The demographics and morphometries of biogenic reefs: important considerations in conservation management

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Modiolus modiolus *L. (horse mussel) reefs are a priority marine habitat of high conservation value that is currently listed as endangered and/or threatened across its European distribution. Population structure, density or shell morphology may influence the biodiversity of a reef, either directly or indirectly. Thus, such metrics are important considerations for successful conservation management of these biodiversity hotspots. Population structure, shell morphology and growth rates were examined in* M. modiolus *reefs across the UK range of the habitat to examine differences between key populations, including those near the Lleyn Peninsula in Wales (southern range), off Port Appin in Western Scotland (mid-range) and in Scapa Flow in the Orkney Isles, Scotland (northern range). Additionally, the influence of physical conditions (temperature and tidal flow) to growth rate and predicted maximum shell length for each population was examined. Growth rates were determined using acetate peels of sectioned shells. Lower juvenile abundance was observed in Scapa Flow. Small, narrow-shaped shells were found to be characteristic of North Lleyn mussels, and larger, globular-shaped shells were characteristic of mussels in Scapa Flow and off Port Appin. Mussels in Scapa Flow were slower growing, yet reached a longer asymptotic length (L$_\infty$) than mussels of Port Appin and North Lleyn. Growth curves from sites within this study were analysed with other published data. A trend of higher L$_\infty$ at higher latitudes and at lower flow rates was observed. Variations in growth and age are discussed in relation to flow regimes, connectivity to other reefs, density and latitude.*

Keywords: *Modiolus modiolus*, biogenic reef, conservation management, growth, climate change, biodiversity hotspots, morphometrics, MPA, demographics

INTRODUCTION

The horse-mussel, *Modiolus modiolus* (Linnaeus, 1758) occurs singularly, in clumps, or as high-density, species-rich biogenic reefs in temperate coastal regions around the world (Rees *et al.*, 2008; Sanderson *et al.*, 2008; Rees, 2009). *Modiolus modiolus* reefs of conservation importance can be identified by their extent, percentage cover of live *M. modiolus*, and associated communities (Morris, 2015). The decline of *M. modiolus* reefs in the North East Atlantic marks them as protected marine conservation features (Rees, 2009; Cook *et al.*, 2013). They are therefore identified under several conservation drivers: The Marine (Scotland) Act 2010; the Habitats and Species Directive (Council Directive 92/43/EEC); the OSPAR Convention; and the Marine Strategy Framework Directive (MSFD; Council Directive 2008/56/EC).

The extent and density of *M. modiolus* reefs have previously been used to determine reef condition (Rees, 2009; Moore *et al.*, 2012; Fariñas-Franco *et al.*, 2014). However, these measures indicate little about their future prospects. Instead, parameters such as size-frequency distribution, morphometries and growth rates may be more appropriate for understanding long-term reef status. An understanding of reef-based differences will also support development of ecologically relevant climate envelope models and aid in illuminating potential impacts (e.g. altered ecosystem function due to shifts in body size) of a changing climate (Peck *et al.*, 2009; Somero, 2010; Sandford & Kelly, 2011).

Growth of *M. modiolus* is usually rapid in the first 4–6 years in order to reach an adult shell length (~35–40 mm) (Anwar *et al.*, 1990). At this size predation pressure is typically reduced (Comely, 1978; Holt *et al.*, 1998) and animals can then spend more of their energy resources on reproduction as opposed to growth. *Modiolus modiolus* are reported to be sexually mature between 4–8 years old (Wiborg, 1946; Rowell, 1967; Jasim & Brand, 1989). Temperature influences growth rates in bivalves, with slower growth rates characteristic of higher latitudes and greater depths (MacDonald & Thompson, 1985; Sato, 1994). Near-bed seawater temperature data for the UK indicates a difference of up to 3–4°C between northern and southern latitudes, and consequently one would expect temperature driven variation in growth rates across *M. modiolus* reef habitats (see Gormley *et al.*, 2013; Seidov *et al.*, 2013). It has also been suggested that gonad development is slower in bivalves in colder temperatures, as such conditions may lead to late maturity and subsequently allow northern populations to attain a larger size before energy is focused on reproduction (Sato, 1994). The availability of food is another factor that may affect growth rates, suggesting

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slower growth rates would be observed in deep-water populations, where food is more limited (MacDonald & Thompson, 1985). Additionally, intertidal *M. modiolus* populations have demonstrated slower growth rates than populations in fast flowing currents, e.g. on oilrigs in the North Sea (Anwar *et al.*, 1990), where increased flow rates reduce the energy required to filter feed (Wildish & Peer, 1983); however, differences in food availability and feeding windows between intertidal and offshore sites may also play a role (Lesser *et al.*, 1994).

Physical conditions also have a strong influence on shell morphology with bivalves generally exhibiting high plasticity in response to local environmental conditions (Seed, 1968; O'Connor, 2010). For example, bivalves with narrow shaped shells reduce the effects of drag and the risk of dislodgement, and are typically found in areas with high flow rates (Seed, 1968, 1980; Steffani & Branch, 2003). Reef density has also been seen to influence the morphology of bivalves, with narrower shells found in denser populations. This may be a response to food availability, disease prevalence and/or physical interference (Alunno-Bruscia *et al.*, 2001; Lauzon-Guay *et al.*, 2005; Caill-Milly *et al.*, 2012). Depth (Etter & Rex, 1990) and substrate type (Seed, 1980) have also been cited as influencing morphology in bivalves. A recent study on the morphology of *M. modiolus* shells found significant differences in shell shape between sites within an enclosed loch, probably due to differences in current speed and sediment type between sites (Fariñas-Franco *et al.*, 2014).

Recruitment of juveniles influences population structure, and effective recruitment relies on successful spawning and settlement of larvae. The spawning season of *M. modiolus* is poorly understood and tends to vary greatly between reefs, though is probably linked to temperature. Settlement of larvae at certain reefs is also highly variable and sporadic between years (Wiborg, 1946; Seed & Brown, 1977; Brown, 1984). Comely (1978) suggested settlement differences between reefs were due to larvae originating from outside the reef area; hence recruitment would be affected by hydrodynamic conditions, particularly as *M. modiolus* larvae can remain within the water column for $\sim$1 month (Schweinitz & Lutz, 1976; Roberts *et al.*, 2011). In addition, a population may act as a larval sink or source, resulting in recruitment differences between reefs (Lipcius *et al.*, 2008). Variation in mussel density on a reef may also influence recruitment. Adult aggregations provide refuge, and consequently can increase post-settlement survival by protecting juvenile *M. modiolus* from predation (Comely, 1978; Holt *et al.*, 1998).

Population structure, density or shell morphology may influence the biodiversity of a given reef, either directly through the abundance and diversity of associated communities (Gutiérrez *et al.*, 2003; O'Connor & Crowe, 2007; Ragnarsson & Burgos, 2012) or indirectly through the reef's capability for habitat modification (Allen & Vaughn, 2011). It is important for such factors to be taken into consideration in Marine Protected Area (MPA) monitoring programmes for successful conservation management of these biodiversity hotspots.

The aim of the present study was to compare population structure, shell morphology and growth rates of *M. modiolus* reef populations from three sites situated across the extent of the UK distribution for the habitat including the Lleyn Peninsula in Wales (southern range), off Port Appin in Western Scotland (mid-range) and in Scapa Flow in the Orkney Isles, Scotland (northern range). The main hypothesis of the work was that sites would vary significantly in these aspects with observed differences related to differences in latitude (as a proxy of temperature), current flow and mussel density. Differences in these population parameters are likely to have important implications for the conservation management of *M. modiolus* populations in a changing climate.

MATERIALS AND METHODS

Mussels were collected by clearing $\sim$1 m² plots on *M. modiolus* 'reefs' (cf. Morris, 2015) using scuba. Four plots were cleared in Scapa Flow (58°53′0.446N 03°11′0.255W; 23 m below chart datum (BCD)), three plots were cleared off Port Appin (56°33′0.029N 05°25′0.468W; 21 m BCD) and four plots were cleared from north of the Lleyn Peninsula (52°56′0.516 N 04°38′0.070W; 30 m BCD); (Figure 1). These sites were chosen as representative of different reef types found in the UK with regards mussel density, geographic location (i.e. latitude) and flow regime.

The North Lleyn reef is currently the largest known *M. modiolus* reef in the UK, with an extent of $\sim$349 ha (Lindenbaum *et al.*, 2008). The reef lies within and forms a feature of the Pen Lŷn a'r Sarnau SAC and is believed to be the most southerly reef in the UK (Lindenbaum *et al.*, 2008). The reef has high densities of *M. modiolus* with raised reef structures present across the reef's extent (Lindenbaum *et al.*, 2008; Sanderson *et al.*, 2008). The Scapa Flow reef is the mostly northerly reef in this study and is less dense than the North Lleyn reef and comprised of three main areas with a combined extent of 42 ha (Sanderson *et al.*, 2014). The Port Appin reef is approximately mid latitude between the other two reefs, and is the smallest of the three reefs with an extent of $\sim$2 ha. The reef is continuous within this area with high densities of *M. modiolus* but lacks the raised structures found on the North Lleyn reef (Moore *et al.*, 2012).

A current meter (MIDAS ECM, Valeport Ltd, Devon, UK) was placed at each site for 6 days during a neap cycle, recording current speed, direction and water depth every 5 s. The densities of the *M. modiolus* reefs were estimated using 0.25 m² photo quadrats using the method and counting rules outlined in Cook *et al.* (2013). Nine and five photo quadrats were taken in 2014 from Scapa Flow and Port Appin reefs, respectively. Photo quadrats could not be taken in 2014 on the North Lleyn reef, so seven photo quadrats taken in 2009 (Cook *et al.*, 2013), were analysed instead.

Length frequency and morphometric data

The maximum shell-lengths of all *M. modiolus* were measured to the nearest 0.1 mm using digital vernier calipers, before being returned to the reef. In addition, width and height of the first 50 mussels were recorded for morphometric analysis. Debris from the cleared plots was washed through a 1 mm sieve in order to include juveniles in the analysis. This was fixed in seawater buffered 10% formaldehyde solution, and subsequently sorted by hand to find juveniles. Juveniles were measured using the same method as described above. Additional length, width and height measurements of
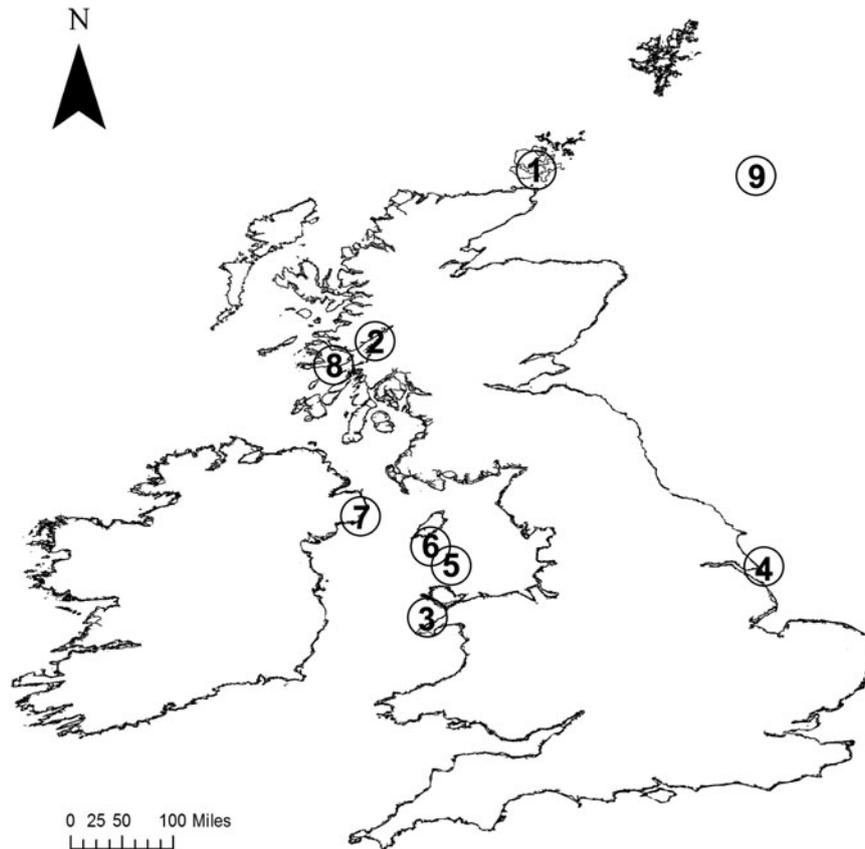
Fig. 1. Study sites: Scapa Flow (1), Port Appin (2) and North Lleyn (3) were sampled in the present study. The Humber Estuary (4), Irish Sea (5), Isle of Man (6), Strangford Lough (7), Isle of Mull (8) and Ling Bank (9) were sampled in the Anwar *et al.* (1990) study.

M. modiolus were collated from historical surveys (2010–2015) at the same sites.

Growth rate data

Thirty mussels of varying lengths were selected from each site across an even size range. Acetate peels were used to age the mussels as described in Richardson *et al.* (1979) and Anwar *et al.* (1990). One valve from each mussel was cut longitudinally, along the umbone-rim axis, using a circular saw. To prevent breakages, shells <60 mm in length were set in clear polyester casting resin before being cut. Once cut, the shell half containing the umbone was sanded, polished and then etched in 1% hydrochloric acid. The edge of the shell was dipped in acetone before being placed on an acetate sheet. After drying, the sheet was pulled from the shell, leaving a 'peel' of the inner nacreous layer. All peels were aged via use of a dissection microscope with each of the dark bands in the middle nacreous layer representing a year of growth (Figure 2).

Analyses

All statistical analyses were completed using the statistical software R (release 3.1.1, 2014). One-way ANOVAs with follow-up pairwise comparisons were used to test for differences in flow rates, collected with the current meter, between the sites. Length frequency measurements were converted to percentage size frequency and plotted for each sampled site along with approximate ages based on the growth curves. One-way ANOVAs, with follow-up pairwise comparisons were then used to test the differences in the mean length of the mussels between sites.

Differences in morphometric ratios between shell measurements were compared between sites. The ratios of height-length were used as a measure of shell elongation, width-height as a measure of shell inflation and width-length as a measure of shell obesity (Zieritz & Aldridge, 2009; Fariñas Franco *et al.*, 2014). Due to the limited number of mussels <50 mm found on some reefs, all mussels <50 mm were removed from the morphometric analysis. These morphometric ratios were not normally distributed; therefore, Kruskal–Wallis tests were used to test for statistically significant differences in the shell shape ratios between sites. Additionally, approximations of the shell shapes of *M. modiolus* at the same age from North Lleyn, Port Appin and Scapa Flow reefs were created according to calculated ratios and growth rates.
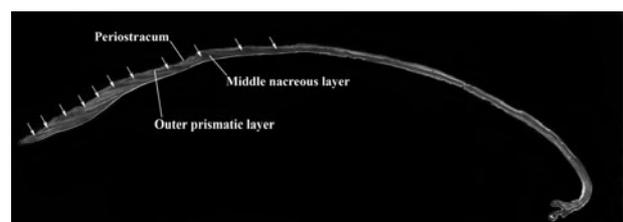

Fig. 2. Acetate peel of a 16-year-old *M. modiolus* specimen. White arrows indicate some of the dark winter bands in the younger half of the shell, laid down each year within the middle nacreous layer.

Values for maximum length (L_∞), growth rate (K) and $t\theta$ were identified to produce growth curves based on von Bertalanffy's growth equation for each of the populations. Starting parameters were estimated using VbStarts in the FSA package within R (Fish R, 2014). These starting values were then used to calculate the coefficients using the non-linear least-squared regression within R. L_∞ and K values were plotted with the best-fit von Bertalanffy growth model superimposed. These values, along with L_∞ and K values from six other populations reported in Anwar *et al.* (1990) (Figure 1), were used to test for correlations with maximum tidal flow and latitude. After assumptions of normality and equal variance were confirmed, a Pearson's Product Moment Correlation test was used to compare these L_∞ and K values against predicted maximum flow rates (BERR, 2008) and latitude of the nine sites. The current meter data was not used in this analysis, as benthic current flow data was not available for the additional six sites. The relationship between latitude and flow was tested separately using Spearman's Rank Correlation.

RESULTS

The mean current speed at the North Lleyn site was 0.244 m s^{-1}, significantly faster than at Scapa Flow (0.029 m s^{-1}, $P < 0.001$) and Port Appin (0.106 m s^{-1}, $P < 0.001$). The current at Port Appin was also significantly

faster than at Scapa Flow ($P < 0.001$). The North Lleyn reef had 24.6 *M. modiolus* per m^2 and 21% coverage, the Port Appin reef had 16 per m^2 and 16% coverage, and the Scapa Flow reef had 11.1 per m^2 and 11% coverage.

Length frequency distributions for each of the sites were bimodal (Figure 3), most pronounced in the Port Appin and North Lleyn populations. The mussels sampled at Scapa Flow were significantly larger (mean 88.75 mm) than those at Port Appin (mean 50.1 mm; $P < 0.001$) and North Lleyn (mean 56.04 mm; $P < 0.001$).

Shell morphometric ratios of inflation, elongation and obesity were found to be significantly different between sites. Mussels from the North Lleyn reef were significantly less elongated than mussels from the Port Appin Reef or Scapa Flow reef (respective Kruskal–Wallis $\chi^2 = 3.614$ and 2.111; $P < 0.001$ and $P < 0.05$). Mussels from the North Lleyn reef were also significantly less inflated (respective Kruskal–Wallis for inflation $\chi^2 = 5.729$ and 4.618; $P < 0.001$), and less obese (respective Kruskal–Wallis for inflation $\chi^2 = 7.733$ and 6.754; $P < 0.001$) than mussels from the Port Appin reef or Scapa Flow reef (Figure 4). Overall, this gave the mussels from the North Lleyn reef a more streamlined profile, having 1% less height and 4.6% less width at a given length compared with the other reefs, and 8.4% less height at a given width compared with the other reefs. The approximate shell shapes of *M. modiolus*, at a similar age, from the three sites are illustrated in Figure 5.

Von Bertalanffy growth curves revealed that *M. modiolus* from the Scapa Flow population had a higher L_∞ (159.8 mm)
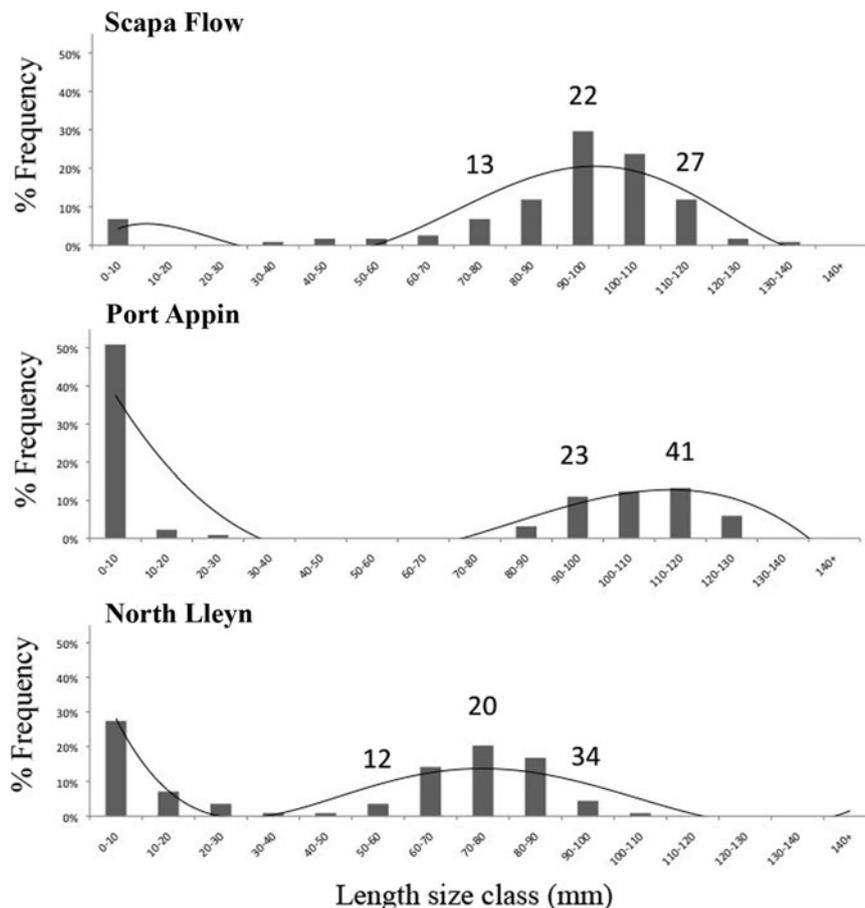

Fig. 3. Percentage size frequency (mm) of *M. modiolus* from Scapa Flow (N = 118), Port Appin (n = 218) and North Lleyn (n = 113). Numbers above bars indicate approximate age of size classes using the growth rates for each site.
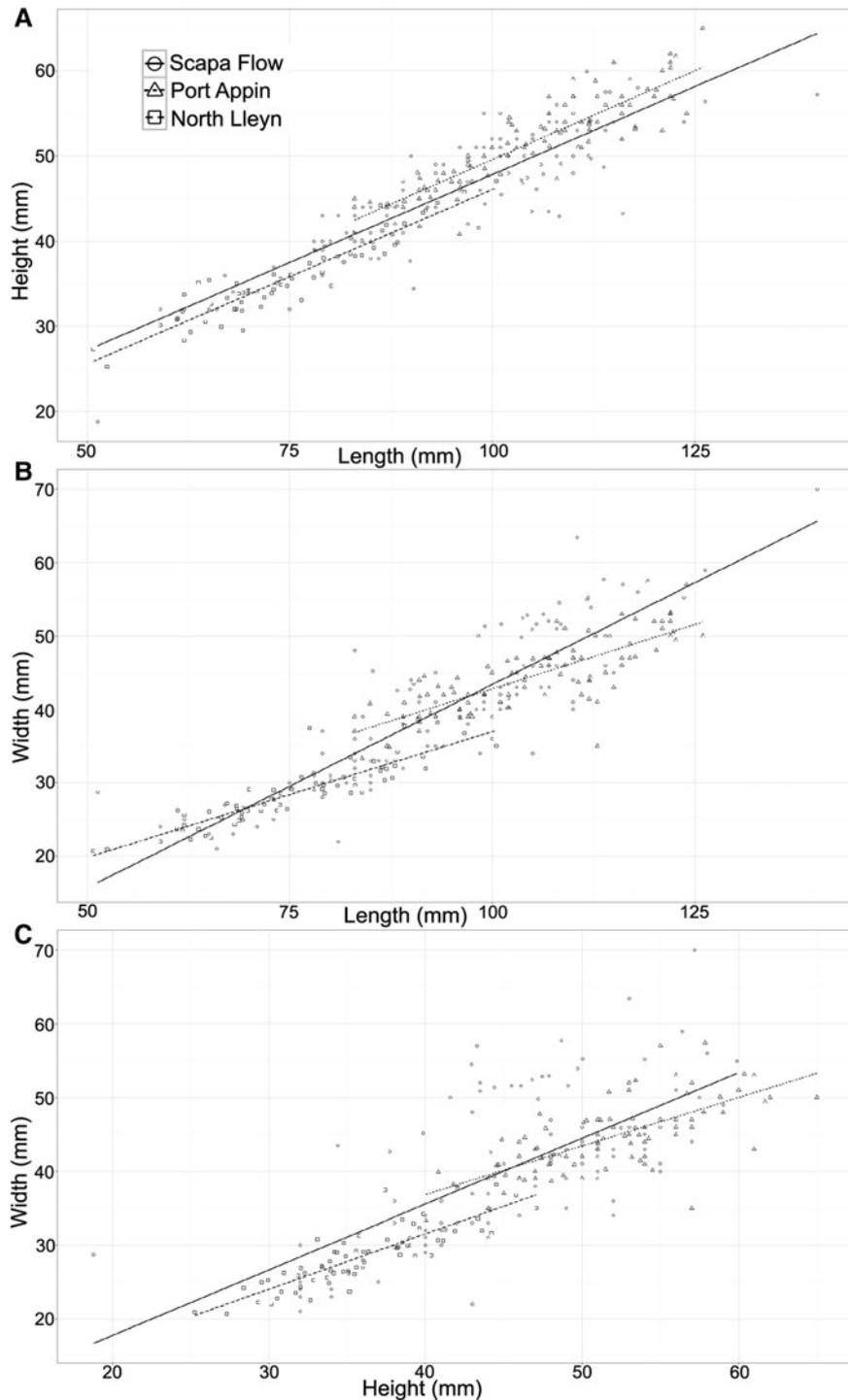
Fig. 4. The relationship between length and height (A), length and width (B), and height and width (C) of *M. modiolus* from Scapa Flow (N = 110), Port Appin (N = 96) and North Lleyn (N = 95).

and a lower K value (0.04) compared with the other sites in this study (Figure 6; Table 1). North Lleyn *M. modiolus* had a lower L_{∞} value (L_{∞} 110.9 mm), and a lower K value (0.059) compared with the Port Appin population (L_{∞} 122.82, K 0.061).

The K and L_{∞} values obtained from the Anwar *et al.* (1990) study are listed in Table 1 with predicted max flow rates and depths. A significant positive relationship was found between latitude and L_{∞} ($r = 0.74$, $t = 2.85$, $P < 0.05$; Figure 6) and a significant negative relationship was found between flow and L_{∞} ($r = -0.82$, $t = -3.4836$, $P < 0.05$; Figure 7). There was

no significant relationship between K and any environmental variable. There was also no significant correlation between flow and latitude ($T = 10$, $P = 0.39$).

DISCUSSION

The present study found that *M. modiolus* from different reefs exhibited different demographic profiles, morphologies and growth rates, that varied with tidal flow and latitude.
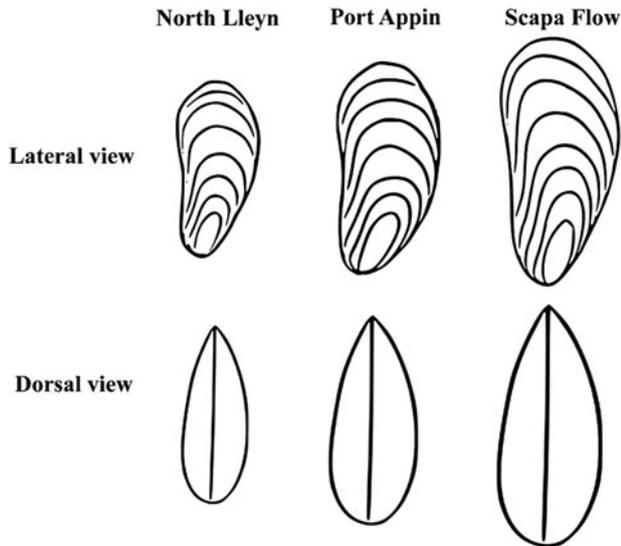
Fig. 5. An approximation of the shell shapes of *M. modiolus* of the same age from North Lleyn, Port Appin and Scapa Flow.

Table 1. L_∞ (mm) and K constant of the von Bertalanffy equation LI $(t) = L_\infty$ $(1-e-K$ $(t-t\theta))$, from the three *M. modiolus* populations studied in this paper as well as the six populations studied by Anwar *et al.* (1990). Depths at which the samples were taken are included, as well as approximate flow rates (BERR, 2008).

Site	K	L_∞ (mm)	Depth (m)	Approx. max. flow rate (m/s)
Scapa Flow	0.040	159.78	21–25.8	0.70
Port Appin	0.061	122.82	21	0.26
North Lleyn	0.059	110.90	30	1.06
Humber Estuary	0.115	89.6	20	1.17
Irish Sea	0.092	81.34	80–90	1.19
Isle of Man	0.079	91.54	–	1.15
Strangford Lough	0.062	120.28	11–16	–
Isle of Mull	0.044	177.55	–	0.10
Ling Bank	0.079	133.95	73–77	0.35
Average	0.070	120.86		

Growth rates and maximum achievable sizes increased with current flow and latitude. Both factors may also directly contribute to the observed variations in juvenile abundance and shell morphology, but indirect impacts via changes to energy budgets should also be considered (Sokolova *et al.*, 2012).

Differences in juvenile abundance are tentatively interpreted here because of the low number of sites studied. Nevertheless, the increased abundance of juveniles at North Lleyn and Port Appin (Figure 3) may be due to the higher current flows observed (Comely, 1978; Brown, 1984). Such conditions may lead to increased connectivity via improved larval supply from other reefs in the Irish Sea (Anwar *et al.*, 1990; Rees *et al.*, 2008; Gormley *et al.*, 2015b) and Loch Linnhe respectively (Rees, 2009; Moore *et al.*, 2012). Conversely, the decreased abundance of juveniles in Scapa Flow may be caused by limited connectivity, due to reduced tidal flow and a lack of known neighbouring reefs (Rees,

2009; Gormley *et al.*, 2015a). Furthermore, while the Scapa Flow population had the largest L_∞, it also had a lower mussel density compared with the Port Appin and North Lleyn reefs. Although gamete production is correlated with body size, population density has been shown to be equally important to fertilization success and reproductive output (Levitan, 1991), and consequently could partially account for lowered abundance of juveniles in the northern population. The higher structural complexity found on reefs with higher densities might also afford more shelter to juveniles from predation (Comely, 1978; Holt *et al.*, 1998). An increase in reef complexity has been shown to increase post-settlement survival in other bivalves (Gutierrez *et al.*, 2003; Nestlerode *et al.*, 2007).

The high mussel density and narrow-shaped shells of mussels from North Lleyn, and low density and globular-shaped shells from Scapa Flow and Port Appin, support the view that crowding leads to narrower shells (Alunno-Bruscia *et al.*, 2001; Lauzon-Guay *et al.*, 2005; Caill-Milly *et al.*, 2012). However, the lower density at Port Appin does not support this hypothesis. Moreover, given that flow rates were significantly higher at North Lleyn than at Port Appin
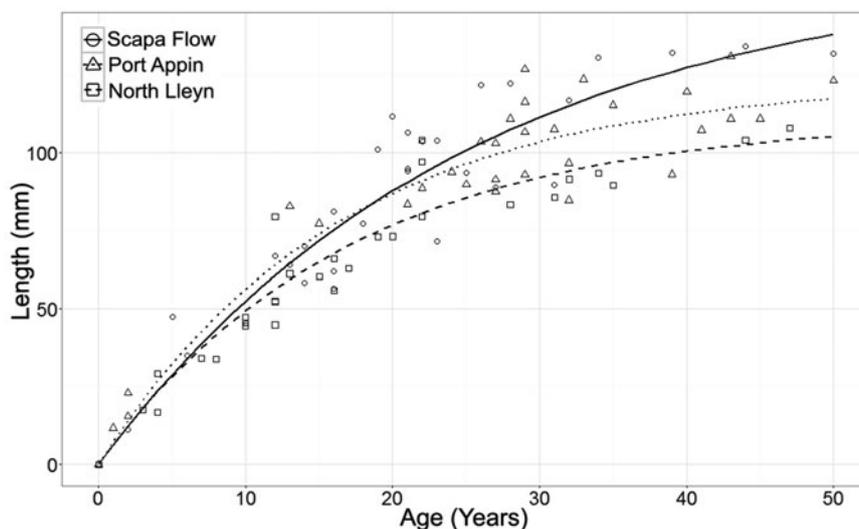

Fig. 6. Von Bertalanffy growth curves of the three *M. modiolus* populations analysed in this study: Scapa Flow, Port Appin and North Lleyn.
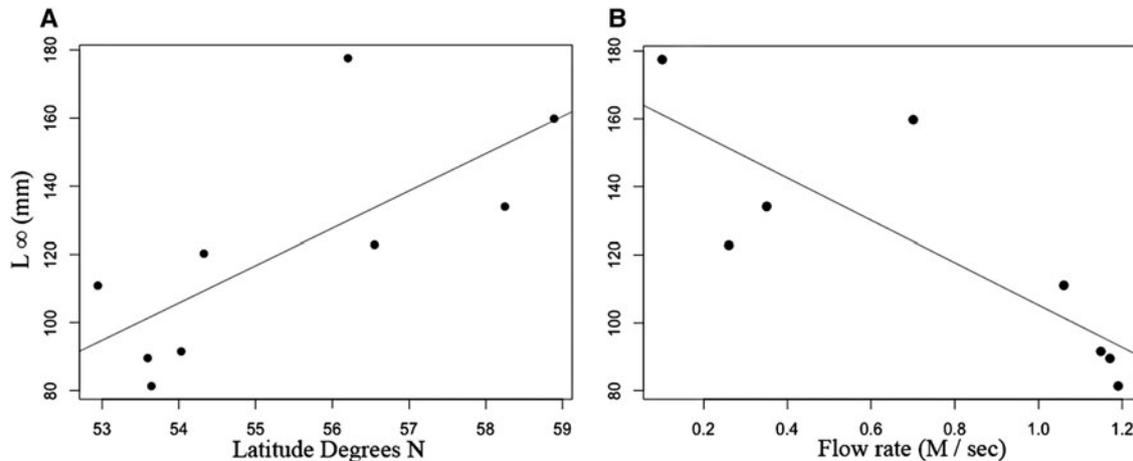
Fig. 7. Relationship between the latitude and the L_∞ (mm) (A), and the chart surface flow and L_∞ (mm) (B), of the respective *M. modiolus* growth curves from each of the sites.

or Scapa Flow, flow rate, rather than density, may be the stronger driver of shell morphology. The narrow-shaped shells from North Lleyn are possibly a morphological adaptation to allow a better hold within the sediment and reduce the risk of dislodgement in fast flowing currents (Seed, 1968, 1980; Steffani & Branch, 2003; Fariñas-Franco et al., 2014).

A significant positive relationship was observed between latitude and L_∞ when including data from the Anwar et al. (1990) study. Bergmann's rule, that a species will demonstrate a larger body size at higher latitudes (i.e. lower temperatures), may explain this relationship (Berke et al., 2013). Oxygen concentration generally limits the size of ectotherm species as surface area to volume ratios decrease with increased body size, thereby reducing gas exchange capability. The increased solubility of oxygen at lower seawater temperatures however, coupled with lowered metabolic demands under such conditions, reduces these size constraints in animals at higher latitudes (Chapelle & Peck, 2004; Makarieva et al., 2005; Moran & Woods, 2012). However, Berke et al. (2013) highlight that there is enormous diversity in size-latitude relationships for marine bivalves. Body size is influenced by a complex interaction of physiological, ecological and evolutionary drivers that affect growth rates, food availability, reproductive output, predation pressure, longevity and various other factors. Under increased thermal stress (e.g. at the edge of a biogeographic range), strain is placed on internal physiological systems. The related costs of energy acquisition, conversion and conservation, impact energy budgets with negative consequences for growth and reproduction (Sokolova et al., 2012). There are numerous studies that demonstrate temperature-induced changes to various aspects of energetics including growth, metabolism, reproductive output and condition index in ectotherm species (Pörtner, 2002, 2012; Lesser & Kruse, 2004; Hofmann & Todgham, 2010; Sokolova, 2013). Additionally, given that shell formation and repair are energetically expensive (Palmer, 1992), increasing temperature may have negative repercussions for shell growth. Elevated temperature may also negatively affect shell biomineralization, particularly when coupled with limited food availability (Mackenzie et al., 2013; Thomsen et al., 2013). Additionally, variation in depth between sites, particularly with regard to those deeper sites examined by Anwar et al. (1990), may influence the growth of mussels at the same latitude but at different depths, especially as previous research has shown that even small changes in temperature can influence bivalve growth (Almada-Villela et al., 1982). Likewise, there are additional abiotic (e.g. photoperiod) and biotic (e.g. food availability) factors which vary with latitude and also influence growth that future work could consider (Strömgren, 1976; Brodte et al., 2006).

A significant negative relationship between flow rate and the maximum theoretical length (L_∞) was also observed in *M. modiolus* when including data from Anwar et al. (1990). Such findings could be an indication of the energetic demands of byssal thread production under high flow conditions, reducing the risk of dislodgement, and reducing scope for growth (Comely, 1978; Okamura, 1986; Anwar et al., 1990; Fariñas-Franco et al., 2014). The findings could also possibly highlight an upper limit to flow conditions that are conducive to efficient food uptake, as current velocity determines the flux of material available for feeding (Lesser et al., 1994).

An increase in global CO_2 concentration has caused sea temperatures to rise, especially in the latter part of the last century and, under current climate change emission scenarios, is predicted to continue to increase ($3–5°C$ by 2100) (IPCC, 2014). For *M. modiolus* reefs at the limit of the species' thermal tolerance (e.g. the North Lleyn reef), warming is likely to be a contributory factor to potential decline. Mean bottom temperature at this southern aspect of the distribution was $11°C$ in 2009 (Gormley et al., 2013) and regional summer seawater temperatures as high as $17–18°C$ have been reported (CEFAS Coastal Temperature Network). Warming is likely to cause range shifts in species and habitats as species align their distributions to match their physiological tolerances (Doney et al., 2012). Consequently, *M. modiolus* reefs may respond to future climate change by shifting distribution further northward. Climate-population models have indicated that changes in population demographics, abundance and size may accompany such climate-driven range shifts (Hare et al., 2010). Results here provide baseline values against which changes in such factors may be monitored thereby aiding detection of potential climate change impacts. Further, where populations are genetically connected (Gormley et al., 2015a, b) and thus may have similar adaptive capacity, consideration of the effects of temperature in more southern regions may give some indication of effects to be expected in more northerly

populations. However, given both the longevity of *M. modiolus* and current acceleration in rates of climate change, many reefs will have limited opportunity for adaptation.

Under the OSPAR Convention for the Protection of the Marine Environment of the North East Atlantic 1992, *M. modiolus* reefs are listed as Priority Marine Habitats (determined as 'threatened and/or declining species and habitats') (OSPAR, 2009). The maintenance of such habitats is therefore key to the achievement of 'Good Environmental Status' under the *European Union (EU) Marine Strategy Framework Directive* (OSPAR, 2012). The findings of the present study have important implications when considering how Marine Protected Areas (MPAs) for these reefs are managed, particularly in a changing climate (Gormley *et al.*, 2013, 2015a). Although the underlying causes of variation in demographics between sites would require further investigation, strong reproduction and post-settlement survival (collectively referred to as recruitment and measurable as juvenile abundance) are nevertheless desirable characteristics for reefs within an MPA. From a cost-benefit perspective, MPAs with stronger recruitment are more likely to achieve conservation objectives. In some cases, maintaining strong recruitment might be a site-specific management consideration (self-recruiting reefs) or it might require the management of larval supply from outside the MPA (cf. Gormley *et al.*, 2015b), thus requiring a network approach. At present, no MPA management plans or conservation objectives give detailed consideration of how recruitment should be managed. For a habitat type that has declined (Rees, 2009), restoration may be necessary to maintain the shellfish reefs within the MPA (cf. Fariñas-Franco *et al.*, 2014) or to create stepping-stones in planned climate migration (Gormley *et al.*, 2015a, b). In such cases, Fariñas-Franco *et al.* (2014) considered that *M. modiolus* ecophenotypes might need to be matched to MPAs if donor populations were to be used in the rehabilitation of declining populations in that MPA. For example, a globular shell shape may not fare well if translocated to an area of greater flow (Hiscock *et al.*, 2002) and morphological adaptation is unlikely to be rapid in these slow growing, long-lived species (Fariñas-Franco *et al.*, 2014). The present study provides widespread evidence of significantly different ecophenotypes linked to flow and latitude and therefore further emphasizes these conclusions.

Significant morphological and demographic variation between locations also gives cause for consideration that, since body size is often linked to fecundity, and population size is clearly linked to total reproductive output (and probably recruitment) some populations may be a higher priority for conservation management than others. Whether it is preferable to direct conservation management effort towards high densities of smaller individuals such as off the North Lleyn (mean length 56.04 mm, 30.8 ind. m²) or reefs with low densities of bigger animals such as in Scapa Flow (mean length of 88.7 mm and 5.80 ind. m²) would require a more detailed analysis of total reproductive outputs and vectors.

This study presents differences between *M. modiolus* populations in terms of their demographics, morphology and growth. Overall the study highlights that conservation management needs to carefully consider the demographics and morphology of protected *M. modiolus* populations in the prioritization of management effort, in assessments of the future prospects of protected areas, and the consideration of restoration. These implications are particularly relevant to planning for a changing climate.

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