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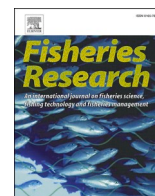
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Re-assessing the growth parameters for the razor clam, *Ensis siliqua*, from Scottish electrofishing grounds using external shell marks and oxygen isotope validation

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ABSTRACT

Landings of razor clams by global capture fisheries have increased by around 15 times since the turn of the century. Harvesting techniques range from hand-picking and use of brine solutions to force the clams to emerge, to more intensive mechanical and hydraulic dredging. In Scotland, electrofishing for the pod razor (*Ensis siliqua*) is presently the focus of a government run scientific trial. Growth estimates are an important component of fisheries management contributing to yield-per-recruit and natural mortality estimation. However, growth rate estimates should be periodically re-evaluated, particularly when harvesting practices have changed. Interpretation of external shell growth increments alongside validation by oxygen isotope analyses was used to generate length-at-age data for *E. siliqua* collected from five sites within the Scottish electrofishing scientific trial. Von Bertalanffy growth curves were then fitted to these data using a hierarchical Bayesian approach. Across all five sites the mean of the asymptotic length (L_{∞}) was estimated to be 191 mm and the mean of the Brody coefficient (k) estimated at 0.27 y^{-1} . The 95 % credible intervals for L_{∞} were from 182 to 206 mm, and for k were between 0.17 and 0.33 y^{-1} . These new estimates are consistent with previous published results from Scottish sites suggesting that recent changes to harvesting practices have not led to substantial changes in *E. siliqua* growth rates.

1. Introduction

Up to the turn of the century reported global landings of razor clams averaged just over 800 tonnes per annum. However, since then there has been an increase of about 15 times so that combined landings from the USA, Pakistan, Spain, Ireland and the UK have averaged 2670 tonnes per annum, while the Netherlands has become the leading producer averaging 4630 tonnes per annum (FAO, 2024). The Netherlands landings include the invasive Atlantic jack-knife clam (*Ensis leei* synonymised names *E. americanus*; *E. directus*) which became established in the southern North Sea after the 1970s (Hervás et al., 2012; Armonies and Reise, 1998). Other countries with minor reported landings of razor clams (< 200 tonnes per annum) include Portugal, Italy, France, Norway, and Mexico (FAO, 2024). However, reported landings are likely to be conservative because artisanal catches often go unrecorded (Hernández Otero et al., 2016) or landings may be included in the generic “clams nei” category (FAO, 2024). Razor clams are also

cultivated e.g. production of the Constricted Tagelus (*Sinonovacula constricta*) in China reached 860,000 tonnes in 2022 (FAO, 2024), thus far exceeding razor clam landings from capture fisheries.

The main species harvested in Scotland is the pod razor, *Ensis siliqua* and the majority of the catch is exported live to the Far East (Scottish Government, 2023). Over the period 2018–2022, annual landings were between 442 and 643 tonnes with a value of £3.4 to £6.4 million (Marine Scotland, 2023). Whilst the razor clam fishery is relatively small in terms of total Scottish fish and shellfish landings (393 to 447 thousand tonnes, worth £520 to £663 million per annum), the razor clam fishery is of local importance for diversification, and for coastal economies and employment.

Ensis siliqua is found in sandy sediments in sheltered to moderately exposed locations where their depth distribution ranges from the shallow inter-tidal down to around 20 m (Holme, 1954). Filter-feeding by the pod razor clam often results in a characteristic keyhole shape in the sediment surface but when disturbed, or during poor weather,

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they can burrow down to depths of around 30 cm (Muir, 2003). Since pod razor clams are normally buried just below the surface harvesting techniques include hand-picking, often combined with the use of brine solutions to force the clams to emerge (Constantino et al., 2009), to more intensive mechanical and hydraulic dredging (Diaz et al., 2011; Vasapollo et al., 2020; Marine Institute, 2022). Traditionally the Scottish razor clam fishery was dominated by the hand-picking or salting techniques, but as European and Far Eastern demand for razor clams grew, fishers began to experiment with more intensive methods such as suction dredging (Bailey et al., 1998; Robinson and Richardson, 1998; Muir, 2003; Hauton et al., 2011). Electricity can also be used to encourage razor clams to emerge onto the surface of the seabed where they can be more easily collected by divers (Breen et al., 2011). Compared with dredging, electrofishing produces a cleaner and less damaged product which increases the marketability. There may also be conservation benefits with electrofishing as undersized clams are left on the seabed where they generally rebury within a few minutes (Murray et al., 2014). In contrast, dredging causes a certain amount of shell damage which can lead to direct mortality or delayed reburying after undersized clams are discarded (Robinson and Richardson, 1998). Habitat disturbance from electrofishing is also lower compared to dredging (Murray et al., 2014, 2016), although others have argued that the benthic communities where razor clams occur are well adapted to both natural and artificial disturbance (Tuck et al., 2000). Of more concern is that both dredging (Hauton et al., 2002, 2007; Fahy and Carroll, 2009) and electrofishing (Fox, 2023) appear to be highly efficient. Since pod razors can potentially live more than 20 years (Bailey et al., 1998; Gaspar et al., 1994; Henderson and Richardson, 1994), maturation takes at least four years (Fahy and Gaffney, 2001), and recruitment is thought to be sporadic (Fahy and Gaffney, 2001), such efficient fishing techniques run the risk of rapid resource depletion unless the fisheries are well managed (Fahy and Carroll, 2007; Gaspar et al., 2011).

Whilst electrofishing remains banned under the European Union Common Fisheries Policy, scientific trials are permitted. After a public consultation the Scottish Government established such a trial from February 2018 to determine whether a sustainable electrofishery for razor clams could be developed (Scottish Government, 2017). Under this scientific trial, harvesting is restricted to fewer than 30 licenced vessels which must operate within defined spatial boundaries, carry Remote Electronic Monitoring (REM) equipment and conform to a daily landing limit of 450 kg (Scottish Government, 2019). Fishing is also only permitted for 110 days each year. The grounds targeted by this fishery are close to shore and harvesting is generally restricted to a maximum depth of approximately 10 m because of bottom-time limits on air-based diving (Scottish Government, 2021; Blackadder et al., 2024). Apart from the Firth of Forth, the permitted harvesting zones are principally located on the Scottish west coast (Blackadder et al., 2024).

The Scottish scientific trial has a number of biological and ecological goals including development of length-based stock assessments which require data on growth parameters (Blackadder et al., 2024). For bivalve shells, the spacing of commarginal incremental growth lines changes with growth rate and this can lead to pronounced features when growth slows or ceases in response to seasonal environmental signals. These features can thus often be interpreted as annuli and used as a basis for age determination (Richardson, 2001). Care is however needed to differentiate annual growth increments from checks produced by other stochastic processes, such as disturbance. Regressing shell lengths against the age estimates then allows average growth curves to be generated.

Previous studies have either fitted growth curves to ages versus total shell lengths determined from individual shells (Bailey et al., 1998; Fahy and Gaffney, 2001; Hauton et al., 2002; Muir, 2003), or to back-calculated shell lengths corresponding to each annual increment within individual shells (Gaspar et al., 1994; Henderson and Richardson, 1994). The first method requires many samples covering the full-size range in the population and also assumes a constant population

Table 1

Details for the *E. siliqua* samples used in this study which were collected by fishers participating in the Scottish electrofishing trial. Sites where a razor clam was used for oxygen isotope ageing validation are indicated by an asterisk.

Site	Date	Lat (deg)	Long (deg)	Shell lengths	
				min (mm)	max (mm)
Broad Bay, Isle of Lewis	31/05/ 23	58.2320	-6.2827	142	206
West of Jura*, Outer Firth of Lorn	08/08/ 22	56.0082	-6.0439	142	214
Irvine Bay*, Firth of Clyde	19/05/ 21	55.6259	-4.7685	151	205
Wigtown Bay, Galloway	31/05/ 23	54.8273	-4.3103	178	198
Elie*, Firth of Forth	18/05/ 21	56.1830	-2.8526	152	166

growth rate. The second approach can extract more information from each individual, but accounting for the individual growth effect has been problematic when fitting growth curves using classical regression (Jones, 2000). However, mixed models (Vincenzi et al., 2020) and hierarchical Bayesian approaches (Morat et al., 2020) have now largely resolved this statistical challenge. The full Bayesian approach also allows previously published growth rate estimates to be incorporated into the estimates via the priors.

In the present study, a hierarchical Bayesian approach was used to fit individual and site-averaged von Bertalanffy growth functions (VBGFs) to samples of *E. siliqua* collected from five areas in the Scottish Government's scientific trial. The new growth parameter estimates were

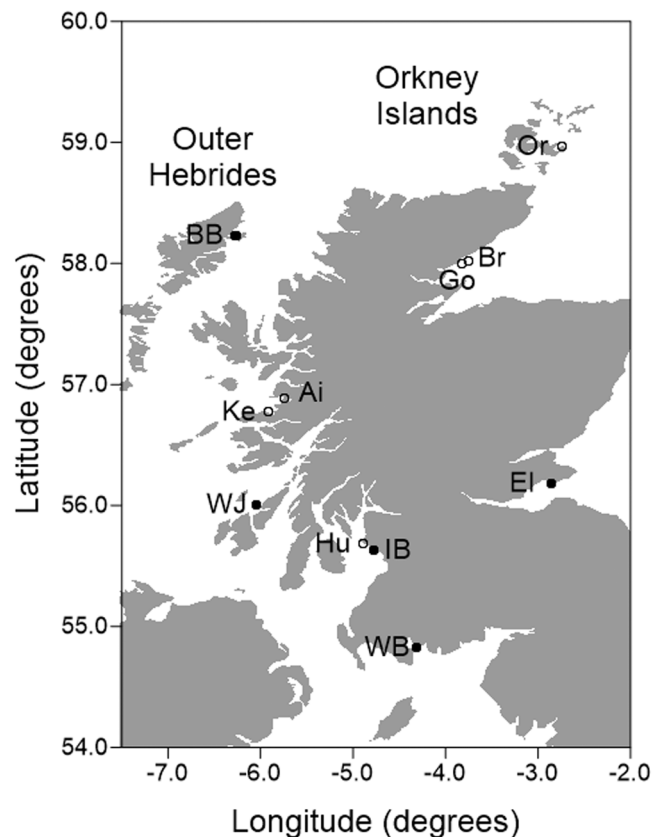


Fig. 1. Locations mentioned in the text. Ai = Ailort; Br = Brora; BB = Broad Bay; E = Elie; Go = Golspie; Hu = Hunterston; IB = Irvine Bay; WJ = West of Jura; Ke = Kintyre; Or = Orkney; WB = Wigtown Bay. Sites where samples were aged in the present study are marked with filled circles, sites where samples were aged in the present study are marked with open circles.

then compared with older published estimates to assess whether the recent changes in harvesting practices have led to noticeable changes in growth rates.

2. Materials and methods

Fishers participating in the Scottish electrofishery trial provided samples of twenty large razor clams (*E. siliqua*) from five harvest sites (Table 1). After delivery to the Scottish Association for Marine Science the samples were stored frozen at -10°C prior to further processing. After thawing, the flesh was removed, the shells gently scrubbed to remove any sand particles, and the shells then dried overnight at room temperature.

2.1. Age determination from growth increments

Growth increments were scrutinised macroscopically from the external surface of the shells. For each shell, the periostracum was carefully removed from the dried left valves using a razor blade. The valve was then placed on a light box which helped to create contrast between opaque (dark) and translucent (lighter) areas. Annuli were identified as darker lines which could be followed around the entire shell. The end of each annual growth cycle was also discerned by slight humps on the shell surface, suggesting the reduction of spacing between striae as growth slowed. The distances from the shell umbo to the start of each dark band were measured along the maximum axis of growth using digital callipers.

2.2. Validation of age determination using oxygen isotope analyses

Three razor clams were selected for isotope analysis, one each from the samples from West of Jura, Irvine Bay, and Elie (Fig. 1). The periostracum had already been removed so the shells were rinsed with ethanol and allowed to air dry. Samples of shell powder were collected by hand micro-drilling the external, convex surface using a pre-cleaned jeweller's scribe under the stereomicroscope. Powder was collected from 80 positions, distributed along the axis of maximum growth. The separation of sampling positions was reduced as the increments narrowed towards the growing edge. From each drill site, approximately 50 – 200 μg of powder was transferred into a 10 ml glass vial and sealed with a silicone rubber septa using a screw cap. The samples were sent to the Godwin Laboratory for Palaeoclimate Research, Department of Earth Sciences, University of Cambridge where they were flushed with CP grade helium, acidified with 104 % orthophosphoric acid (Burman et al., 2005) for 1 hour at 70°C , and then analysed using a Thermo Gasbench preparation system attached to a Thermo Delta V Advantage mass spectrometer in continuous flow mode. Each sample run was accompanied by 10 reference carbonates (Carrara Z) and two control samples (Fletton Clay). Carrara Z has been calibrated to Vienna Pee Dee Belemnite (VPDB) using the international standard NBS19. The results are reported with reference to the international VPDB standard, and the precision is better than ± 0.10 per mil for $^{18}\text{O}/^{16}\text{O}$.

2.3. Fitting the growth curves

For organisms such as *E. siliqua*, which release planktonic larvae in the spring that then settle as juveniles part-way through the year, it can be more meaningful to recode the first winter growth mark as age 0. This results in L_0 becoming the estimated average shell length at the end of the first growth phase, i.e. after around six to nine months with subsequent length increments representing complete years of growth. This recoding does not affect the estimates of L_{∞} or k . The age and length data were modelled using the 'fishgrowbot' package (Schiettekatte, 2021) in R v4.1.1 (R Core Team, 2022). This package fits the 'specialized' VBGF which assumes that anabolism scales with mass to the $2/3$ power and mass scales with the cube of size (Vincenzi et al., 2020). Fitting using

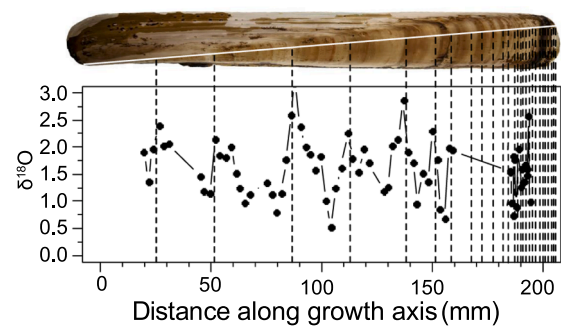


Fig. 2. Stable oxygen isotope ratio profiles for the razor clam (*E. siliqua*) from West of Jura analysed for ageing validation. Solid dots indicate the isotope ratio with reference to the Vienna Pee Dee Belemnite (VPDB) standard; Dashed vertical lines indicate the visually identified annual growth increments. Photograph of the shell with the periostracum removed and photographed on a lightbox to increase the contrast of the increments. The solid white line indicates the axis of growth.

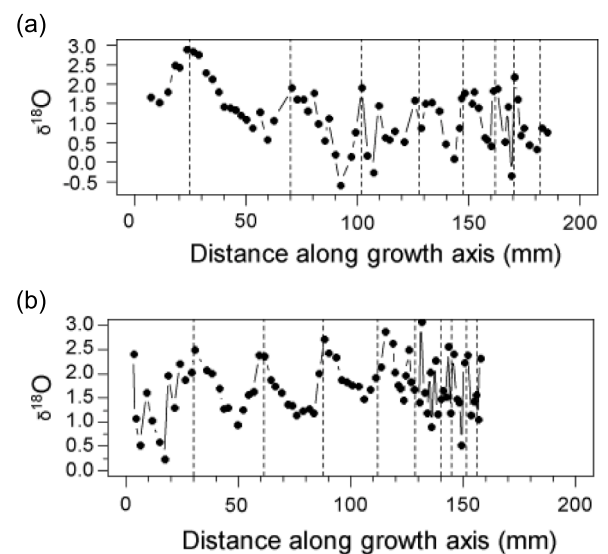


Fig. 3. Stable oxygen isotope ratio profiles for the *E. siliqua* analysed for ageing validation from (a) Irvine Bay and (b) Elie. Solid dots indicate the isotope ratio with reference to the Vienna Pee Dee Belemnite (VPDB) standard; Dashed vertical lines indicate the visually identified annual growth increments.

'fishgrowbot' estimates the joint distribution of the three parameters (L_{∞} , k and L_0) in Eqn [2] where $E(L|t)$ is the expected shell length (mm) at age t (y), L_{∞} is the asymptotic average size in mm, L_0 is the length at age zero (mm) and k is the Brody growth coefficient (y^{-1}).

$$E(L|t) = L_{\infty} - (L_{\infty} - L_0) e^{-kt} \quad (2)$$

The 'fishgrowbot' package applies a hierarchical Bayesian approach where growth curves are first fitted to individuals, followed by an overall population curve. Fitting uses a dynamic Hamiltonian Monte-Carlo Markov Chain (MCMC) as implemented via RStan (ver2.32.6). Because the *E. siliqua* data directly related shell lengths to their equivalent ages, the back-calculation function ('bcalc') in 'fishgrowbot' was not used and the length-at-age data were submitted directly for growth curve fitting ('growreg'). Gaussian priors were set at 194 ± 10 mm (mean \pm SD) for L_{∞} and 37 ± 5 mm (mean \pm SD) for L_0 based on previous VBGF parameter estimates for *E. siliqua* from Scotland (Hauton et al., 2002). Posterior sampling used 4 chains with 10,000 iterations and a 50 % warm-up.

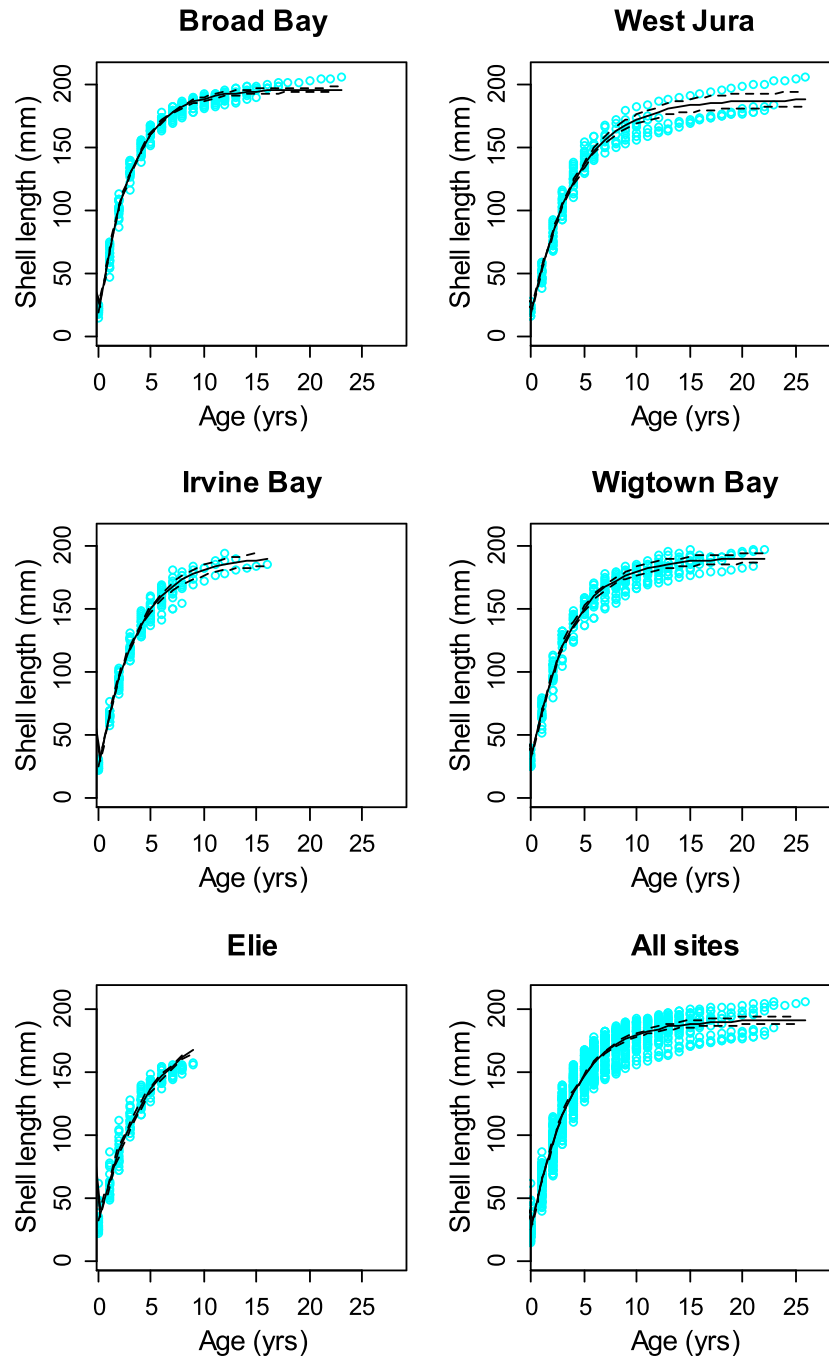


Fig. 4. Raw length at age data and fitted VBGF growth curves for razor clams, *E. siliqua*, by site. Dashed lines indicate the 95 % credible intervals for the fitted growth curves.

3. Results

3.1. Validation of age determination from visual shell increments

Taking the first annual increment as equivalent to age 0, the visually estimated age of the razor clam sampled for validation from West Jura was 26 years (Fig. 2), the razor clam from Elie was 8 years (Fig. 3) and the one from Irvine Bay was 7 years (Fig. 3). For the Elie sample, a single anomalously low $\delta^{18}\text{O}_c$ sample (spot 19) was removed before further data analysis. The oxygen isotope profiles for all three razor clams

showed regular asymmetric patterns between each pair of visually identified annuli (Figs. 2 and 3). For the razor clams from Elie and Irvine Bay these regular patterns encompassed the whole shell but for the oldest parts of the West of Jura shell the growth increments became too close together to resolve the oxygen isotope pattern beyond 160 mm shell length (Fig. 2). The regular patterns in the $\delta^{18}\text{O}$ profiles for all three shells supported the visual identification of the annual growth lines. In biogenic aragonite, the $\delta^{18}\text{O}$ ratio is expected to increase with decreasing water temperature (Grossman and Ku, 1986) so that the coincidence of high $\delta^{18}\text{O}$ values with the visually identified annual

Table 2

Previously published growth rate estimates for the razor clam, *E. siliqua*. L_{∞} is theoretical maximum average length; k is the Brody growth coefficient; L_0 is the shell length at first annual growth increment. 'na' indicates parameter estimate was not reported. Data sources: ^a Gaspar et al# (1994); ^b Henderson and Richardson (1994); ^c Fahy and Gaffney (2001); ^d Hauton et al# (2002). For the Kentra site, Hauton et al# (2002) analysed separate samples collected in April and Nov 2001.

Site	L_{∞} (mm)		K (d^{-1})		L_0 (mm)	
	mean	SE	mean	SE	mean	SE
	(mm)	(mm)	(d^{-1})	(d^{-1})	(mm)	(mm)
Portugal ^c	139.6	NA	0.65	NA	58.0	na
North Wales ^b	154.7	6.1	0.53	0.07	63.4	na
Ireland ^a	178.2	NA	0.26	NA	31.6	0.04
Kentra Nov 2001 ^d	180.0	7.1	0.44	0.295	63.5	na
Golspie ^d	185.6	5.8	0.15	0.037	25.2	na
Lewis ^d	188.3	2.3	0.22	0.025	37.6	na
Ailort ^d	189.8	6.0	0.23	0.064	38.2	na
Kentra Apr 2001 ^d	191.8	14.5	0.22	0.061	37.3	na
Brora ^d	196.3	8.2	0.11	0.031	19.9	na
Hunterston ^d	206.6	18.7	0.27	0.158	48.1	na
mean Scottish	193.9	3.3	0.22	0.031	37.1	na

growth lines suggests that these form when water temperatures reach their minima during winter to early spring (Cardoso et al., 2013).

3.2. Growth curves

While razor clam samples from Broad Bay, West of Jura and Wigtown Bay included several clams up to 20 + years of age (Fig. 4), nearly all the specimens from Irvine Bay and Elie were estimated to be younger than 10 years. VBGF curves generally had good fits to the length at age data for individual shells (Supplementary Figures 1 to 5), but negative divergence was noticeable above about 150 mm shell length (e.g. Broad Bay sample 16; Wigtown Bay sample 8). Chain mixing during MCMC fitting was considered acceptable (Supplementary Figures 6 to 11) as was the linearity of the sampled parameter spaces (Supplementary Figures 12 to 17). Posterior predictive checks appeared acceptable (Supplementary Figure 18), although the site level model underestimated the size of the youngest ages for West of Jura. The distributions of the posterior draws (Supplementary Figures 19 to 24) yielded credible intervals of L_{∞} from 182 to 206 mm, and for the Brody growth coefficient between 0.17 and 0.33 y^{-1} (Table 3). Comparing the site level growth curves with the raw length at age data suggests that the VBGFs adequately captured the *E. siliqua* growth patterns up to about 15 years of age but there was evidence that beyond this age growth does not slow as fast as predicted (Fig. 4).

For L_{∞} the new growth estimates showed good agreement with earlier published results for *E. siliqua* from Scottish mainland sites (Fig. 5). The pattern of broadly decreasing L_{∞} moving from north to south as noted by Hauton et al. (2002) is also maintained by the addition of these new estimates. Similarly estimates for k are close to those previously published for *E. siliqua* from Scottish sites. Estimates of L_0 were more variable although the range of credible intervals for the new estimates encompassed, or were very close to, those of previous published

Table 3

Parameter estimates for the VBGF fitted by site. LCI and UCI are the upper and lower boundaries of the 95 % credible intervals.

Site	L_{∞} (mm)			K (d^{-1})			L_0 (mm)		
	mean	LCI	UCI	mean	LCI	UCI	mean	LCI	UCI
Broad Bay	196	194	198	0.32	0.31	0.33	19.1	17.3	20.9
West of Jura	188	182	195	0.24	0.22	0.25	18.1	16.0	20.2
Irvine Bay	192	186	198	0.28	0.26	0.29	26.1	24.5	27.8
Wigtown Bay	191	187	198	0.28	0.27	0.28	31.8	30.0	33.6
Elie	189	182	197	0.22	0.19	0.24	32.1	29.3	35.0
All	191	188	194	0.27	0.26	0.28	25.4	23.7	27.2

results.

4. Discussion

4.1. Validation of annual growth increments

In this study, validation of visual age determination was confirmed for the pod razor clam (*E. siliqua*) using oxygen isotope analysis. This corroborates conclusions regarding the reliability of visual ageing of the Atlantic jack-knife clam (*E. leei*) sampled from the southern North Sea (Cardoso et al., 2013). In that study the authors were also able to reproduce the seasonal patterns in water temperature from their oxygen isotope data using the biogenic $\delta^{18}O$ temperature regression of Grossman and Ku (1986). This suggested that shell growth in *E. leei* slows or ceases below about 6°C. We would expect similar results for *E. siliqua* but because of a lack of long-term salinity timeseries for the Scottish inshore sites, we were unable to estimate corresponding environmental temperatures from our oxygen isotope data. In Cardoso et al. (2013) the maximum age of the razor clams analysed was five years with a minimum inter-annuli spacing of about 50 mm so they were able to sample at high spatial resolution along the whole growth axis. In contrast, because the inter-annuli spacing became so narrow it became impossible to resolve the interannular material in the oldest parts of our validation sample from the West of Jura (Fig. 2). Our validation of visual ageing therefore assumes that the characteristic appearance of the annual lines validated for up to 6 or 7 years of age continues throughout the growth of *E. siliqua*.

4.2. Approaches to ageing razor clams

Various methods have been used to age *Ensis* spp. including length cohort analysis (Bailey et al., 1998), identification of annual increments using acetate peels of longitudinal shell sections (Gaspar et al., 1994; Henderson and Richardson, 1994; Robinson and Richardson, 1998), and identification of annual increments using thin-sections of shells from the umbo region (Bailey et al., 1998; Hauton et al., 2002). Issues with visual age determination were noted by Gaspar et al. (1994) who found that analysing internal versus external shell marks produced slightly different growth curves, and Henderson and Richardson (1994) who reported that their shells of inter-tidal origin contained sub-annual increments related to periods of immersion and emersion. However, Cardoso et al. (2013) concluded that external shell lines can be reliably interpreted as annuli as demonstrated in *E. leei*, although they also recommended that validation be included in future applications of visual age determination.

4.3. *E. siliqua* growth rates

Organism growth rates are an important consideration in fisheries management as they affect potential harvest yields and are correlated with age at maturity, which itself affects the resilience of populations to exploitation. Growth rates are also used in yield-per-recruit analyses, to infer natural mortality rates, and provide a basis for setting reference points such as F_{msy} (the fishing mortality associated with maximum

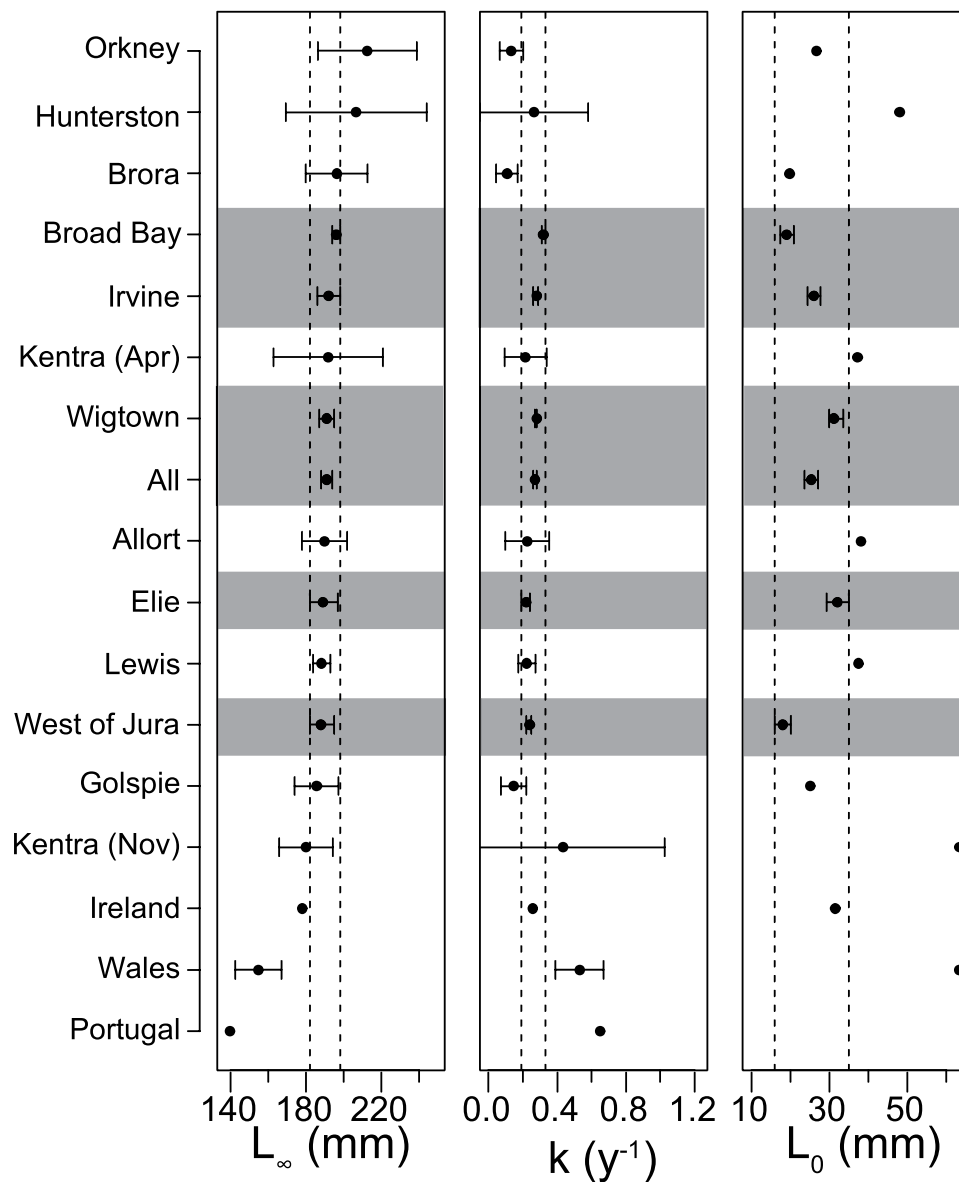


Fig. 5. Comparison of Bayesian VBGF parameter estimates with previously published estimates from data cited in Table 2. New results from the present study are highlighted in grey and sites ordered by decreasing L_{∞} (Length at infinity). For previous studies approximate 95 % confidence intervals are shown based on information provided in those publications while for the Bayesian estimates the 95 % credible intervals are shown.

sustainable yield). Growth rates should however be periodically re-evaluated because they can be affected by changes in food availability, population density, or trends in environmental factors (Dmitriew, 2011). Such re-evaluations are particularly important when there has been a change in the harvesting regime as density-dependent growth effects may become apparent (Croll et al., 2023).

It is known that growth rates of *E. siliqua* can differ by sex with females growing slightly slower than males (Fahy and Gaffney, 2001). However, determining the sex of razor clams is challenging and requires gonadal smears or histology on the partially ripe or ripe gonads (Darriba et al., 2005; Cross et al., 2014). In Scottish waters, gametogenesis occurs during the winter and recent histological results show spawning activity in April and May (Blackadder et al., 2024). This would be similar to Ireland where Cross et al. (2014) suggested spawning occurs between March to July and northwestern Spain where Darriba et al. (2005) reported spawning occurs during April to May. Hermaphroditism can also occur but tends to be rare (Darriba et al., 2005; Blackadder et al., 2024).

Although some papers suggest the colour of the gonads in mature specimens differs slightly (Muir, 2003; Darriba and Patiño, 2011), we were unable to reliably see this difference in our samples which were not all collected at times when the gonads would be expected to be mature. Our growth rate estimates are thus based on unsexed samples but because fishers do not distinguish razor clams by sex during collection, combined male-female growth rates are used in the management of this fishery (Blackadder et al., 2024).

As with several other species of bivalves (Gosling, 2003), growth in *E. siliqua* appears to be indeterminate. The analysis of samples in the present study suggests that the asymptotic VBGF may not capture growth of *E. siliqua* beyond around 15 years as this age appears to form a breakpoint after which shell growth continues at a more constant rate than predicted (Fig. 4). Such a pattern is less likely to be revealed in studies where total shell lengths are regressed against total age data, but it can be seen when individual growth curves are reconstructed. However, as the samples analysed in the present study contained relatively

few older specimens it may be pre-emptive to apply a different growth model and previous published razor clam growth rates have also all used the VBGF (Table 2). For fishery management purposes growth during the younger ages has the most influence on stock resilience and yields and this part of the growth of *E. siliqua* does appear to be captured by the VBGF. However, it may be worthwhile considering alternative growth models which have been suggested as being more suitable for long-lived bivalves (Richardson, 2001, Klinck et al., 2023).

Bivalve growth rates are influenced by multiple factors including those which are site specific, such as water depth and sediment composition; temporal changes in factors such as temperature, salinity and food supply; and occurrence of disease (Gosling, 2003). In addition, variable recruitment and patchy settlement have the potential to generate density-dependent growth effects. For example, Weinberg (1998) showed a clear link between local density and both L_{∞} and k in the surf clam (*Spisula solidissima*). However, other studies have noted that levels of density-dependent growth suppression in bivalves are often quite small. In quahog (*Merccenaria mercenaria*) Peterson and Beal (1989) reported an average decrease in growth of 18 % for larger quahog and 10 % for smaller sizes associated with an eight-fold increase in density (10–80 individuals m^{-2}). In the Pacific oyster (*Crassostrea virginica*) Puckett and Eggleston (2012) did detect a density-dependent effect on growth, but the growth rates were highly variable between sites and the density effect appeared to be confounded with settlement year. Studying cockles (*Cerastoderma edule*) in the Wadden Sea, Beukema and Dekker (2015) reported that growth in tissue dry weight was only suppressed in a few years which had anomalously high densities. Generally, it seems that intraspecific competition for resources may be quite weak in suspension-feeding bivalves, as long as densities are not extremely high (Beukema and Dekker, 2015). Furthermore, because high densities of razor clams typically only occur within small patches (Fox, 2023), any localised suppression of growth will tend to be averaged out across larger areas.

Historical estimates of razor clam densities around Scotland are limited so it is difficult to know exactly how densities have changed since the early 2000s. Furthermore, the local densities where the samples in the present study were collected are not known, but there has likely been a general reduction in the abundance of older individuals in the fished sites as it is the larger clams which are preferentially harvested (Fox, 2023; 2024). However, any changes in *E. siliqua* densities or environmental conditions in the trial sites do not appear to have resulted in substantial effects on pod razor clam growth rates since the re-assessed VBGF parameter estimates were in good agreement with historical results from a variety of Scottish mainland sites (Hauton et al., 2002).

CRedit authorship contribution statement

Blackman Chloe: Writing – review & editing, Writing – original draft, Investigation. **Fox Clive:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Conceptualization. **Blackadder Lynda:** Writing – review & editing, Project administration, Funding acquisition. **Harper Elizabeth M.:** Writing – review & editing, Writing – original draft, Resources, Methodology.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Chloe Blackman reports financial support was provided by a SUPER Doctoral Training Partnership (<https://superdtp.st-andrews.ac.uk/>) grant - Organism and Ecological Impacts of Electrofishing in Scottish Shallow Coastal Habitats. The other authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.fishres.2025.107294](https://doi.org/10.1016/j.fishres.2025.107294).

Data availability

Data will be made available on request.

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