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The population structure and biology of the ocean quahog, *Arctica islandica*, in Belfast Lough, Northern Ireland

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The spatial distribution, density, growth rate, longevity, mortality and recruitment patterns of the long-lived clam Arctica islandica *in Belfast Lough, Northern Ireland, UK are described. The* A. islandica *population at Belfast Lough appears to be restricted to a small area at the mouth of the Lough. Additional searches for specimens further into the Lough and into deeper waters found no evidence of a larger more widespread population and we report population densities of 4.5 individuals* m^{-2}*. The ages of the clams were determined from the number of internal annual growth lines in acetate peel replicas of shell sections. The population growth curve was fitted using the Von Bertalanffy growth equation:* $L_t = 93.7$ *mm* $(1-e^{-0.03(t-1.25)})$*. Based on catch curve analysis, the Belfast Lough population has an estimated longevity of 220 years and a natural mortality rate of 0.02. We compare growth characteristics and life history traits in this population with other analogous* A. islandica *populations. The overall growth performance and the phi-prime index were used to compare growth parameters with data from the literature and we observed no significant relationship between the growth performance indices and longevity or latitude. Analysis of the age-structure and reconstructed dates of settlement indicate that this population has experienced almost continual recruitment over the last century with a gap in successful recruitment into the population 90–100 years ago and another 140–150 years ago. The size-structure revealed a scarcity of small individuals which we believe may be an artefact of the dredge sampling process.*

Keywords: *Arctica islandica*, distribution, density, recruitment, mortality, longevity

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INTRODUCTION

The ocean quahog, *Arctica islandica* (Linnaeus, 1767), is a large long-lived suspension feeding infaunal bivalve mollusc found burrowed in the top 5 cm or deeper of sand and muddy substrates in the shelf seas of the North Atlantic, commonly at a water depth of 25 to 80 m (Mann & Wolf 1983). In Europe the species occupies a wide latitudinal range from the Bay of Biscay in the south (48°N), to Icelandic waters (66°N) and even as far north as of the southern coast of the Svalbard (76°N) in the Arctic Ocean (Dahlgren *et al.*, 2000), whilst on the eastern coast of North America it occupies a latitudinal range from Labrador to Cape Hatteras (Franz & Merrill, 1980).

The ocean quahog is of both commercial and academic interest. Commercially it is harvested in the USA, Canada and Iceland; conversely it is not a very marketable species in European waters and no commercial fisheries exist. Academically, however it is becoming an increasingly important species being utilized both as a high resolution marine palaeoclimate archive (Wanamaker *et al.*, 2008; Butler *et al.*, 2009) and a model organism for research about ageing (Strahl *et al.*, 2007; Abele *et al.*, 2008). The species has recently piqued the interest of biogerontologists because it is not just the longest-lived bivalve, it is also the longest lived non-colonial animal known to science (Wanamaker *et al.*, 2008). The known maximum life span potential (MLSP) for this clam continues to increase (Thompson *et al.*, 1980a; Jones, 1983; Ropes, 1985; Schöne *et al.*, 2005; Scourse *et al.*, 2006) and currently stands at 410 years (Wanamaker *et al.*, 2008).

As a result of commercial and academic interest, research on the population characteristics of *A. islandica* has become increasingly important in the past two decades. Knowledge of the species population-structure, recruitment history, mortality rates, longevity and reproductive cycle has largely been obtained from those regions where the species is commercially harvested. For example the age of the species has been investigated for the Mid-Atlantic Bight population (Thompson *et al.*, 1980a, b; Kennish *et al.*, 1994), near New York (Ropes *et al.*, 1984), eastern Canadian waters (Kilada *et al.*, 2007) and in Iceland (Steingrimsson & Thorarinsdóttir, 1995; Thorarinsdóttir & Steingrimsson, 2000; Kilada *et al.*, 2007) and the population-structure and seasonal reproductive cycle were described for the southern New England shelf (Mann, 1982), New Jersey (Fritz, 1991; Kennish & Lutz, 1995), Iceland (Thorarinsdóttir & Einarsson, 1996; Thorarinsdóttir & Johannesson, 1996; Thorarinsdóttir, 2000), the Baltic Sea (Zettler *et al.*, 2001), Georges Bank (Lewis *et al.*, 2001) and the northern North Sea (Witbaard & Bergman, 2003). Despite this wealth of knowledge there have been no investigations into the population structure of any Irish Sea populations.

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For the clam to be effectively utilized as a model organism in research about ageing there is a pressing need to catalogue its life history traits throughout its latitudinal range. Understanding how longevity is associated with growth rate, maximum size, recruitment conditions and local environmental conditions will facilitate our understanding of ageing in this important species. It is also still to be ascertained what type of senescence this animal experiences (negligible as proposed by Finch (1990) or rather radically the negative as proposed by Vaupel *et al.* (2004)). A way to document the type of senescence experienced is through in-depth demographic analysis of variations in mortality rate with age. However, before such work can be initiated there is a need to understand recruitment patterns in clam populations and their age-structure. Harding *et al.* (2008) documented decadal trends in age-structure and recruitment patterns of *A. islandica* from the Mid-Atlantic Bight in relation to water temperature and Butler *et al.* (2009) reported long periods with no recruitment for a population of *A. islandica* from Isle of Man waters.

Although *A. islandica* is currently not commercially exploited in UK waters, the continuing decline in traditional white fin fisheries and commercial shellfisheries could see the targeting of alternative species, which could feasibly include *A. islandica*. The species is abundant in the Irish Sea and North Sea (Witbaard, 1996; Butler *et al.*, 2009, respectively) and both these areas may support fisheries, as discussed by Witbaard & Bergman (2003), but information on age composition, mortality, and growth rate would be required to estimate levels of sustainable harvest. Therefore growth rate investigations are warranted to indicate how much time is required to reach a certain marketable size (Urban, 2000), and the relationship between size and age is essential to implement appropriate management strategies (Keller *et al.*, 2002). Knowledge of growth parameters is essential for understanding the biology and productivity of bivalves (Moura *et al.*, 2009). Studying vital rates (namely growth) is necessary for modelling population dynamics, which, in turn, is crucial to exploitation and management (Laudien *et al.*, 2003; Peharda *et al.*, 2007) and to the recommendation of effective measures for the protection of the species (Katsanevakis, 2007).

In this paper we describe the geographical distribution, density, growth rate, longevity, mortality and recruitment patterns of *A. islandica* in Belfast Lough, Northern Ireland, UK. We also compare growth characteristics and life history traits of this population with other analogous populations.

MATERIALS AND METHODS

Belfast Lough (Figure 1A) is a fully marine inshore body of water which experiences annual seawater temperature ranges of between 6 and 15°C (Evans *et al.*, 2003). *Arctica islandica* were collected from a site at 20–25 m depth at the mouth of Belfast Lough (54°42.10N 5°35.25W) (Figure 1A; Station C) in July and September 2008 and April 2010, using a customized rigid-toothed dredge, 1 m wide with a 25 mm mesh, deployed from the RV 'Prince Madog'. The dredge is designed to equally sample all size-classes of *A. islandica* greater than 25 mm shell height. Potential dredge sites were surveyed using side-scan sonar prior to deployment in order to avoid obstacles. The presence of *A. islandica* at this location was initially identified during Northern Ireland scallop surveys which were confirmed by a previous visit by the RV 'Prince Madog' in 2005. The site was of specific interest due to the high population density (inferred due to the high capture rate previously reported compared with other sampled populations of *A. islandica*) and the large size-range of clams that had previously been obtained.

To assess the spatial distribution of the population within Belfast Lough seven locations were identified (Figure 1B). The strategy was to initially dredge each location to assess the presence or absence of the species and if present to undertake quantitative a grab sampling protocol. Twenty Day grabs were undertaken, the protocol was to position the boat on the identified coordinates and perform five Day grabs with the drift of the boat providing random sampling, before the boat was repositioned and another five grabs undertaken until a total of twenty grabs were completed. All grab samples were sieved through a 2 mm sieve. To compare the 'availability' to the dredge of *A. islandica* during each visit we compared the capture rate of *A. islandica* by the dredge during each of the three visits. The sum of individuals captured during each visit was divided by the cumulative duration of the dredge tows to estimate the relative abundance of clams during each visit.

A total of 850 live *A. islandica* collected in the dredge tows were measured to determine the population size–frequency distribution. The shell height (maximum distance from umbo to the ventral margin) was measured to the nearest 0.01 mm with a digital Vernier calliper and a size–frequency distribution constructed. The relative number of clams in each size-class was used to calculate how many of each size-class should be aged; a random number generator was then used to select the shells for ageing from within each size-class. The age of 125 of these individuals obtained in July 2008 was determined. The flesh was removed and small pieces of gonad removed and inspected microscopically in squash preparations to determine clam gender and whether the animal was sexually mature.

The age and growth rate of *A. islandica* were determined from acetate peels of the sectioned shells (see Richardson, 2001). Clean, dry shells were embedded in resin and sectioned along the major growth axis using a diamond saw. The cut surface was ground on increasingly finer grades of wet and dry paper, polished and then etched for 5 minutes in 0.1M hydrochloric acid. Acetate peel replicas were prepared using the methodology described by Richardson (1989) and Wanamaker *et al.* (2008) and viewed in a transmitted light microscope. The ages of the 125 *A. islandica* were estimated by counting the number of clear annual growth lines present in the hinge region of acetate peels of the shell sections and the population age structure constructed. The Von Bertalanffy growth function (VBGF) ($L_t = L_\infty\ (1-e^{-k(t-to)})$) was fitted to the shell length-at-age data, and the growth constant (K) and asymptotic maximum shell length (L_∞) determined using the fisheries program Fishparm (Prager *et al.*, 1987). Growth data estimated in this study were compared with data available from the literature for other *A. islandica* populations. With known dates of death and ages ascribed to each shell the year of settlement for the 125 *A. islandica* was then determined.

Instantaneous natural mortality rate (M) was estimated on the basis of age–frequency distributions (Ricker, 1975). As Station C is believed to have no history of commercial fishing it was assumed that total mortality (Z) was equivalent

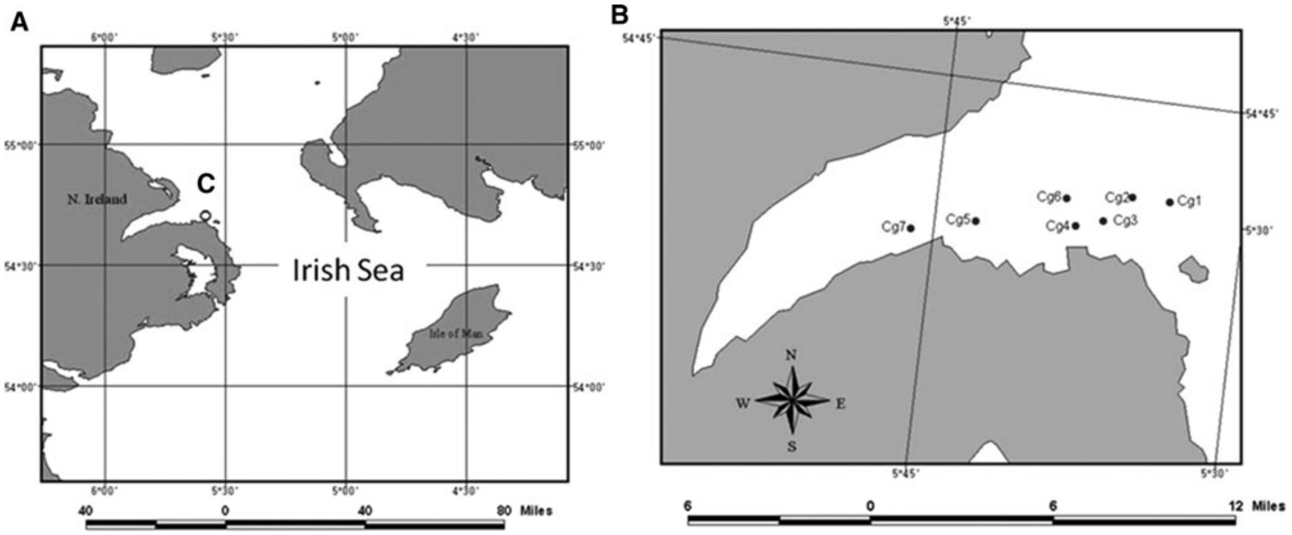

Fig. 1. Location of *Arctica islandica* populations in Belfast Lough. (A) Sampling Station C, in the mouth of Belfast Lough; (B) location of grab sampling Stations (Cg1 – Cg 7) in Belfast Lough for quantitative sampling of the *Arctica islandica* population. Cg2 was the site of dredge sampling.

to natural mortality. Z was estimated by calculating the slope of the regression between the natural log of the frequency at age data. The analysis was restricted on the descending right limb of the age – frequency curve; we believe this is an artefact of size selectivity by the dredge. Longevity was also estimated from the catch curves. Longevity and mortality estimates were obtained from analysis of age frequencies based entirely on the 125 aged animals and from the clam ages estimated from length at age curve, using the VBGF, for the rest of the 850 live *A. islandica* collected.

Due to the non-linearity of the growth process, the comparison of growth amongst different organisms is often complex (Moura *et al.*, 2009). To overcome this problem, several growth performance indices have been used, namely, the overall growth performance (P) and the growth performance index phi-prime (φ') (Pauly, 1979; Munro & Pauly, 1983). The overall growth performance P ($P = \log(K \times L_\infty^3)$) and the phi-prime index (φ') ($\varphi' = \log K + 2 \text{ x } \log L_\infty$), were used as measures of growth performance and for comparing growth data obtained during the present study with that obtained from the literature.

RESULTS

Distribution and abundance

Dredge sampling for *A. islandica* at six additional locations around Station C and further into Belfast Lough confirmed that the population was restricted to Station C (grab site Cg2). Because no *A. islandica* were captured in the dredges at these other locations, grab sampling was only undertaken at Station C. The quantitative assessment of the *A. islandica* populations at Station C by the grab sampling demonstrated that the population density was 4.5 individuals m^2.

Dredging was undertaken over three visits between 2008 and 2010. The relative abundance of *A. islandica* during the September 2008 visit (1.03 individuals.min^{-1}) was significantly lower than during the other two months (2.21 individuals.min^{-1} and 2.61 individuals.min^{-1} for July 2008 and April 2010 respectively) (Mann – Whitney *U*-test; $P = 0.05$).

Growth

Counting the number of internal growth increments provided age estimates ranging between 6 and 217 years old. The population VBGF growth equation fitted using data from the annual internal growth increments provided an estimate asymptotic size (L_∞) of 93.7 mm ($\pm$0.918 SE), a growth rate (K) of 0.03 yr^{-1} ($\pm$0.00197 SE) and $t_o = -1.25$ (Figure 2). The growth curve depicts a period of rapid growth until around 20 years when the growth rate continues to decline until around 80 years of age; from then on the species displays a low rate of indeterminate growth.

The gonad maturation state of the 125 clams whose age was determined indicated that the maximum size that the clams were immature was ~40 mm shell height and between 6 and 7 years old. Two other 7 year old *A. islandica* (>40 mm shell height) produced gametes indicating that they had attained sexual maturity, or were at least at the intermediate

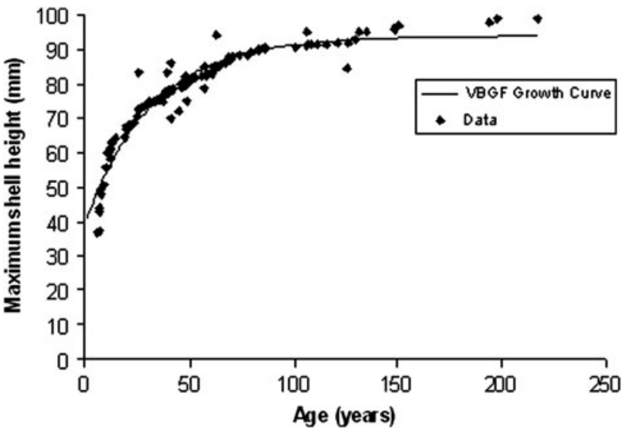

Fig. 2. Variation in maximum shell height with age in 125 *Arctica islandica*. The growth curve was fitted using the Von Bertallanffy growth equation ($L_t = 93.7\text{mm}\ (1 - e^{-0.03(t-1.25)})$).

stage. Thus we assume that sexual maturity in clams from Belfast Lough occurs at ~40 mm shell height, i.e. around 7 years old.

Population structure

The size–frequency histogram for Belfast Lough (Figure 3) shows a unimodal peak in shell height at the 80.1–85 mm size-class, and declines steeply from there; the maximum shell height observed was 106.3 mm and was the only individual >100 mm shell height. There was also an observed absence of small individuals. However, the analysis of the age–frequency histogram (Figure 4) for Belfast Lough shows more of a bi-modal height distribution, with a clear peak in the 41–60 year age-class, and a much smaller secondary peak at the 101–120 year age-class. Over 15% of the total population had lived in excess of a century.

Catch curve analysis from aged individuals provided mortality and longevity estimates of 0.02 and 220 years respectively (Figure 4). Age estimated from size using the parameters of the VBGF for the remaining 740 clams whose age had not been determined using shell sections produced a similar longevity estimate of 217, but a higher mortality rate of 0.04 (data not presented).

Due to the asymptotic growth nature displayed in longevous bivalves, shell size is a poor predictor of age. It was therefore decided that estimates of longevity and mortality were more reliable when based entirely on clams for which individual ages were accurately ascribed, rather than the ages of clams of known length whose ages had been estimated from the VBGF.

For example, two similar sized clam shells whose age had been estimated using growth lines and had shell heights of 85.3 and 90.8 mm, had estimated ages of 149 and 61 years respectively. This demonstrates how similar sized animals can be of vastly different ages and that size is an unreliable predictor of longevity.

Settlement

With a known date of death and accurate ages determined it was possible to ascribe an estimated date of settlement for the 125 individuals that had been aged and produce a curve reflecting cumulative settlement (Figure 5). Analysis of the curve suggests the *A. islandica* population at Belfast Lough has experienced almost continuous recruitment over the last 90 years, but with two significant gaps in recruitment, one 90–100 years ago and another 140–150 ago.

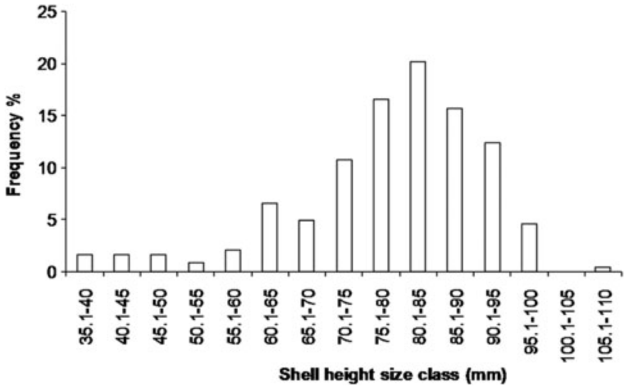

Fig. 3. Size–frequency distribution of *Arctica islandica* (in 5 mm size-classes) collected in the dredge tows in Belfast Lough.

Fig. 4. Age–frequency distribution for the *Arctica islandica* population at Station C, Belfast Lough. This graph is based on the 125 animals whose age was determined using sclerochronological techniques. Regression analysis of the natural log (LN) frequency data provides estimations of Longevity (the x axis intercept) and mortality (the slope).

DISCUSSION

Distribution and abundance

The *A. islandica* population at Belfast Lough appears to be restricted to a small area at the mouth of the Lough. Additional searches for specimens further into the Lough and into deeper waters found no evidence of a larger more widespread population and at Station C we report population densities of 4.5 individuals m^{-2}. For the waters of the UK this is a relatively dense population, and only in the central Fladen Ground (northern North Sea), with an average density of 12 individuals m^{-2}, comprising up to 75% of the total biomass, have higher densities been reported (De Wilde *et al.*, 1986). In fact, when the Station was re-sampled by Witbaard & Bergman (2003) using a Triple-D dredge which accurately quantitatively samples the benthos they estimated local densities of up to 286 individuals (>10 mm) m^{-2} in the northern cluster.

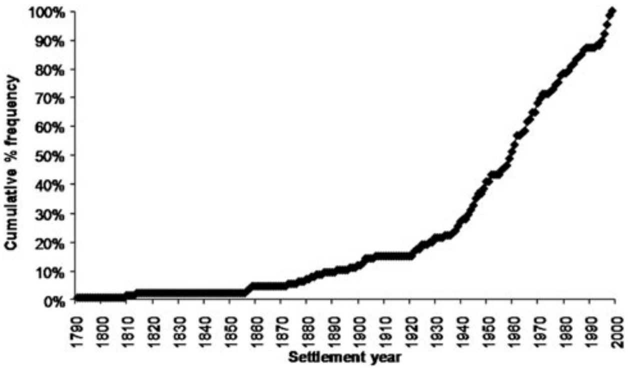

Fig. 5. Cumulative frequency of the occurrence of successful settlement and recruitment into the population of *Arctica islandica* from Belfast Lough from 1790–1990.

The Belfast Lough population is probably near the southern limit of the population in the Irish Sea. The bottom waters in this region occasionally exceed 16°C (Evans *et al.*, 2003) which has been reported as the upper limit for population survival (Merrill *et al.*, 1969). Similarly in the southern North Sea Witbaard & Bergman (2003) reported that the southern limit of *A. islandica* coincides with the southernmost limit of the summer stratified water mass where bottom water temperatures never exceed 16°C.

An interesting observation to arise from the present study is the significantly reduced dredge capture rate during the September 2008 sampling period. One of the only plausible reasons for the temporary significant reduction in the dredge capture rate we observed in September 2008 is that the population had undergone a synchronized burrowing period, and were less 'available' to the dredge. It was hypothesized that synchronous burrowing behaviour of the clams would reduce their availability to the dredge; therefore this data would provide preliminary evidence of when synchronous burrowing occurs in *A. islandica* populations in Belfast Lough. It is known that many species of burrowing bivalves display a seasonal pattern of burrowing behaviour (for example in *Macoma balthica* (Reading & McGrorty, 1978) and *Mya arenaria* (Englund & Heino, 1994). Although *A. islandica* is known to burrow, its burrowing behaviour has been reported as being unsynchronized (Taylor, 1976).

September is also the time when the growth increment in the shell is believed to form when shell growth ceases (Jones, 1980). We hypothesize that some cue causes *A. islandica* to burrow into the sediment, lose contact with the sediment–surface water interface and therefore stop shell growth and form the annual growth line; this cue might be the maximum annual seawater temperature (Mann, 1982), or breakdown of the thermocline leading to high organic matter and anoxic bottom waters (Mann, 1982). Additionally, both Dunca *et al.* (2009), studying an *A. islandica* population from the west coast of Sweden, and Weidman *et al.* (1994), studying a Georges Bank population, reported isotopic measurements that indicate that growth line formation occurs in the autumn when the seawater temperature has begun to decrease. Dunca *et al.* (2009) reported that the onset of shell growth began around the end of October and ceased (producing the annual growth line) the following year between August and September. Although these findings are preliminary and our work here requires repeating, it is one of the first reports of a seasonal change in population abundance of *A. islandica* associated with a synchornized burrowing in a bivalve population. The burrowing event possibly coincides with the timing of growth line formation. Support of the timing of this event comes from the experimental tanks at the Royal Netherlands Institute of Sea Research where burrowing in *A. islandica* has been investigated. Preliminary results suggest the largest proportion of animals buried deep in the sediment (with no siphons visible) at the end of summer (in the months of August and September) (Witbaard, personal communication, 2010).

Growth

In the present study we report an L_∞ value of 93.7 mm. This represents an intermediate value compared to other populations. Whereas in some areas higher L_∞ values have been reported (e.g. 99.6 mm in north-west Iceland by Thorarinsdóttir & Jacobson, 2005), other research had documented values as low as 86 mm (north-east Iceland; Strahl *et al.*, 2007) and 87.6 mm (St Mary's Bay, eastern Canada; Kilada *et al.*, 2007) (see Table 1). Our estimate of the VBGF K (0.03) is also an intermediate value; other population estimates of K have ranged between ~0.02 in north-west Iceland (Thorarinsdóttir & Jacobson, 2005) and 0.06 at Georges Bank (Lewis *et al.*, 2001) and north-east Iceland (Strahl *et al.*, 2007). The overall growth performance and the growth performance index calculated for the Belfast Lough *A. islandica* population are also similar to other estimates (Table 1). Perhaps surprisingly no significant relationship between the overall growth performance (P) and the growth performance index phi-prime (φ') with either longevity or latitude was observed.

Population structure

Analysis of the size-structure revealed that smaller clams were rare in the population. A similar situation has previously been observed amongst populations collected along the American east coast (Murawski *et al.*, 1982), north-west Iceland (Thorarinsdóttir & Einarsson, 1996) and the North Sea (Witbaard *et al.*, 1997). Murawski *et al.* (1982) suggested that skewed size–frequency distributions probably result from either irregular recruitment or low recruit survival. However, it has previously been reported by Thorarinsdóttir *et al.* (2010) that commercial *A. islandica* dredges are selective for larger sized animals and therefore the skewed size–frequency distribution may be an artefact of the sampling process.

Table 1. Von Bertalanffy growth parameters and other parameters by area for ocean quahogs from this study and published reports. Asymptotic shell length (L_∞ mm), Von Bertalanffy growth constant (K yr^{-1}), phi-prime (φ'), overall growth performance (P), latitude (Lat °N), estimate of population longevity (T_{max}) and reference source.

Population	L_∞	K	φ'	P	Lat °N	T_{max}	Reference
Belfast Lough	93.7	0.03	2.420	4.392	54.42	220	Present study
Georges Bank	97.6	0.06	2.757	4.747	41	90	Lewis *et al.* (2001)
Iceland (north-west)	99.9	0.02	2.298	4.296	66	202	Thorarinsdóttir & Jacobson (2005)
Mid-Atlantic Bight	97.3	0.03	2.453	4.441	40.5	90	Lewis *et al.* (2001)
Iceland (north-east)	86	0.06	2.647	4.582	66.03	192	Strahl *et al.* (2007)
Iceland (north-west)	92.5	0.03	2.409	4.376	65.83	100	Kilada *et al.* (2007)
St Mary's Bay	87.6	0.05	2.584	4.526	44.25	72	Kilada *et al.* (2007)
Sable Bank	90.48	0.05	2.612	4.569	44	210	Kilada *et al.* (2007)
Kiel Bay	93.6	0.07	2.788	4.759	54.5	n/a	Brey *et al.* (1990)

Analysis of the age-composition of the catch demonstrated that the oldest animal caught was 217 years old; this corresponded well with our longevity estimate of 220 years from catch curve analysis. Additionally, an age estimate based on only 125 individuals should probably be considered an underestimate (Beukema, 1988). Nevertheless we have demonstrated that even at the southern limit of its distribution, and in relatively shallow waters of 25 m depth, that this species still exhibits an exceptional longevity in excess of 200 years.

The annual mortality rate for offshore populations of *A. islandica* is generally assumed to be 1–3% (NEFSC, 2004; Kilada *et al.*, 2007). Catch curve analysis provided a very similar estimate of 0.02 for the Belfast Lough population. For the actuarial definition of rates of senescence we really need a comprehensive understanding of age-related changes in mortality rate. Whilst this has ecological implications, a strong interest in the mortality rates of *A. islandica* comes from the biogerontological community, who are keen to accurately determine the type of senescence experienced by this unique clam species. Finch (2009) acknowledges the difficulty defining mortality rates at later ages in natural populations because of the small sample sizes, which are necessarily sacrificed for the observation of age. Whilst researchers such as Kilada *et al.* (2007) have used huge clam sample sizes (in excess of 300,000), their ages have necessarily been estimated from age/length keys and are unreliable and too coarse at advanced ages to permit accurate analysis of changes in age-related mortalities. A concerted effort to accurately age many more shells from a specific population is needed if we are to be able to determine age-related changes in mortality rates for this species.

Settlement

Harding *et al.* (2008) recently reported on decadal trends of successful recruitment into *A. islandica* populations off the east coast of America. In Belfast Lough we observed almost continuous recruitment into the population over the last 100 years, with two possible breaks in recruitment, one at 90–100 years ago and another 140–150 years ago. Harding *et al.* (2008) propose that observed recruitment patterns in ocean quahogs are strongly related to bottom water seawater temperature patterns. However, Seymour & Doncaster (2007) theorized that density-dependence factors may be a determining factor for the exceptional longevity of *A. islandica*, predicting longer reproductive lifespan in response to severely limited recruitment opportunities (for example clam larvae may only be able to secure a foothold in suitable sediment where space is released by an adult death). Currently it is unclear what factors or suite of factors are driving recruitment in long-lived marine bivalves and whether gaps in recruitment represent failures in gamete production, larval settlement or juvenile survival.

CONCLUSIONS

We have documented the growth and population structure of an *A. islandica* population towards the southern limit of its distribution and have demonstrated that even at these southern latitudes the animal demonstrates exceptional longevity, in excess of two centuries. Parameters of the Von Bertalanffy growth formula and indices of growth are comparable to figures observed for mid-Atlantic and Icelandic populations. It is possible that we have detected a synchronized burrowing event which may be related to growth line formation.

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