



Drivers of growth in a keystone fished species along the European Atlantic coast: The common cockle *Cerastoderma edule*

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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 study the spatial and temporal variabilities in common cockle growth across latitudes were assessed and compared with historical data. Six locations were examined at bimonthly intervals over 19 months; three Irish, two Welsh and one French, spanning the latitudes 54°N to 44°N. The results demonstrated that local abiotic and biotic factors have a larger impact on cockle growth than latitude. Cockles at similar latitudes grew at different rates and sizes, possibly due to factors such as density, fishing activity and interspecific competition. Cockles (0–3 years) impacted by low salinity and parasites (trematodes), exhibited reduced growth in later years. At the warmest, southernmost 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. The results opposed previously literature which demonstrated significantly greater growth at lower latitudes. These findings affirm that cockle growth and size is variable due to local abiotic (reduced salinity) and biotic (potentially trematode infection) 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 northern cockles reaching smaller maximum sizes.

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 a keystone species 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 addition, there is a strong commercial interest in the species, In Europe, *C. edule* has the potential to provide an additional \$11.5 M a year from meat, ecosystem services and by-products,

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such as shell aggregate and nutrient removal (Carss et al., 2020). Management of common cockle fisheries is particularly topical, considering the increasingly frequent boom and bust cycles observed in populations of this species (Burdon et al., 2014; Morgan et al., 2013). In terms of fisheries, cockle management schemes typically set minimum capture sizes to safeguard future generations of cockles and sustainable harvests. 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 historically 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 (Gobler et al., 2014). Biotic factors such as competition (Beukema and Dekker, 2005; de Fouw et al., 2020; Jensen, 1993; Jensen, 1992; Masski and Guillou, 1999), predation (de Fouw et al., 2020) 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). 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 (Gam et al., 2009). These parasites can negatively impact cockle condition and survival (Longshaw and Malham, 2013), particularly when coupled with environmental stressors, 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 growth. 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 relationships that these (a)biotic variables had with 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 since the findings of Iglesias and Navarro (1990) 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 ($n = 2133$) were gathered from six locations (three Irish ($n = 1174$), two Welsh ($n = 720$), and one French ($n = 239$; Fig. 1). Two Irish locations (Dundalk Bay and Cork Harbour) were sampled at two distinct sites (Fig. 1). At every site (six in total), cockles were opportunistically collected from the intertidal areas with rakes and by hand, at low tide. At Carlingford and Cork, cockles



Fig. 1. Locations (and sites within) studied in a 19-month survey of growth rates in *Cerastoderma edule*. At each location, one site was examined with the exceptions of two sites at Dundalk and Cork Harbour.

were collected from the sediment surface due to the rocky substrate, which made raking difficult. At the remaining locations both surfaced and buried cockles were collected. Deviations to the sampling scheme (<30 cockles) occurred due to difficulty locating cockles due to low densities or tidal constraints.

2.2. Spatial variation in abiotic variables

Environmental data (sea temperature, salinity and primary productivity (net primary production of carbon, $\text{mg}/\text{m}^3/\text{day}$) were obtained from the Atlantic-Iberian Bay Irish Ocean Physics Analysis and Forecast (Copernicus, 2020). Monthly means of this daily dataset were obtained from the nearest coordinates within the bay or estuary where sampling occurred. These oceanographic models agreed with actual measurements. For example, temperature at Arcachon was similar in previous studies (de Montaudouin and Lancelleur, 2011), and low salinities have been recorded previously at Carlingford (Wilson, 1977; Wilson and Seed, 1974).

The conservation/protected area status, land usage, and types of fishing activity were recorded (Table 1). At Dundalk Bay a cockle fishery exists from July to October (Tully and Clarke, 2016), with a razor clam *Ensis siliqua* fishery occurring downshore (Marine Institute, 2016). No large scale fishery for cockles exists at Carlingford, with the exception of occasional light hand-harvesting. Samples were obtained from an oyster *Crassostrea gigas* farm. Depending on stock surveys, a fishery occurs year-round at the Burry Inlet (Natural Resources Wales, 2013) and between June and December at the Dee Estuary (Hough and Holt, 2012). At Arcachon, hand raking was not occurring during the sampling period due to low numbers of cockles in the area.

Table 1

Description of the five locations and the sites examined within each location (only for Cork Harbour and Dundalk Bay), including information on cockle fisheries, with the type of fishery and minimum capture size (MCS) i.e. minimum shell length for capture. 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	Location	Site	n	Coordinates	Fishery type	MCS (mm)	Activities	Protections	Sporocyst Prevalence (%) ^a	Metacercarial Prevalence (%) ^a
Ireland	Carlingford	Oyster Farm	229	54°01'N, 6°09'W	Occasional light hand-harvesting	17	Shipping, aquaculture, agriculture Razor clam fishery	SAC, SPA, Ramsar	4.80	81.66
		Dundalk	Annagassan	269	53°52'N, 6°20'W	Suction dredging		22	SAC	2.92
	Cork	Cooley	269	54°00'N, 6°17'W	Unfished	17	Industry, shipping	SPA	4.60	15.48
		Cuskinny	240	51°51'N, 8°15'W					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, agriculture	National Reserve	12.13	34.73

^a Mahony et al., 2021

2.3. Spatial variation in biotic variables

2.3.1. Cockle morphometrics

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 calipers (Supplementary Material, S1 Figure).

2.3.2. Cockle growth

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 because $L = 0$ does not exist) (Gosling, 2015; Ogle, 2015).

Von Bertalanffy growth parameters were estimated using the 'FSA' package in R Version 1.2.5033 (R Core Team, 2019), with nonlinear least squares estimates (Ogle et al., 2020).

Finally, growth performance indices (ϕ') were calculated for each population, following the formula of Pauly and Munro, 1984:

$$\phi' = 2 \times \log_{10}(L_\infty) + \log_{10}(k)$$

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

2.3.3. Density

On one occasion during the entire sample period, in winter 2018/2019, cockle density was randomly recorded from the low shore at low tide at each location, 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 was obtained for Dundalk Bay from The Marine Institute and Bord Iascaigh Mhara (2020). Data from this survey was obtained during July 2019 using 0.25 m² quadrats. Average density was calculated from record within a 1 km radius of the sampled sites.

2.3.4. Stable isotopes of cockle tissue

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 site (except at Ringaskiddy and Carlingford) in preparation for stable isotope analyses. Cockles were rinsed externally with fresh water. The cockles were subdivided (by visual inspection) 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 placed in clean (10% HCl) and pre-combusted (4 h at 450 °C) 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. 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 ($^{13}\text{C}/^{12}\text{C}$).

2.3.5. 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, Table 1).

2.4. Statistical analysis

2.4.1. Spatial variation in biotic and abiotic variables

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.

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 locations.

Linear and quadratic equations were examined to determine the relationship between length and weight in cockles across all sites. Both equations were fit 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.

Differences in growth models were then compared using the 'fish-methods' package (Nelson, 2019). A general model (most complex model including L_{∞} , t_0 and k) and four submodels (examining which growth parameters differ between groups) 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.

2.4.2. Drivers of spatial variation of growth

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 sites (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).

2.5. Historic spatio-temporal trends of cockle growth

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, location and sampling location (subtidal, intertidal).

Mixed effects models were employed to examine the impact of latitude and decade on historical growth parameters (L_{∞} , k). Final models were chosen using top down selection of p values (Zuur et al., 2009).

3. Results

3.1. Spatial variation in extrinsic variables

Median salinity differed significantly across sites ($H = 103.98$, $df = 7$, $p < 0.001$) and was significantly lower at Carlingford compared to

Table 2

Descriptive statistics for all variables measured in this study (April 2018 – October 2019). Median values are presented, with the exception of density and $\delta^{13}\text{C}$, as non-parametric statistics were conducted. Density estimates were gathered during winter 2018/2019. SD indicates standard deviation. Maximum values between locations for each variable indicated in bold, minimum indicated in italics. For trematode data see Table 1.

Location	Site	Latitude	Measure	Shell Length (mm)	Shell Height (mm)	Shell Width (mm)	Wet Weight (g)	Growth Rings	Salinity	Seawater Temperature °C	Primary Productivity mg C/ m ³ / day	Density ind/m ²	$\delta^{13}\text{C}$	
Carlingford Lough (Ireland)	Oyster Farm	54°N	Median	34	32.0	26.7	15.96	4	<i>12.4</i>	<i>12.1</i>	22	–	–	
			SD	3.9	3.3	3.4	4.7	1.6	10.4	2.4	30.5			
			Minimum	21.0	20.2	14.9	4.0	1	11.6	8.2	0	99		
			Maximum	45.8	40.4	39.2	32.5	11	34.2	15				
Dundalk Bay (Ireland)	Annagassan	53°N	Median	33.22	29.96	24.53	14.15	3	30.7	12.2	89	93.7	–18.6	
			SD	6.2	5.5	5.1	7.7	1.5	0.9	3.6	63.3	156.6	0.2	
			Minimum	17.2	15.0	11.5	1.3	0	28.9	6.4	6	0	–18.8	
	Cooley	53°N	Maximum	47.7	41.4	35.4	37	9	32.0	17.6	186	547.5	–18.4	
			Median	32.0	29.28	23.74	12.91	3	30.6	12.2	67	30.9	–17.9	
			SD	6.0	5.0	4.8	8.2	1.5	0.7	3.3	41.9	34.9	0.3	
Wales	Dee	53°N	Minimum	20	18.2	13.8	2.1	0	29.3	6.6	6	0.25	–18.2	
			Maximum	49.1	43.1	37.5	50.4	8	31.8	17.1	132	106.25	–17.6	
			Median	28.09	21.74	17.18	5.4	1	27.6	14.3	373	608.7	–19.5	
	Burry	51°N	SD	3.6	3.1	3.0	3.0	0.7	1.9	5.7	217.9	392.5	0.3	
			Minimum	18.3	15.5	10.9	1.8	1	24.9	4.3	21	211.7	–19.6	
			Maximum	35.8	31.2	25.5	17.2	5	30.9	21.9	610	1249.7	–19.1	
Cork Harbour (Ireland)	Cuskinny	51°N	Median	23.74	20.97	16.7	4.8	2	27.6	13.9	296	3525.3	–18.0	
			SD	3.0	2.6	2.5	2.1	0.7	1.5	4.6	235.1	2373.0	0.2	
			Minimum	17.5	15.4	11.5	1.8	1	24.2	6.4	26	201.6	–17.3	
	Ringaskiddy	51°N	Maximum	33.3	27.9	24.0	13.7	5	29.3	20.6	840	6933.7	–17.0	
			Median	35.47	32.73	26.05	18.71	4	33.9	12.1	97	9.6	–18.0	
			SD	8.3	7.1	6.2	10.2	1.9	0.7	2.5	47.1	8.3	0.2	
Arcachon (France)	Arguin	44°N	Minimum	11.8	10.4	8.4	0.8	0	31.9	8.5	9	0	–18.1	
			Maximum	49.9	43.2	35.6	46.3	13	34.8	16.5	161	28	–17.7	
			Median	33	31.01	24	14.9	3	33.8	11.9	90	–	–	
	Ringaskiddy	51°N	SD	8.2	7.2	6.5	9.1	1.6	0.8	2.5	47.5			
			Minimum	9.5	9.6	6.6	0.4	0	31.6	8.5	10			
			Maximum	46.3	42.9	38	47.7	8	34.9	16.6	171			
Arguin	44°N	Median	28.9	26.5	22.23	8.4	3	33.3	16.3	24	14	–17.3		
		SD	4.5	4.0	3.3	3.6	1.4	0.4	3.5	23.2	14.0	0.1		
		Minimum	16.2	15.5	11.2	1.4	0	32.6	11.1	6	0	–17.3		
Maximum	40.0	39.6	31.0	25.7	7	34	22.2	91	40	–17.2				

Arcachon, Cuskinny and Ringaskiddy ($p < 0.001$ in all cases, Supplementary Material Table S1). Carlingford also exhibited the largest range in salinity values (Table 2). Median sea temperature differed significantly across sites ($H = 17.766$, $df = 7$, $p = 0.013$), with significant differences between Arcachon and the northernmost sites Carlingford and Cooley ($p = 0.004$ and $p = 0.020$ respectively, Supplementary Material Table S2). Finally in terms of abiotic variables, median primary productivity also differed significantly across sites ($H = 67.334$, $df = 7$, $p < 0.001$). Primary productivity was significantly higher, or trending higher at the Burry Inlet and the Dee Estuary, relative to all other sites (Supplementary Material Table S3).

3.2. Spatial variation in cockle characteristics

3.2.1. Cockle morphometrics

Median shell length of cockles differed significantly across sites ($H = 725.91$, $df = 7$, $p < 0.001$). A post hoc Dunn test revealed that cockles were smallest at the Burry Inlet, when compared to all other sites ($p \leq 0.001$ in all cases, Supplementary Material Table S4). The largest cockles were found at Cuskinny ($p < 0.05$ in all cases, with the exception of Carlingford and Annagassan, which did not differ significantly from Cuskinny). Therefore, no relationship between length and latitude was observed (Table 2).

Weight also differed significantly between sites ($H = 876.44$, $df = 7$, $p < 0.001$). As was the case with length, mean wet weight of Welsh cockles was lower than all other sites ($p < 0.001$ in all cases, Supplementary Material Table S5). Cockles at Cuskinny were significantly heavier than all other sites, except for Carlingford. Like with cockle length, no relationship was observed between wet weight and geographic proximity as evidenced by the Dunn tests (Supplementary Material Table S5).

3.2.2. Cockle growth

The estimates for L_{∞} (asymptotic average length), k (Brody growth rate coefficient), t_0 (age at size 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. Sites within the same location (i.e. sites within Cork Harbour and Dundalk Bay), exhibited similar growth curves (Fig. 2).

Following analysis of multiple nonlinear growth models, there was a significant difference between the simplest model (where no growth parameters differed between sites), and the most complex, where all parameters differed. This suggested that growth parameters varied between sites ($\chi^2 = 308.29$, $df = 18$, $p < 0.001$, 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 sites. However, L_{∞} was not found to significantly differ among sites.

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 site.

Table 3

Growth parameters estimated using the von Bertalanffy growth model for *Cerastoderma edule*, from five Irish sites, one Welsh site (Dee) and one French site (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 age at size 0, and ϕ' is the growth performance index.

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

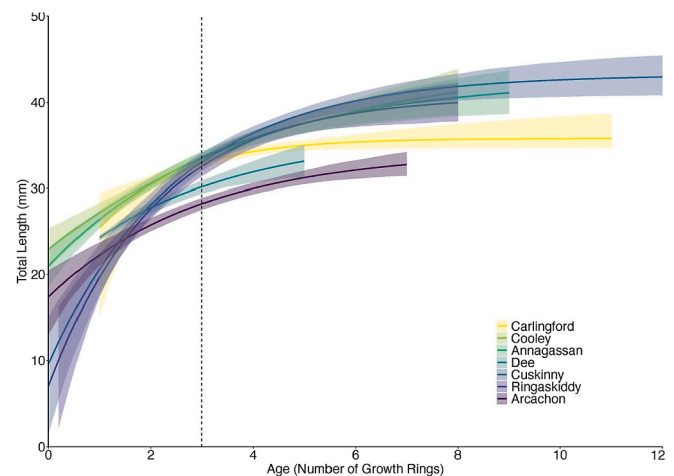


Fig. 2. Estimated von Bertalanffy growth curves of cockles at five Irish beds, one Welsh bed and one French bed. The dashed line indicates three growth rings, when variations in growth curves became evident. Shaded areas around the curve indicate the 95% confidence intervals.

However, at Carlingford, t_0 was low initially and growth appeared relatively slow in cockles >3 years (Fig. 2). Carlingford also exhibited the lowest primary productivity (differing significantly from all sites except for Arcachon; Table 2). Mean salinity also appeared to be lowest compared to the other sites, combined with a large range in salinity (Table 2). Conversely, in terms of growth parameters, both sites at Dundalk took the longest to reach maximum average length (L_{∞} ; Annagassan: 0.29 yr^{-1} and Cooley: 0.22 yr^{-1}). However, at Dundalk cockles had reached larger sizes by year three (Fig. 2). Annual temperatures were highest at Arcachon, significantly higher than Carlingford ($p = 0.004$) and Cooley ($p = 0.02$), with a trend for lower temperatures at Annagassan ($p = 0.04$ at a significance level of 2.5%). Primary productivity was generally highest at the Welsh locations, which was 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).

3.2.3. Stable isotopes of cockle tissue

The mean $\delta^{13}\text{C}$ value of cockles of all size classes differed significantly between sites ($F = 41.65$, $df = 5$, $p < 0.001$). All sites differed significantly in $\delta^{13}\text{C}$ values according to post hoc tests, with the exception of three comparisons (Burry vs Arcachon, Cooley vs Arcachon and Cuskinny vs Cooley, Supplementary Material Table S6). The sites with the lowest $\delta^{13}\text{C}$ values corresponded with the highest primary productivity (Burry and Dee, Table 2).

3.3. Drivers of spatial variation of growth

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

3.4. 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 (Fig. 3, Table 4), with lower latitudes more frequently studied since the 1990s. A total of ten studies detailing L_{∞} and k were included in this analysis (Table 4). L_{∞} tended to generally 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, Fig. 3A). However, not all locations exhibited an increase in L_{∞} over time, as demonstrated by a reduction at Arcachon

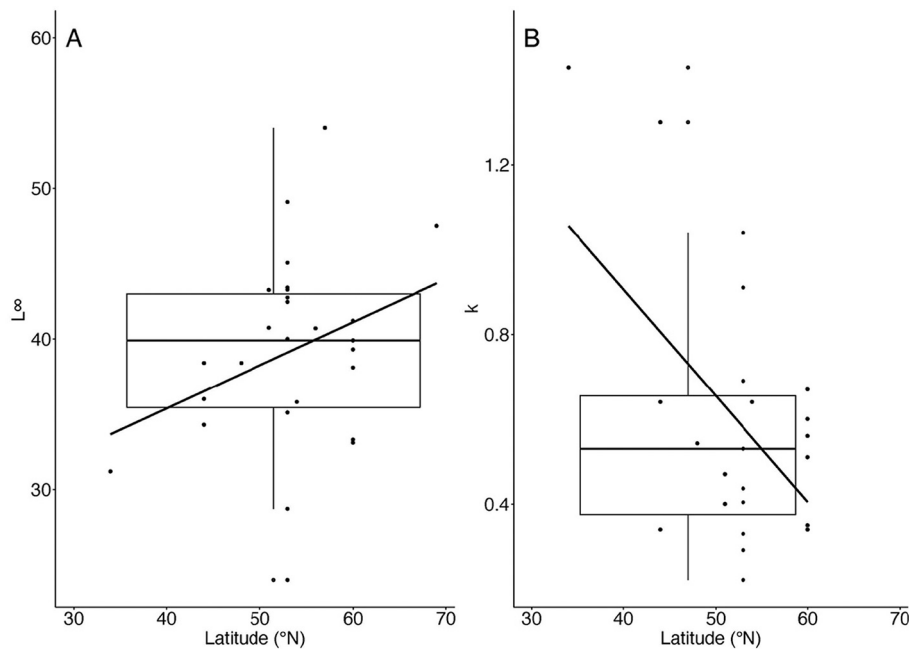


Fig. 3. Relationship between latitude and (A) L_{∞} and (B) k , based on mixed effects models. Values for L_{∞} and k were obtained from the current study and historic studies. The boxplots demonstrate the median values, the boxes extend from the 25th to 75th percentile of each distribution of values, and whiskers show the largest and smallest values within 1.5 times the interquartile range.

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 et al., 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	Netherlands	2001–2003	53	Intertidal	Cardoso, 2007
43.26	1.04	3.3	Wadden Sea	Netherlands	2001–2003	53	Subtidal	Cardoso, 2007
49.10	0.44	2.7	Dundalk	Ireland	2003–2004	53	Intertidal/Subtidal	Fahy et al., 2004
42.74	0.29	2.2	Dundalk (Annagassan)	Ireland	2018–2019	53	Intertidal	This Study
45.04	0.22	1.9	Dundalk (Cooley)	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 et al., 1987
28.73	0.69	2.6	Traeth Melynog	Wales	1986	53	Mid Shore	Sanchez-Salazar et al., 1987
35.10	0.53	2.5	Traeth Melynog	Wales	1986	53	Low Shore	Sanchez-Salazar et al., 1987
42.45	NA	NA	Traeth Melynog	Wales	1976–1997	53	Intertidal	Richardson et al., 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	Ponsoero et al., 2009
36.00	0.64	2.7	Arcachon	France	1997–2014	44	Intertidal	Magalhães et al., 2016
38.40	1.30	3.4	Arcachon	France	2005–2007	44	Intertidal	Gam et al., 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 et al., 2010

between this study and a previous study from 2005 and 2007 (Table 4). The Brody growth rate coefficient (k) decreased significantly at higher latitudes (i.e. cockles reached L_{∞} in less time at lower latitudes; $p = 0.04$, Fig. 3B). Only two locations 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 the present study.

4. Discussion

This field survey further affirmed the variability among 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 growth curves. This finding is most likely due to a reduced representation of larger cockles in the population caused by local fishing activities. However the historic survey indicated that latitude (and likely temperature) may potentially impact cockle growth parameters, with cockles reaching larger asymptotic average length (L_{∞}) at northern sites. Furthermore, these results may agree with a previous study where cockles grew faster (to smaller sizes) 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, populations at the same latitude did not always have similar growth rates (e.g. Dundalk vs the Dee). Therefore, it is more important to consider the influence of local abiotic and biotic drivers influence growth, more so than latitudinal variations.

4.1. Spatial variation in abiotic drivers of cockle growth

Cockles at Dundalk Bay reached >30 mm earliest compared to all other sites, supporting a productive fishery here. However, Dundalk also exhibited among the lowest growth performance indices. Furthermore, while strictly speaking, cockles at Carlingford (lightly fished) exhibited the highest growth performance, the growth rate never exceeded that of other sites and cockles here had a small asymptotic average length (L_{∞}). Additionally, cockles at all three unfished/lightly fished sites (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. While growth performance was not lowest at Carlingford, the growth curve demonstrated slow growth initially.

The slow growth in later years at the lowest salinity site, Carlingford, may demonstrate the role of abiotic drivers on cockle growth. At Cork, where salinity was highest, cockles 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). Considering the potential for increased precipitation events in combination with increasing water temperatures due to climate change (Beniston et al., 2007), this negative impact of low salinity is a potential threat for the future growth of cockles. Nevertheless, 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.

4.2. Spatial variation in biotic drivers of cockle growth

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 due to potentially 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. 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 for speciation would be beneficial to determine the species present at these sites. Furthermore, it would also be useful to conduct surveys in these locations to determine the impacts

of other pathologies or pollutants.

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 location 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.

4.3. Interactions between biotic and abiotic variables

In many cases, it is likely that the relationship between drivers of cockle growth act additively, synergistically or antagonistically. For example, it would 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 previously been demonstrated in cockles, likely due to food availability (Beukema et al., 2017). As mentioned, high metacercarial prevalence in combination with low salinity at Carlingford was potentially detrimental to growth. This is concerning, due to the possibility of increased trematode transmission resulting from warming seawater (de Montaudouin et al., 2016).

4.4. Historic spatio-temporal trends of cockle growth

Examining the historic spatio-temporal trends was possible due to comparisons among the current and historical literature. In particular, previous studies have been conducted at Arcachon and Dundalk, allowing for a comparison between current and past growth rates at these sites. 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 possibly 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). 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, potentially due to the influence of temperature on spawning (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).

4.5. Conclusions

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 size trajectories as currently experienced at warmer, southern locations. This may consequently disrupt the production of cockles at northern latitudes, damaging fisheries. Therefore, it would be beneficial to conduct similar field studies at the extreme high and low latitudes. Finally, due to the local differences, growth patterns appeared to vary 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.

Declaration of competing interest

The authors have no conflicts of interest to declare.

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Appendix A. Supplementary data

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