to be heavier and larger.

Finally, age differed significantly between sites (H=682.0, df=5. p<0.001, **Figure 11C**). All pairwise comparisons were significant except for Cork (mean= 3.56 rings) vs Arcachon (mean= 3.36 rings, i.e. mean age did not differ significantly between Cork and Arcachon). However, a larger age range was evident at Cork (**Figure 11C**). The mean number of growth rings of cockles at Carlingford (mean= 4.20 rings) was significantly higher than all other sites. Conversely, cockles at Dee (mean= 1.48 rings) were significantly younger than all other sites (**Figure 11C**).

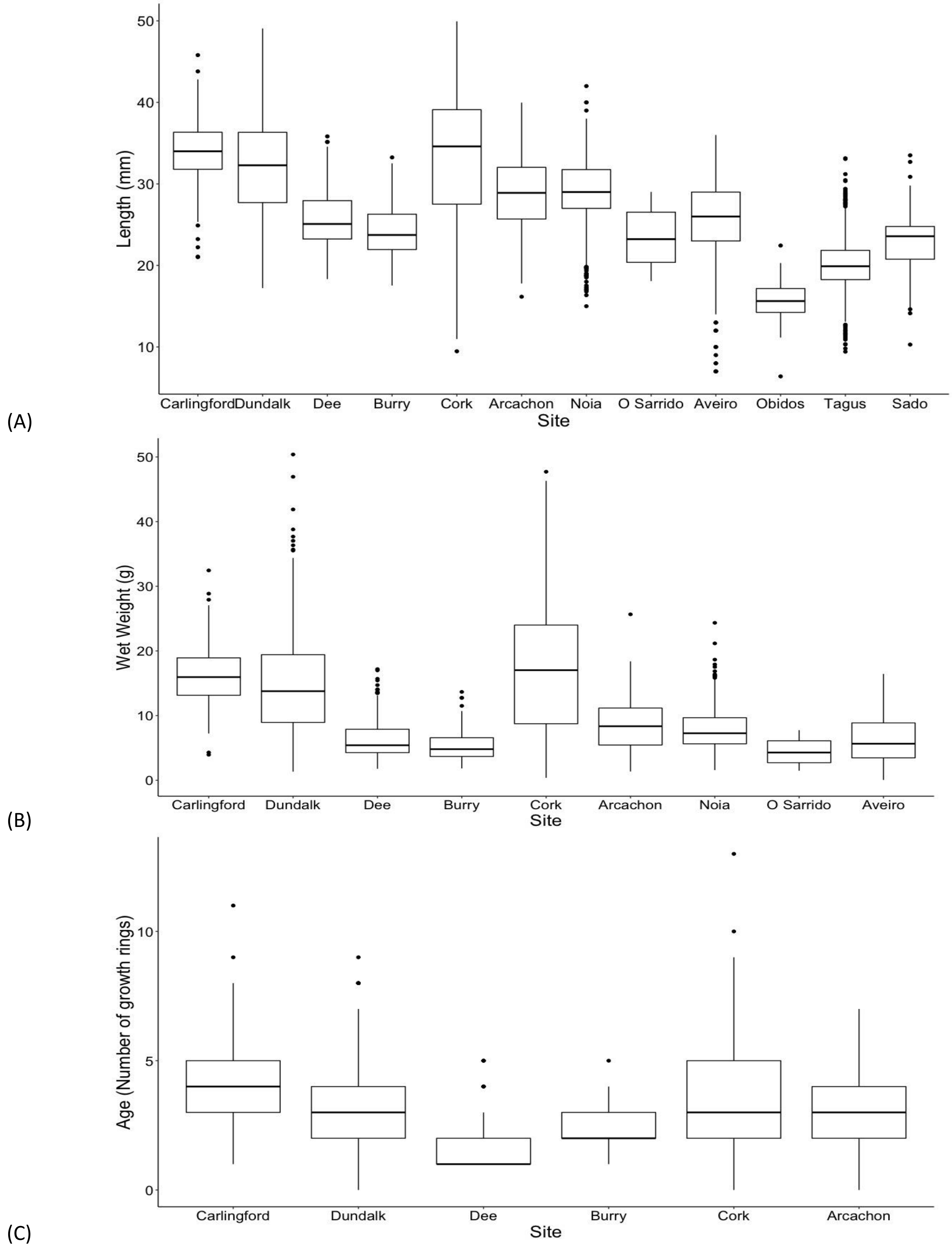

Figure 11. Mean length **(A)**, wet weight **(B)** and age **(C)** of cockles studied at each site.

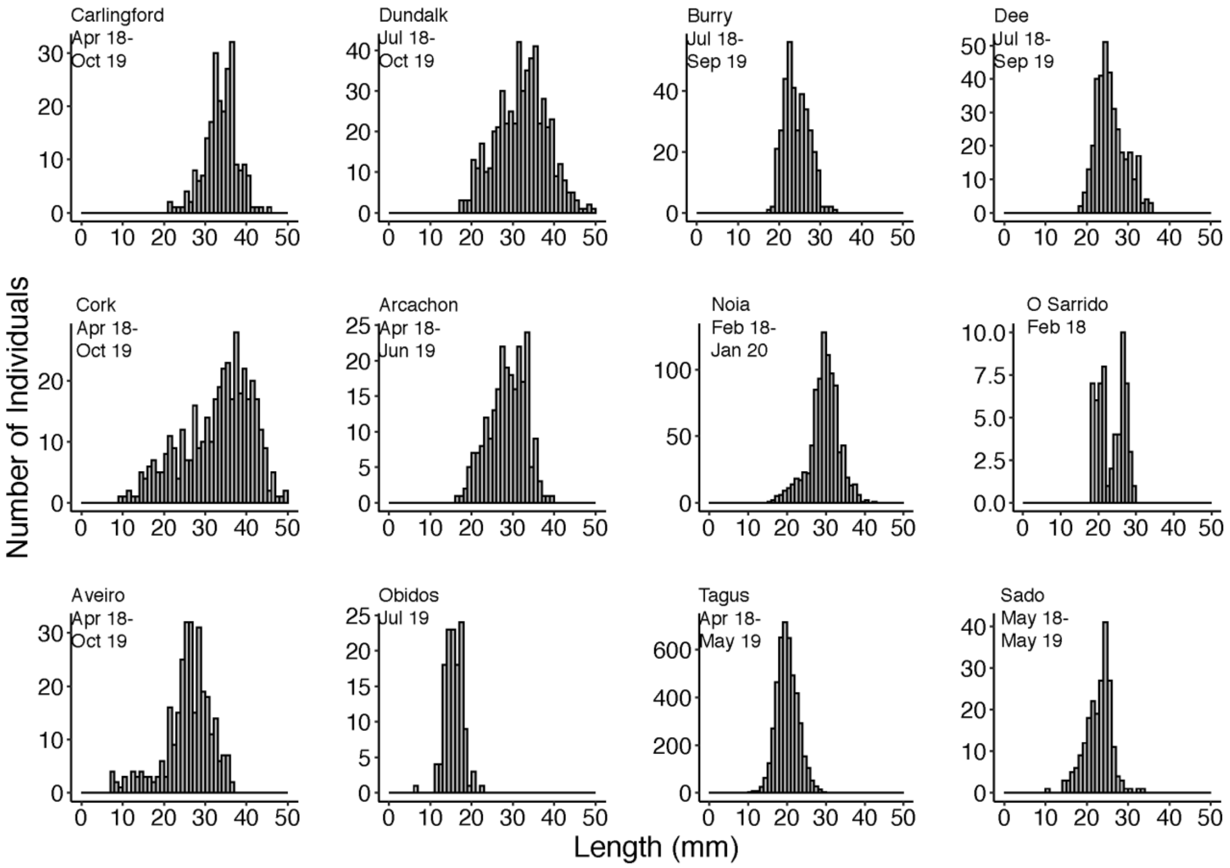

Figure 12. Shell length frequency distributions of all cockles studied for population dynamics. Note the differences in Y axes. Cockles were sampled over varying time periods, indicated on the graph. Further maps displaying length frequency distributions geographically, are included at the end of this report.

Cockles at nine beds in Ria Formosa, Portugal were analysed separately. Overall, 4,350 individuals were sampled with a broad size range (7 – 35 mm) corresponding to a mean shell length of 22.5 ± 3.2 mm. In general, the populations demographic structure was dominated by commercially-undersized cockles (minimum conservation reference size = 25 mm: Olhão = 66.2–90.9% < Minimum Conservation Reference Sizes (MCRS); Faro = 52.7–61.4% < MCRS; Fuseta = 37.3–60.8% < MCRS; **Figure 13**).

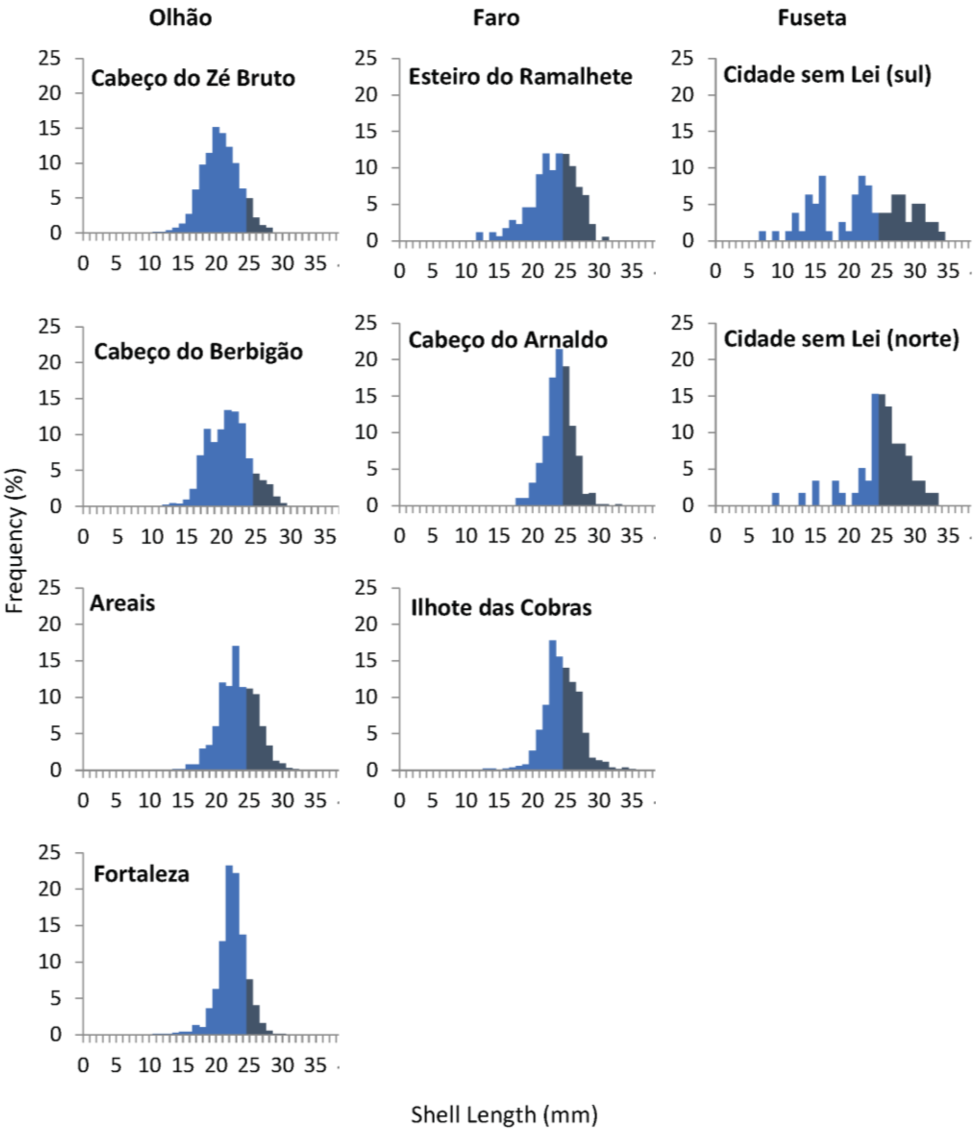

Figure 13. Shell length frequency distributions of cockles at nine beds in Ria Formosa, Portugal. Light blue indicates below minimum capture size and dark blue indicates shell length above minimum capture size.

Figure 14 shows additional size distribution of cockles from Sarrido on three different dates. Annual outbreaks of marteiliosis detected in this bed caused mass mortality of every annual newly recruited cockle cohort significantly impairing the number of cockles reaching minimum legal commercial size (25 mm). See **Section 7 - MAPS** for additional depictions of length frequency distributions.

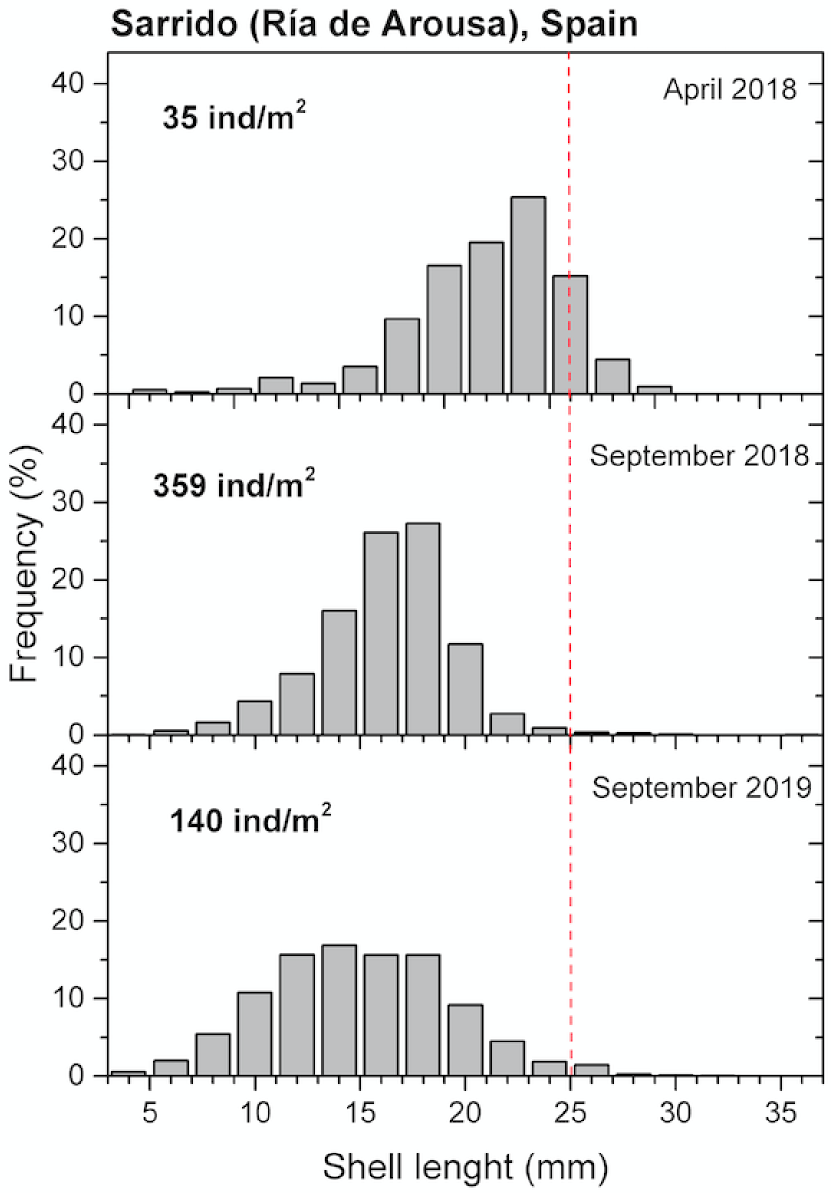

Figure 14. Shell length frequency distributions of cockles sampled in Sarrido. Cockles were sampled over varying time periods, indicated on the graph. Vertical red dashed line indicates the minimum legal size of cockles in Galicia (25 mm).

4.5. Investigation 4: Population dynamics - cockle growth

The estimates for $L\infty$ (asymptotic average length, i.e. average maximum length), k (Brody growth rate coefficient, i.e. speed at which average maximum length is reached) and t_0 (size at age 0) are indicated in **Table 8**. Growth parameters could not be estimated for Burry Inlet due to a lack of older individuals, resulting in a linear fit. Beds within the same sites (i.e. beds at Cork and Dundalk), exhibited similar growth curves (**Figure 15**).

Table 8. Growth parameters estimated using the von Bertalanffy growth model for *Cerastoderma edule*, from Irish cockle beds, one Welsh cockle 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 size at age 0, and ϕ' is the growth performance index.

Site	**Latitude**	L_∞ **(mm)**	k **(yr^{-1})**	t_0 **(yr)**	ϕ'
Carlingford	54°N	35.7994	0.6354	-0.9542	2.72
Cooley	53°N	45.0353	0.2185	-3.2349	1.99
Annagassan	53°N	42.7378	0.2884	-2.3392	2.18
Dee	53°N	36.1528	0.3426	-2.2544	2.19
Cuskinny	51°N	43.2443	0.3986	-0.6290	2.48
Ringaskiddy	51°N	40.7380	0.4722	-0.4013	2.57
Arcachon	44°N	34.2873	0.3419	-2.0657	2.13

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 (χ^2=308.29, df=18, p<0.001). There was a significant difference in both k and t_0 (p<0.001) between sites. The highest ϕ' and the highest k were found at Carlingford, indicating that it took shortest for cockles in Carlingford to reach $L\infty$ (average maximum length). Conversely, both sites at Dundalk reached $L\infty$ the slowest (Annagassan= 0.29 yr^{-1} and Cooley= 0.22 yr^{-1}). The highest $L\infty$

was observed in Cooley, followed by Cuskinny and then Annagassan while the lowest $L\infty$ was observed in Arcachon (34.3 mm), with a similar value at Carlingford (35.8 mm; **Table 8**). However, $L\infty$ was not found to significantly differ statistically between sites.

The impact of primary productivity, salinity, temperature and trematodes (metacercariae and sporocysts) and density on the cockle growth performance index (ϕ') were also tested. Following model reduction, no significant relationships were observed.

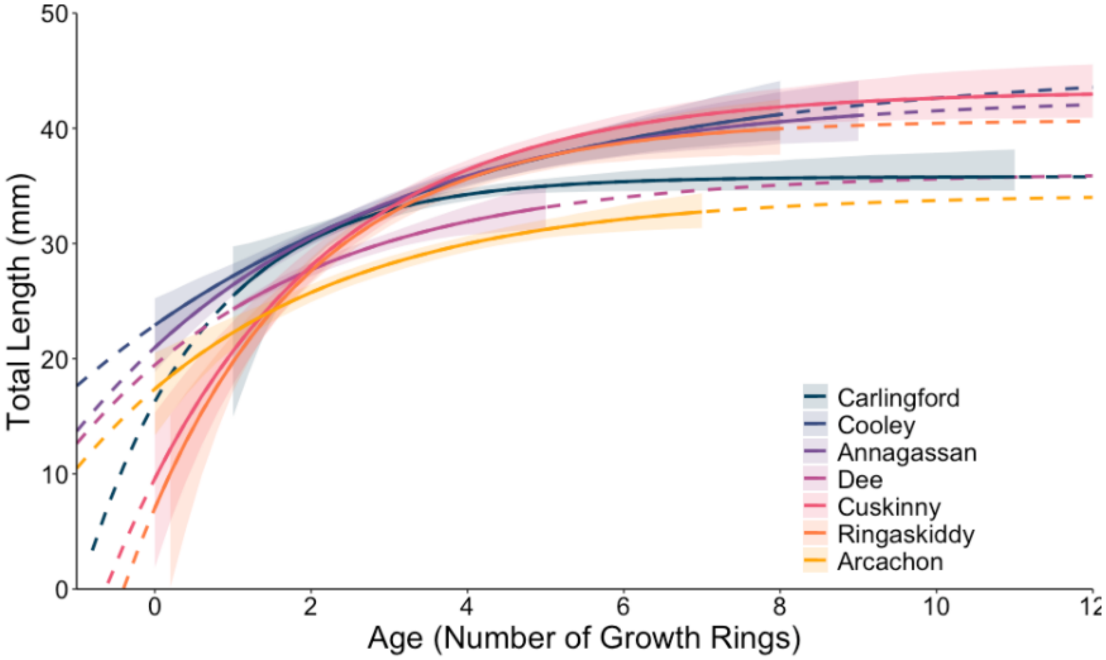

Figure 15. Estimated von Bertalanffy growth curves of cockles at five Irish (Carlingford, Cooley Annagassan, Cuskinny, Ringaskiddy), one Welsh (Dee) and one French (Arcachon) site.

5. DISCUSSION

The vulnerability of European cockle populations has been recognised for over a decade now and a great effort has been made to improve resilience through designating site protection in many areas (Ponsero et al., 2009). However, there are no European-wide regulations for exploitation and capacity for site-specific management schemes are often lacking (McLaughlin et al., 2007). To enable the development of effective management strategies and focus resources to maximise sustainable exploitation of this resource, concrete data of current distribution, abundance and population dynamics are imperative. This study has further affirmed the variability of cockle populations, in terms of size, growth and density, as well as the variation of external environmental (temperature, salinity, food availability, density) drivers on this commercially and ecologically important species. Although the maps in this study show that *C. edule* exhibits an extensive range (at least 15°N to 71°N; note: due to identification errors, it is possible that not all records may be correctly identified as *C. edule*, e.g. in the Mediterranean Sea), surveys showed that the densest populations are located in Wales and northern France. Similar high densities in these regions were noted in COCKLES **Deliverable 4.1** throughout the 1990s to 2010s. Contrastingly, densities didn't remain consistent across time in other locations, with densities in Galicia in the 1980s and 2000s greater than those seen today (2018 – 2020). Spatial and temporal variability of sampling impair comparison, but the incidence of the disease marteliosis in 2012 in the southern rias of Galicia, which caused heavy mortalities, provide an explanation for this downward trend in cockle density.

Environmental parameters (salinity, sea temperature and primary productivity) varied significantly between AA sites, confirming that *C. edule* populations proliferate across wide environmental ranges. However, it was found that *C. edule* experiencing environmental stressors such as low salinity and high parasite levels may be slower growing in early life, and these drivers can be compounding. These are important findings that should be monitored into the future to enable management and mitigation of potentially harmful effects, particularly with regards to predicted changes due to climate change. Such findings support the suggestion that more regular monitoring of this iconic fishery throughout the AA is required to ensure sustainability.

Significant variation in the length, wet weight and age of cockles at different sites was also found. Interestingly, average length and weight tended to decrease with latitude. However, no latitudinal relationship was observed in frequency of age classes. The Burry Inlet and Dee Estuary had the youngest populations on average, and these sites were also some of the most densely populated in the current survey, as well as historically (COCKLES **Deliverable 4.1**). These sites are managed by Natural Resources Wales, with a minimum landing size set at 10 mm riddle in the Burry (following years of recurrent mortality; Burdon et al., 2014) and 20 mm for the Dee. With the small landing size for the cockles in the Burry, the finding of the Burry having the youngest cockles is in keeping with the current management regime. However, the regime in the Dee is for a larger landing size. It may be that the cockles from the Dee were from an area with more recently settled cockles.

5.1. Ireland

Three sites (five beds) were sampled in Ireland and large variations in abundance were noted between them. Density at Dundalk (the primary site for cockle fishing in Ireland), was much higher than at Cork or Carlingford, which experience low fishing pressure. Previous studies have shown that active fisheries may reduce cockle population density (Piersma et al., 2001), however, density at Dundalk was higher than the unfished sites in Ireland. Therefore, it is unlikely that fishing pressure is influencing density in Ireland, confirming that the Total Allowable Catches (TACs) employed in Dundalk (Tully and Clarke, 2016) are effective at supporting recruitment. Interestingly, density was notably lower here than at the Welsh sites of a similar latitude, which also experience fishing pressure, suggesting that other factors are important drivers of population density. Sediment type varied between Irish sites, a factor that may have influenced density. Cockle density is positively correlated with mud content (Whitton et al., 2015) and at stonier sites, at Carlingford and Cork, a reduced number of cockles were present, potentially due to less space for settlement. This further highlights the importance of sediment type for cockle populations, as well as the necessity of protecting suitable environments. In terms of population dynamics, cockles in Carlingford were oldest compared with all other sites, despite the low and fluctuating salinity and low seawater temperature. This older population may be a result of reduced recruitment in the area. It is worth investigating if low salinity is having a greater impact on juvenile cockles, leading to their under representation. At Dundalk, cockles were young relative to Carlingford. While fishing pressure was unlikely to have influenced density at Dundalk, it is very likely that it influenced the age distribution at this site. Finally, cockles at Cork reached the largest sizes of all cockles studied, as well as having a low density. It is probable that the Cork cockles were able to attain large sizes due to the lack of density dependent competition, which commonly restricts growth (Beukema and Dekker, 2015).

Cockles at Dundalk grew fastest in the initial life stages, according to the von Bertalanffy growth models in this study, but growth appeared to slow after three growth rings, in comparison with the nearby site of Carlingford. This can be explained by a reduced representation of larger cockles in the population, most likely due to fishing activity here (minimum capture size= 22 mm). It was expected that cockles at Carlingford would experience the lowest growth performance, due to low salinity increasing valve closure times, reducing food intake and reducing the energy available for growth (Domínguez et al., 2020). Consequently, due to the diversion of energy to maintenance (Peteiro et al., 2018), cockles at Carlingford may be unable to allocate as much energy to their immune systems, potentially explaining the high prevalence of metacercariae here. This high prevalence may also be attributed to the presence of a high number of birds (i.e. final hosts, Hechinger and Lafferty, 2005) due to the RAMSAR classification. However, cockles at Cork, which features a nature reserve for birds, did not experience such high prevalence. Although, cockles at Carlingford exhibited the highest growth performance, the growth rate did not exceed that of other sites until year three and cockles here had the smallest L_∞. Furthermore, cockles at all three unfished beds (Cuskinny, Ringaskiddy and Carlingford), initially exhibited slowest growth. The lack of older individuals is a common phenomenon impeding model fitting with a VGBF (Ogle et al., 2015). This lack of older individuals results in an attempt to fit a nonlinear function to an erroneously linear model (Ogle et al., 2015). Therefore, the hypothesis of fluctuating salinity and parasitism influencing growth may still be valid. This is of concern because, increased precipitation (and subsequently lower salinity) have been reported in Ireland (Lynch et al. 2020) as well as globally (Kharin et al., 2013) in recent years. Results from this study suggest that these climatic changes may further negatively impact cockle growth in the future. Furthermore, transmission of trematodes may be increased due to warming seawater (de Montaudouin et al., 2016), which, in combination with reduced immune function resulting from low salinity, may be detrimental to many cockle populations.

5.2 Wales

In Wales, commercially fished beds in the Burry Inlet and the Dee were sampled for the project. The samples from Wales demonstrated the highest densities of all locations sampled in the AA. It is possible that these high densities are a result of larval retention and hydrography (Young et al., 1998) which would be the case for the Burry Inlet but not necessarily for the Dee (Coscia et al., 2020). This hypothesis was beyond the scope of this report but will be interesting to examine as part of **COCKLES Work Package 6**, which aims to investigate larval dispersal.

The cockles from the Burry and the Dee were significantly smaller than the Irish cockles of similar latitude. As mentioned, the riddle size (i.e. minimum capture size) for the Burry is set at 10mm whereas in the Dee it is set at 20mm. Although the small riddle size for the Burry may explain the smaller cockles for the Inlet, the riddle size for the Dee is double that of the Burry and yet these cockles were smaller and younger. Cockles do show patchiness and this maybe the cause of the smaller cockles collected in the Dee sample, as could a slight difference in sediment type between the two sites. The Dee also recorded lower salinity potentially affecting growth (Domínguez et al., 2020). However, this does not correlate with the observation that the Welsh sites had the highest primary productivity compared with all other sites. The Dee site, in particular, had lower than expected growth given the productivity of the area. While it is expected the high primary productivity would result in larger cockles due to energy availability it may also be possible that the high densities have resulted in density dependent competition (Beukema and Dekker, 2015).

Previous work in the Burry (Elliott et al., 2012) highlighted the apparent switch of the Burry cockle population from a stable population of several year classes to one of high recruitment of first year cockles with good growth. These cockles suffered very high recurrent mortality shortly after reproduction with potential influencing factors ranging from density and overcrowding to parasite load, energy and/or condition loss. This work also highlighted the good growth of young cockles under the nutrient and organic condition in the Burry at the time of the study (Elliott et al., 2012). Contrasting with the Burry, the Dee cockles had lower density compared to the Burry Inlet although overall cockle growth was slower than in the Burry with generally larger cockles in the Dee. More recent work has indicated the Burry Inlet may be starting to return to a state of more age classes and less mortality.

5.3 France

In France, density at Arcachon Bay was in the middle of the study's recorded range from all the sites. At Banc d'Arguin - a semi-sheltered site, morphometric analysis was also undertaken. However, since this study was undertaken, density has been reported as very low in Arcachon Bay, highlighting the temporal variability in cockle abundance. Temporal variation is frequently locally isolated and, in contrast, when examining temporal variability in northern France, densities at the Seine Estuary remained similar between 2017 and 2018.

Monthly sampling performed at Arcachon since 1998 has shown that cockle abundance fluctuates significantly, with some prosperous years (Magalhães et al. 2016). However, since 2012 all cohorts failed in the first six months after recruitment. There is no demonstrated reason for the recent settlement failure of the cockle population in Banc d'Arguin (Arcachon). The main hypotheses are a positive North Atlantic Oscillation during this period, but also an increase in disease prevalence, like disseminated neoplasia (Le Grand et al. 2010) and deleterious trematodes, i.e. *Bucephalus minimus* (de Montaudouin et al. 2012). A recent unpublished study reported that an increase in the seagull nesting population (*Larus* spp.) could be partly responsible for increasing cockle mortality.

Despite the large difference in seawater temperatures between Cork and Arcachon, cockles did not differ in size between these sites. In terms of growth rate, growth performance was low at Arcachon. While more southern sites were not examined, making conclusions difficult to derive, it is possible that temperature had an impact here. It is also possible that growth at Arcachon is influenced by the allocation of energy to gametogenesis, rather than somatic growth, with spawning occurring nearly all year at this location (COCKLES **Deliverable 4.3**). Regardless, cockles at Arcachon, and perhaps cockles in general, are reputed to display a large inter-individual variation in growth rate: within 10 months, the length increment of a young cockle can vary by a factor of up to five, in the same environmental conditions (de Montaudouin et al. 2012).

5.4 Spain

In Galicia, density variation was analysed in Sarrido, a shellfish bed affected by the disease marteiliosis. Large temporal differences observed in cockle densities were associated to heavy mortalities caused by disease outbreaks. Annual outbreaks of marteiliosis detected in this bed produce mass mortality of every annual newly recruited cockle cohort, significantly impairing the number of cockles reaching minimum legal commercial size (25 mm) and the recovery of the fishery.

The physiological effects exerted by the pathogen *Marteilia cochillia* could also be assessed at Sarrido, since the analysed cockles, picked in February 2018, just when an outbreak of marteiliosis occurred at this bed, weighed the least. However, this site was not notable in terms of any of the studied environmental variables. This agrees with the infection pattern of the parasite that heavily affects the digestive gland of cockles, impairing the absorption of food and causing starvation.

These results showed that, since the first detection in Galicia in 2012, marteiliosis was the main driver of cockle population dynamics in those beds affected by the disease.

5.5 Portugal

In Portugal, abundance was generally variable within a single system, potentially due to location within these systems. With the exception of Óbidos Lagoon, all the Portuguese systems studied (Ria de Aveiro, Tagus and Sado estuaries and Ria Formosa) are quite large in terms of total area covered, ranging from 83 km^2 in Ria de Aveiro to 320 km^2 at the Tagus Estuary (Cabral et al. 2019). Consequently, the intra-variability of the abiotic factors (such as sediment composition, hydrodynamics, temperature and salinity) will result in different abundances of the bivalve populations, particularly cockle populations. The highest densities in Portugal were observed at Barra in the Ria de Aveiro, as well as Seixal in the Tagus Estuary. This might be explained by the fact that highest densities of cockles are usually in sites characterized by fine sand or mud (Maia and Gaspar, 2014; Soissons et al., 2019). Furthermore, according to Freire et al. (2007), Seixal recorded the lowest median diameter of grain size at the Tagus Estuary. However, a more likely scenario is that higher salinity at Aveiro is favourable for cockle populations, as median grain size in Vagueira (lower density) is thinner when compared to Barra (higher density). Additionally, considering that Seixal is in a semi-enclosed sheltered bay, the hydrodynamic stress is usually reduced in these areas, potentially leading to self-recruitment and low dispersion of the larvae (de Fouw et al., 2020), similar to the Burry Inlet, Wales.

The smallest cockles in terms of mean length noted in this study were found at Óbidos. This might indicate that the cockle populations at the Óbidos Lagoon are being overfished, since low abundances and a size structure composed mainly by small individuals are the most common consequences of overfishing. In fact, according to official statistics of professional harvesters provided by DGRM (Direção-Geral de Recursos Naturais, Segurança e Serviços Marítimos) for the year of 2019, Foz do Arelho (the closest fishing port of Óbidos lagoon) recorded the third highest quantity of commercial landings for cockles in Portugal, surpassed only by fishing ports at Ria de Aveiro and Ria Formosa. Nevertheless, it is important to highlight that both Ria de Aveiro and Ria Formosa contain much larger exploitable areas. At Óbidos, salinity was higher than other sites due to the narrow inlet (± 1.5km in length) with a sandy barrier that connects to the Atlantic Ocean and the low input of freshwater discharges that are negligible in summer (Pereira et al., 2009). However, this was not outside the range of tolerance for cockles (12.5 - 38.5; Russell and Petersen, 1973).

At the Ria Formosa, the prevalence of individuals below the MCRS apparently reveals an adequate recruitment in these areas, especially at the sampling sites with higher abundances and densities. Conversely, the low proportions of individuals above the MCRS might be related to reduced growth rates under high population densities (e.g. due to space limitation and food scarcity), coupled with the continuous removal of commercially-sized cockles during the intensive fishing activity that leads to resource overexploitation in some preferential harvesting areas.

In the Ria Formosa lagoon, cockles are harvested both manually with hand knifes and by hand-dredges. In general, cockle harvesting by hand-dredge is a patchy activity scattered throughout the lagoon, performed in heterogeneous harvesting areas. Highly variable fishing yields (CPUE’s) reveal the spatially diverse abundance/biomass and diverse harvesting effort, with the cockle beds exploited until the profitability limit. Indeed, the population demographic structure (high proportion of cockles below the MCRS) confirms the overexploitation of the resource in some preferential harvesting areas. In addition, local professional harvesters sometimes report high natural mortality rates in harvesting areas with remarkably high abundance / density of cockles.

6. CONCLUSION

The findings of **Deliverable 4.2** are valuable due to its large-scale focus, especially considering cockles are rarely studied beyond a national scale. Populations at the same latitude did not always have similar growth rates or population dynamics (e.g. Dundalk vs the Dee). This highlights that local abiotic and biotic drivers/inhibitors influence cockle populations, more so than geographic trends. It was evident that cockles were spatially variable in growth, density and population structure, and much of this variation was caused by local environmental factors, in particular salinity, temperature and productivity: factors that may exert so far undetermined effects on cockle growth in the context of climate change. It is also likely that all the environmental variables may be acting concurrently (Gosling, 2015), however; it is difficult to uncouple this in a field study. Nevertheless, with the potential for temperatures to increase at higher latitudes, northern cockles may follow similar, slower growth trajectories as currently experienced at warmer, southern locations. This may consequently disrupt the production of cockles at higher latitudes, limiting fisheries. Furthermore, salinity appeared to be a key driver of growth, which may be altered at local scales due to increased precipitation or increased storm frequency (Beniston et al., 2007).

A key outcome of this deliverable, is the proposal of recommendations for managers. Due to the local differences, it was evident that density, population dynamics and growth rate varied greatly at different sites, even within close proximity, highlighting the importance of carrying out local and frequent surveys. It is recommended to conduct these surveys at least yearly, to record any temporal variability of cockle populations. Second, such surveys should be conducted at a fine scale, on a bed to bed basis, rather than on a regional scale (i.e. bay or estuary basis). This is necessary due to the fine scale spatial variation in cockle populations, evidenced in this study. These regular, fine scale surveys should ultimately be employed to determine the most suitable minimum capture size, as has occurred in other invertebrate species (Sulardiono et al., 2012), as well as for the development of Total Allowable Catches, which have proved beneficial at Dundalk Bay (COCKLES **Deliverable 4.3**). Due to the lack of older individuals at harvested populations, it is not recommended to focus solely on the VBGM parameters for interpreting growth. Instead, growth curves should be examined carefully, taking into account minimum capture size at specific beds. Finally, it is strongly recommended to widely and freely share any gathered data from these surveys in order to provide a holistic overview of cockle populations, over their entire range. These data will be beneficial in protecting cockle populations into the future.

The key conclusions for COCKLES **Deliverable 4.2** are as follows:

- The distribution range of AA *C. edule* has remained consistent with few occurrences of disappearance/collapse of populations. Such a finding highlights the resilience of *C. edule* populations, despite the many challenges (abiotic, biotic, anthropogenic, meteorological etc.) that they have had to overcome and currently experience are considered (**Investigation 1**).
- The densest populations of cockles occur in Wales and northern France, both historically and from this study. Density fluctuations have occurred at other locations. At Galicia, density has reduced due to marteliosis, in those rias affected by this parasite. Furthermore, at Arcachon, cockles have been impacted by climate, disease and predation. These findings support previous studies that indicate that climate change and pathogens are driving declines in certain populations of cockles. It was also found that these factors are likely to work additively, with cockles facing high prevalence of metacercariae and low environmental salinity experiencing reduced growth rates in early life. This will have implications for cockles given the trend of increased precipitation resulting from climate change (**Investigation 2**).
- Large variability in terms of biological factors (population structures, growth and density) were observed in combination with significant variation in environmental parameters (salinity, sea temperature and primary productivity). This confirms that *C. edule* can tolerate a wide range of environments and fluctuating conditions. This may be advantageous to cockles in a changing marine environment (**Investigations 2 and 3**).
- Variations in length, wet weight and age were observed across the cockle populations, with smaller cockles at more southern latitudes. This relationship was not apparent with age. It is likely that at southern populations, cockles divert more energy to reproduction rather than growth, supporting the findings of COCKLES **Deliverable 4.3** – ‘Cockle reproductive health’ (**Investigation 3**).
- Cockle growth was not influenced by primary productivity as strongly as expected. Instead, high density appeared to be a more important driver of population dynamics, resulting in smaller cockles (**Investigation 4**).
- These findings highlight the importance of management occurring at a site-specific level, due to the large variations in environmental and biological factors evidenced across the range of *C. edule*.
- A knowledge sharing platform for key stakeholders would provide a tool for the exchange of information and expertise to support a sustainable AA cockle sector.

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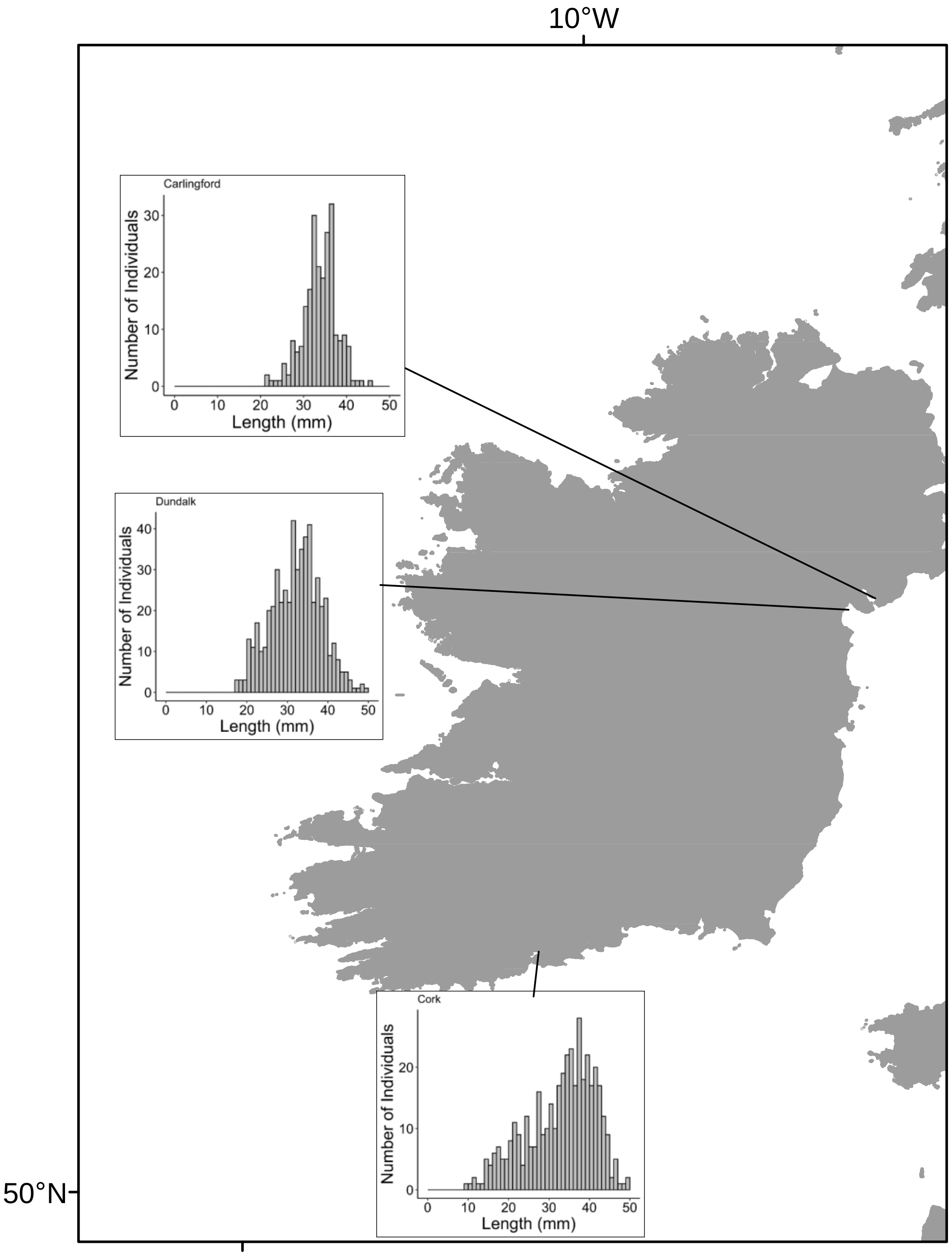
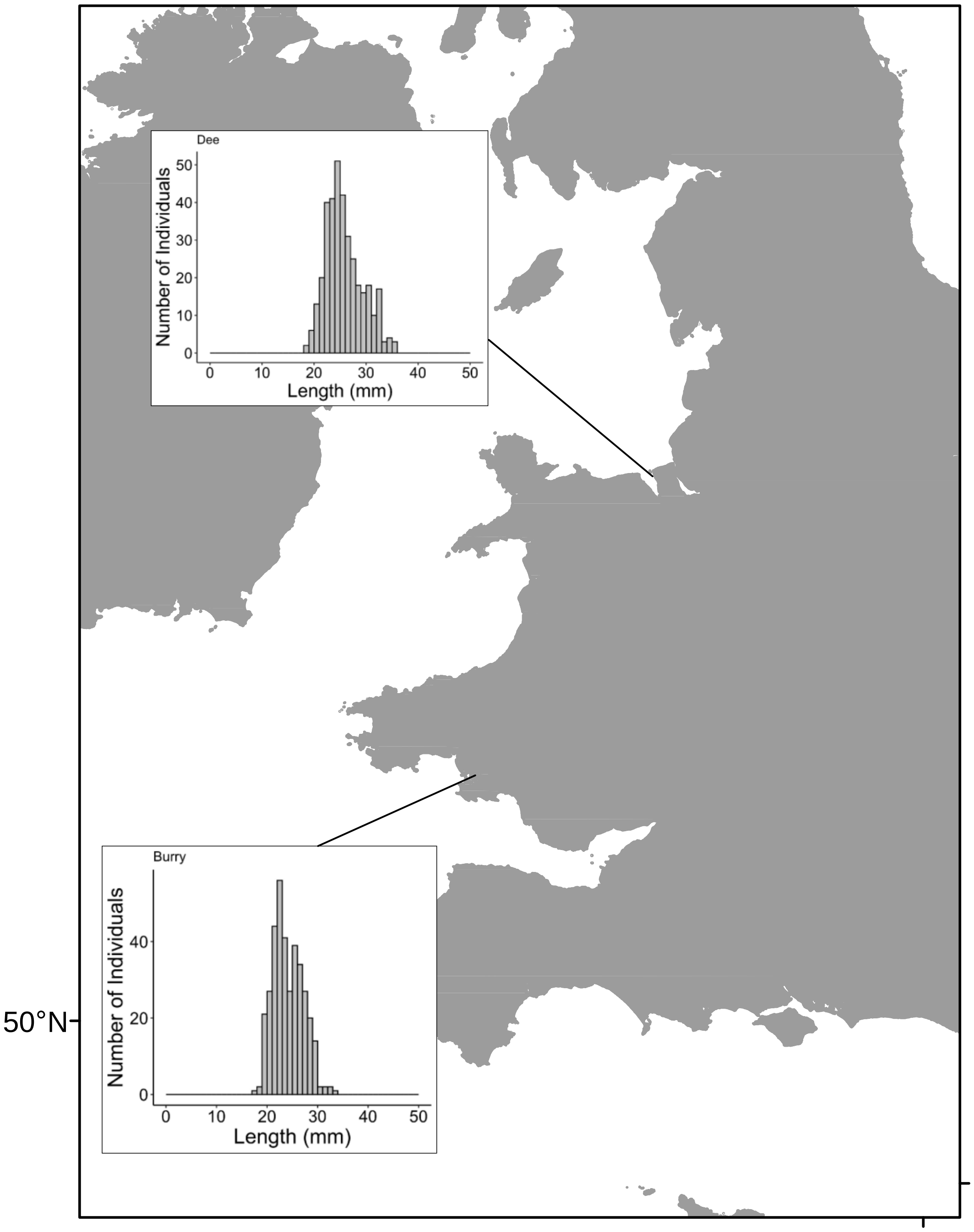
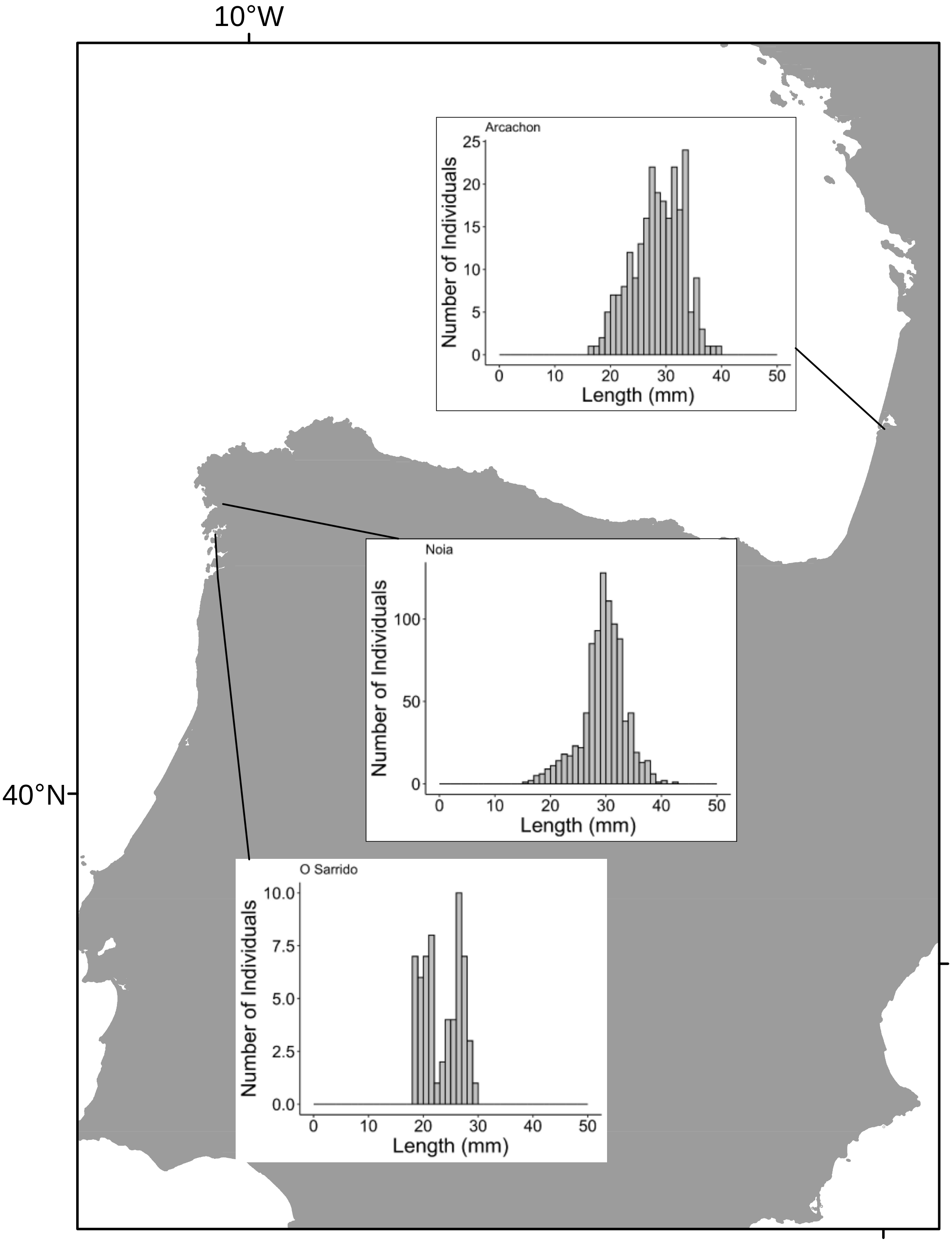
8. MAPS



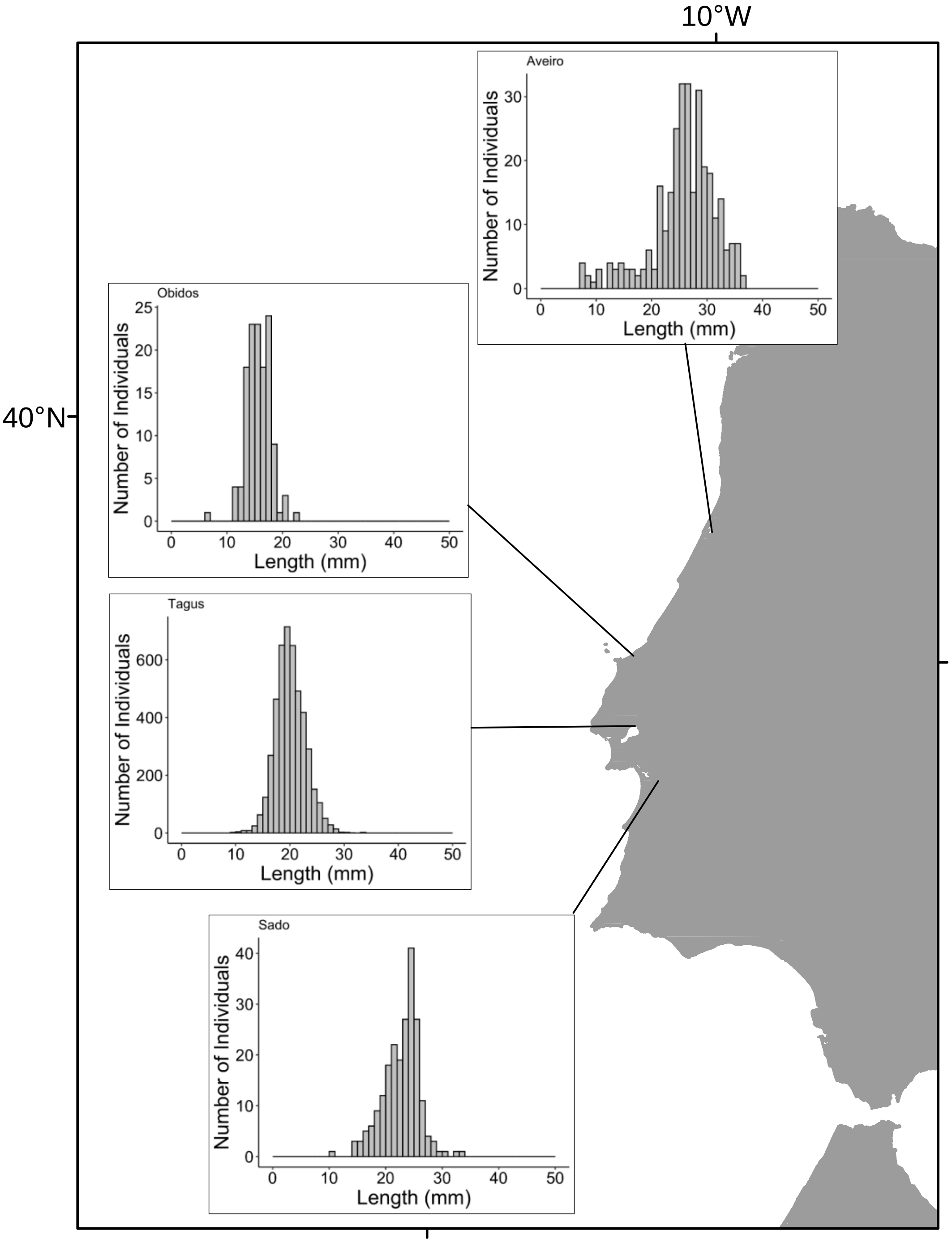
Map 1. Length frequency distributions for *Cerastoderma edule* sampled in Ireland (2018-2019)



Map 2. Length frequency distributions for *Cerastoderma edule* sampled in Wales (2018-2019)



Map 3. Length frequency distributions for *Cerastoderma edule* sampled in France (2018-2019) and Galicia (Spain), Sarrido (February 2018) and Noia (2018-2020)



Map 4. Length frequency distributions for *Cerastoderma edule* sampled in Portugal (2018-2019, with the exception of Obidos which was sampled in July 2019)

9. APPENDIX

Table A.1. Trematode prevalences (%) (obtained from COCKLES **Deliverable 4.3**), used as a predictor variable in a mixed effects model examining the influence of biotic and abiotic drivers on cockle growth.

Bed	Metacercariae	Sporocysts
Carlingford	81.66	0.05
Annagassan	20.00	2.92
Cooley	15.48	4.60
Cuskinny	19.58	2.92
Ringaskiddy	7.19	2.99
Arcachon	34.73	12.13
Dee	NA	NA

Table A.2. Result of Dunn Tests (*p* values) with Bonferroni correction to determine if median salinity differed between beds. Results are significant where p = 0.025.

	Anna	Arc	Aveir	Burry	Carl	Cool	Cusk	Dee	Noia	Sarri	Obid	Ring	Sado
Arc	0.52	-	-	-	-	-	-	-	-	-	-	-	-
Aveir	**<0.01**	0.99	-	-	-	-	-	-	-	-	-	-	-
Burry	0.99	**<0.01**	**<0.01**	-	-	-	-	-	-	-	-	-	-
Carling	0.99	0.02	**<0.01**	0.99	-	-	-	-	-	-	-	-	-
Cooley	0.99	0.58	**<0.01**	0.99	0.99	-	-	-	-	-	-	-	-
Cuskin	**<0.01**	0.99	0.99	**<0.01**	**<0.01**	**<0.01**	-	-	-	-	-	-	-
Dee	0.99	**<0.01**	**<0.01**	0.999	0.99	0.99	**<0.01**	-	-	-	-	-	-
Noia	**<0.01**	0.99	0.99	**<0.01**	**<0.01**	**<0.01**	0.99	**<0.01**	-	-	-	-	-
Sarri	**<0.01**	0.70	0.99	**<0.01**	**<0.01**	**<0.01**	0.99	**<0.01**	0.99	-	-	-	-
Obid	**<0.01**	**<0.01**	0.99	**<0.01**	**<0.01**	**<0.01**	0.99	**<0.01**	0.99	0.99	-	-	-
Ring	**<0.01**	0.99	0.99	**<0.01**	**<0.01**	**<0.01**	0.99	**<0.01**	0.99	0.99	0.43	-	-
Sado	**<0.01**	**<0.01**	0.05	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	0.14	0.21	0.99	**<0.01**	-
Tagus	0.99	**<0.01**	**0.01**	0.99	0.99	0.99	**<0.01**	0.99	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**

Table A.3. Result of Dunn Tests (*p* values) with Bonferroni correction to determine if median temperature differed between beds. Results are significant where *p* = 0.025.

	Anna	Arca	Aveiro	Burry	Carl	Cool	Cusk	Dee	Noia	Sarri	Obid	Ring	Sado
Arc	**0.01**	-	-	-	-		-	-	-	-	-	-	-
Aveir	**0.02**	0.99	-	-	-	-	-	-	-	-	-	-	-
Burry	0.99	0.46	0.73	-	-	-	-	-	-	-	-	-	-
Carl	0.99	**<0.01**	**<0.01**	0.99	-	-	-	-	-	-	-	-	-
Cool	0.99	**<0.01**	**0.01**	0.99	0.99	-	-	-	-	-	-	-	-
Cusk	0.99	0.03	0.06	0.99	0.99	0.99	-	-	-	-	-	-	-
Dee	0.99	0.19	0.31	0.99	0.99	0.99	0.99	-	-	-	-	-	-
Noia	0.16	0.99	0.99	0.99	**0.02**	0.09	0.33	0.99	-	-	-	-	-
Sarri	0.03	0.99	0.99	0.75	**<0.01**	**0.01**	0.06	0.32	0.99	-	-	-	-
Obid	**<0.01**	0.99	0.99	0.20	**<0.01**	**<0.01**	**0.01**	0.07	0.99	0.99	-	-	-

Ring	0.99	0.03	0.05	0.99	0.99	0.99	0.99	0.99	0.29	0.05	**<0.01**	-	-
Sado	**<0.01**	0.99	0.99	0.03	**<0.01**	**<0.01**	**<0.01**	**<0.01**	0.99	0.99	0.99	**<0.01**	-
Tagus	**<0.01**	0.99	0.99	0.10	**<0.01**	**<0.01**	**<0.01**	0.04	0.99	0.99	0.99	**<0.01**	0.31

Table A.4. Result of Dunn Tests (*p* values) with Bonferroni correction to determine if median primary productivity differed between beds. Results are significant where *p* = 0.025.

	Anna	Arc	Aveiro	Burry	Carl	Cool	Cusk	Dee	Noia	Sarri	Obid	Ring	Sado
Arc	0.04	-	-	-	-	-	-	-	-	-	-	-	-
Aveiro	0.99	0.99	-	-	-	-	-	-	-	-	-	-	-
Burry	0.23	**<0.01**	**<0.01**	-	-	-	-	-	-	-	-	-	-
Carl	**<0.01**	0.99	0.99	**<0.01**	-	-	-	-	-	-	-	-	-
Cool	0.99	0.99	099	**<0.01**	0.19	-	-	-	-	-	-	-	-
Cusk	0.99	0.08	0.99	0.12	**<0.01**	0.99	-	-	-	-	-	-	-
Dee	0.99	**<0.01**	**<0.01**	0.99	**<0.01**	0.04	0.63	-	-	-	-	-	-
Noia	0.99	0.04	0.99	0.21	**<0.01**	0.99	0.99	0.99	-	-	-	-	-
Sarri	0.99	**<0.01**	**<0.01**	0.99	**<0.01**	0.43	0.99	0.99	0.99	-	-	-	-
Obid	0.99	0.99	0.99	**<0.01**	0.57	0.99	0.99	**<0.01**	0.99	0.14	-	-	-
Ring	0.99	0.09	0.99	0.11	**<0.01**	0.99	0.99	0.58	0.99	0.99	0.99	-	-
Sado	0.99	0.99	0.99	**<0.01**	0.99	0.99	0.99	**<0.01**	0.99	0.03	0.99	0.99	-
Tagus	0.99	**<0.01**	0.42	0.60	**<0.01**	0.99	0.99	0.99	0.99	0.99	0.99	0.99	0.99

Table A.5. Result of Dunn Tests (*p* values) with Bonferroni correction to determine if median length differed between sites. Results are significant where *p* = 0.025.

	Arca	Aveiro	Burry	Carl	Cork	Dee	Dundalk	Noia	Sarri	Obid	Sado
Aveir	**<0.01**	-	-	-	-	-	-	-	-	-	-
Burry	**<0.01**	0.99	-	-	-	-	-	-	-	-	-
Carling	**<0.01**	**<0.01**	**<0.01**	-	-	-	-	-	-	-	-
Cork	0.99	**<0.01**	**<0.01**	**<0.01**	-	-	-	-	-	-	-
Dee	**<0.01**	0.99	**<0.01**	**<0.01**	**<0.01**	-	-	-	-	-	-
Dundalk	**<0.01**	**<0.01**	**<0.01**	0.15	0.99	**<0.01**	-	-	-	-	-
Noia	0.99	**<0.01**	**<0.01**	**<0.01**	0.99	**<0.01**	**<0.01**	-	-	-	-
Sarrid	**<0.01**	0.44	0.99	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	-	-	-
Obid	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	-	-
Sado	**<0.01**	**<0.01**	0.09	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	0.99	**<0.01**	-
Tagus	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**

Table A.6. Result of Dunn Tests (*p* values) with Bonferroni correction to determine if median wet weight differed between sites. Results are significant where *p* = 0.025.

	Arca	Aveiro	Burry	Carl	Cork	Dee	Dundalk	Noia
Aveir	**<0.01**	-	-	-	-	-	-	-
Burry	**<0.01**	**<0.01**	-	-	-	-	-	-
Carling	**<0.01**	**<0.01**	**<0.01**	-	-	-	-	-
Cork	**<0.01**	**<0.01**	**<0.01**	**<0.01**	-	-	-	-
Dee	**<0.01**	0.99	**<0.01**	**<0.01**	**<0.01**	-	-	-

Dundalk	**<0.01**	**<0.01**	**<0.01**	**<0.01**	0.99	**<0.01**	-	-
Noia	0.99	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	-
Sarrid	**<0.01**	**<0.01**	0.99	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**

Table A.7. Result of Dunn Tests (*p* values) with Bonferroni correction to determine if median number of growth rings differed between sites. Results are significant where *p* = 0.025.

	Arcachon	Burry	Carlingford	Cork	Dee
Burry	**<0.01**	-	-	-	-
Carlingford	**<0.01**	**<0.01**	-	-	-
Cork	0.99	**<0.01**	**<0.01**	-	-
Dee	**<0.01**	**<0.01**	**<0.01**	**<0.01**	-
Dundalk	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**