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1 **The demographics and morphometries of biogenic reefs:** 2 **important considerations in conservation management**

3
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8
9 *Modiolus modiolus* L. (horse mussel) reefs are a priority marine habitat of high
10 conservation value that is currently listed as endangered and/or threatened across its
11 European distribution. Population structure, density or shell morphology may
12 influence the biodiversity of a reef, either directly or indirectly. Thus, such metrics are
13 important considerations for successful conservation management of these biodiversity
14 hotspots. Population structure, shell morphology and growth rates were examined in
15 *M. modiolus* reefs across the UK range of the habitat to examine differences between
16 key populations, including those near the Lleyn Peninsula in Wales (southern range),
17 off Port Appin in Western Scotland (mid-range) and in Scapa Flow in the Orkney Isles,
18 Scotland (northern range). Additionally, the influence of physical conditions
19 (temperature and tidal flow) to growth rate and predicted maximum shell length for
20 each population was examined. Growth rates were determined using acetate peels of
21 sectioned shells. Lower juvenile abundance was observed in Scapa Flow. Small,
22 narrow-shaped shells were found to be characteristic of North Lleyn mussels, and
23 larger, globular-shaped shells were characteristic of mussels in Scapa Flow and off
24 Port Appin. Mussels in Scapa Flow were slower growing, yet reached a longer
25 asymptotic length (L_{∞}) than mussels of Port Appin and North Lleyn. Growth curves
26 from sites within this study were analysed with other published data. A trend of higher
27 L_{∞} at higher latitudes and at lower flow rates was observed. Variations in growth and
28 age are discussed in relation to flow regimes, connectivity to other reefs, density and
29 latitude.

30
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33 34 INTRODUCTION

35
36 The horse-mussel, *Modiolus modiolus* (Linnaeus, 1758) occurs singularly, in clumps,
37 or as high-density, species-rich biogenic reefs in temperate coastal regions around the
38 world (Rees *et al.*, 2008; Sanderson *et al.*, 2008; Rees, 2009). *M. modiolus* reefs of
39 conservation importance can be identified by their extent, percentage cover of live
40 *M. modiolus*, and associated communities (Morris, 2015). The decline of *M. modiolus*
41 reefs in the North East Atlantic marks them as protected marine conservation features
42 (Rees, 2009; Cook *et al.*, 2013). They are therefore identified under several
43 conservation drivers: The Marine (Scotland) Act 2010; the Habitats and Species
44 Directive (Council Directive 92/43/EEC); the OSPAR Convention; and the Marine
45 Strategy Framework Directive (MSFD; Council Directive 2008/56/EC).

46
47 The extent and density of *M. modiolus* reefs have previously been used to determine
48 reef condition (Rees, 2009; Moore *et al.*, 2012; Fariñas-Franco *et al.*, 2014). However,
49 these measures indicate little about their future prospects. Instead, parameters such as

50 size-frequency distribution, morphometries and growth rates may be more appropriate
51 for understanding long-term reef status. An understanding of reef-based differences
52 will also support development of ecologically relevant climate envelope models and aid
53 in illuminating potential impacts (e.g. altered ecosystem function due to shifts in body
54 size) of a changing climate (Peck *et al.*, 2009; Somero, 2010; Sandford & Kelly, 2011).

55
56 Growth of *M. modiolus* is usually rapid in the first 4-6 years in order to reach an adult
57 shell length (i.e. approximately 35-40 mm) (Anwar *et al.*, 1990). At this size predation
58 pressure is typically reduced (Comely, 1978; Holt *et al.*, 1998) and animals can then
59 spend more of their energy resources on reproduction as opposed to growth. *M.*
60 *modiolus* are reported to be sexually mature between 4-8 years old (Jasim & Brand,
61 1989; Wiborg, 1946; Rowell, 1967). Temperature influences growth rates in bivalves,
62 with slower growth rates characteristic of higher latitudes and greater depths
63 (MacDonald & Thompson, 1985; Sato, 1994). Near-bed seawater temperature data for
64 the UK indicates a difference of up to 3-4 °C between northern and southern latitudes,
65 and consequently one would expect temperature driven variation in growth rates across
66 *M. modiolus* reef habitats (see Seidov *et al.* 2013; Gormley *et al.*, 2013). It has also
67 been suggested that gonad development is slower in bivalves in colder temperatures, as
68 such conditions may lead to late maturity and subsequently allow northern populations
69 to attain a larger size before energy is focused on reproduction (Sato, 1994). The
70 availability of food is another factor that may affect growth rates, suggesting slower
71 growth rates would be observed in deep-water populations, where food is more limited
72 (MacDonald & Thompson, 1985). Additionally, intertidal *M. modiolus* populations
73 have demonstrated slower growth rates than populations in fast flowing currents, e.g.
74 on oilrigs in the North Sea (Anwar *et al.*, 1990), where increased flow rates reduce the
75 energy required to filter feed (Wildish & Peer, 1983); however, differences in food
76 availability and feeding windows between intertidal and offshore sites may also play a
77 role (Lesser *et al.*, 1994).

78
79 Physical conditions also have a strong influence on shell morphology with bivalves
80 generally exhibiting high plasticity in response to local environmental conditions (Seed,
81 1968; O'Connor, 2010). For example, bivalves with narrow shaped shells reduce the
82 effects of drag and the risk of dislodgement, and are typically found in areas with high
83 flow rates (Seed, 1968; Seed, 1980; Steffani & Branch, 2003). Reef density has also
84 been seen to influence the morphology of bivalves, with narrower shells found in denser
85 populations. This may be a response to food availability, disease prevalence, and/ or
86 physical interference (Alunno-Bruscia *et al.*, 2001; Lauzon-Guay *et al.*, 2005; Caill-
87 Milly *et al.*, 2012). Depth (Etter & Rex, 1990) and substrate type (Seed, 1980) have
88 also been cited as influencing morphology in bivalves. A recent study on the
89 morphology of *M. modiolus* shells found significant differences in shell shape between
90 sites within an enclosed loch, likely due to differences in current speed and sediment
91 type between sites (Farinas-Franco *et al.*, 2014).

92
93 Recruitment of juveniles influences population structure, and effective recruitment
94 relies on successful spawning and settlement of larvae. The spawning season of
95 *M. modiolus* is poorly understood and tends to vary greatly between reefs, though is
96 likely linked to temperature. Settlement of larvae at certain reefs is also highly variable
97 and sporadic between years (Wiborg, 1946; Seed & Brown, 1977; Brown, 1984).
98 Comely (1978) suggested settlement differences between reefs were due to larvae
99 originating from outside the reef area; hence recruitment would be affected by

100 hydrodynamic conditions, particularly as *M. modiolus* larvae can remain within the
101 water column for approximately one month (Schweinitz & Lutz, 1976; Roberts *et al.*,
102 2011). In addition, a population may act as a larval sink or source, resulting in
103 recruitment differences between reefs (Lipcuis *et al.*, 2008). Variation in mussel density
104 on a reef may also influence recruitment. Adult aggregations provide refuge, and
105 consequently can increase post-settlement survival by protecting juvenile *M. modiolus*
106 from predation (Comely, 1978; Holt *et al.*, 1998).

107

108 Population structure, density or shell morphology may influence the biodiversity of a
109 given reef, either directly through the abundance and diversity of associated
110 communities (Gutiérrez *et al.*, 2003; O'Connor & Crowe, 2007; Ragnarsson & Burgos,
111 2012) or indirectly through the reef's capability for habitat modification (Allen &
112 Vaughn, 2011). It is important for such factors to be taken into consideration in Marine
113 Protected Area (MPA) monitoring programmes for successful conservation
114 management of these biodiversity hotspots.

115

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

125

126 MATERIALS AND METHODS

127

128 Mussels were collected by clearing ~1 m² plots on *M. modiolus* 'reefs' (*cf* Morris 2015)
129 using SCUBA. Four plots were cleared in Scapa Flow (N 58° 53' .446, W 03° 11' .255;
130 23 m below chart datum (BCD)), three plots were cleared off Port Appin (N 56° 33'
131 .029, W 05° 25' .468; 21 m BCD) and four plots were cleared from north of the Lleyn
132 Peninsula (N 52° 56' .516, W 04° 38' .070; 30m BCD); (Figure 1). These sites were
133 chosen as representative of different reef types found in the UK with regards mussel
134 density, geographic location (i.e. latitude) and flow regime.

135

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

148

149 A current meter (MIDAS ECM, Valeport Ltd., Devon, UK) was placed at each site for
150 6 days during a neap cycle, recording current speed, direction and water depth every 5
151 seconds. The densities of the *M. modiolus* reefs were estimated using 0.25m² photo
152 quadrats using the method and counting rules outlined in Cook *et al.* (2013). Nine and
153 five photo quadrats were taken in 2014 from Scapa Flow and Port Appin reefs. Photo
154 quadrats could not be taken in 2014 on the North Lleyn reef, so seven photo quadrats
155 taken in 2009 (Cook *et al.*, 2013), were analysed instead.

156

157 **Length frequency and morphometric data**

158 The maximum shell-lengths of all *M. modiolus* were measured to the nearest 0.1 mm
159 using digital vernier callipers, before being returned to the reef. In addition, width and
160 height of the first 50 mussels were recorded for morphometric analysis. Debris from
161 the cleared plots was washed through a 1 mm sieve in order to include juveniles in the
162 analysis. This was fixed in seawater buffered 10% formaldehyde solution, and
163 subsequently sorted by hand to find juveniles. Juveniles were measured using the same
164 method as described above. Additional length, width and height measurements of *M.*
165 *modiolus* were collated from historical surveys (2010-2015) at the same sites.

166

167 **Growth rate data**

168 Thirty mussels of varying lengths were selected from each site across an even size
169 range. Acetate peels were used to age the mussels as described in Richardson *et al.*
170 (1979) and Anwar *et al.* (1990). One valve from each mussel was cut longitudinally,
171 along the umbone-rim axis, using a circular saw. To prevent breakages, shells <60 mm
172 in length were set in clear polyester casting resin before being cut. Once cut, the shell
173 half containing the umbone was sanded, polished and then etched in 1% hydrochloric
174 acid. The edge of the shell was dipped in acetone before being placed on an acetate
175 sheet. After drying, the sheet was pulled from the shell, leaving a 'peel' of the inner
176 nacreous layer. All peels were aged via use of a dissection microscope with each of the
177 dark bands in the middle nacreous layer representing a year of growth (Figure 2).

178

179 **Analyses**

180 All statistical analyses were completed using the statistical software R (release 3.1.1,
181 2014). One-way ANOVAs with follow up pairwise comparisons were used to test for
182 differences in flow rates, collected with the current meter, between the sites. Length
183 frequency measurements were converted to percentage size frequency and plotted for
184 each sampled site along with approximate ages based on the growth curves. One-way
185 ANOVAs, with follow up pairwise comparisons were then used to test of differences
186 in the mean length of the mussels between sites.

187

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

198

199 Values for maximum length (L_{∞}), growth rate (K) and $t\theta$ were identified to produce
200 growth curves based on Von-Bertalanffy's growth equation for each of the populations.
201 Starting parameters were estimated using VbStarts in the FSA package within R (Fish
202 R, 2014). These starting values were then used to calculate the coefficients using the
203 nonlinear least-squared regression within R. L_{∞} and K values were plotted with the
204 best-fit Von Bertalanffy growth model superimposed. These values, along with L_{∞} and
205 K values from 6 other populations reported in Anwar *et al.* (1990) (Figure 1), were used
206 to test for correlations with maximum tidal flow and latitude. After assumptions of
207 normality and equal variance were confirmed, a Pearson's Product Moment Correlation
208 test was used to compare these L_{∞} and K values against predicted maximum flow rates
209 (BERR, 2008) and latitude of the nine sites. The current meter data was not used in this
210 analysis, as benthic current flow data was not available for the additional 6 sites. The
211 relationship between latitude and flow was tested separately using Spearman's Rank
212 Correlation.

213

214 RESULTS

215

216 The mean current speed at the North Lleyrn site was 0.244 m/sec significantly faster
217 than at Scapa Flow (0.029 m/sec, $P < 0.001$) and Port Appin (0.106 m/sec, $P < 0.001$).
218 The current at Port Appin was also significantly faster than at Scapa Flow ($P < 0.001$).
219 The North Lleyrn reef had 24.6 *M. modiolus* per m^2 and 21% coverage, the Port Appin
220 reef had 16 per m^2 and 16% coverage and the Scapa Flow reef had 11.1 per m^2 and 11%
221 coverage.

222

223 Length frequency distributions for each of the sites were bimodal (Figure 3), most
224 pronounced in the Port Appin and North Lleyrn populations. The mussels sampled at
225 Scapa Flow were significantly larger (mean 88.75 mm) than those at Port Appin (mean
226 50.1 mm; $P < 0.001$) and North Lleyrn (mean 56.04 mm; $P < 0.001$).

227

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

240

241 Von Bertalanffy growth curves revealed that *M. modiolus* from the Scapa Flow
242 population had a higher L_{∞} (159.8 mm) and a lower K value (0.04) compared to the
243 other sites in this study (Figure 6; Table 1). North Lleyrn *M. modiolus* had a lower L_{∞}
244 value (L_{∞} 110.9 mm), and a lower K value (0.059) compared to the Port Appin
245 population (L_{∞} 122.82, K 0.061).

246

247 The K and L_{∞} values obtained from the Anwar *et al.* (1990) study are listed in Table 1
248 with predicted max flow rates and depths. A significant positive relationship was found

249 between latitude and L_{∞} ($r=0.74$, $t=2.85$, $P<0.05$; Figure 6) and a significant negative
250 relationship was found between flow and L_{∞} ($r=-0.82$, $t=-3.4836$, $P<0.05$; Figure 7).
251 There was no significant relationship between K and any environmental variable. There
252 was also no significant correlation between flow and latitude ($T=10$, $P=0.39$).

253

254 DISCUSSION

255

256 The present study found that *M. modiolus* from different reefs exhibited different
257 demographic profiles, morphologies and growth rates, that varied with tidal flow and
258 latitude. Growth rates and maximum achievable sizes increased with current flow and
259 latitude. Both factors may also directly contribute to the observed variations in juvenile
260 abundance and shell morphology, but indirect impacts via changes to energy budgets
261 should also be considered (Sokolova *et al.*, 2012).

262

263 Differences in juvenile abundance are tentatively interpreted here because of the low
264 number of sites studied. Nevertheless, the increased abundance of juveniles at North
265 Lleyn and Port Appin (Figure 3) may be due to the higher current flows observed
266 (Comely, 1978; Brown, 1984). Such conditions may lead to increased connectivity via
267 improved larval supply from other reefs in the Irish Sea (Anwar *et al.*, 1990; Rees *et al.*,
268 2008; Gormley *et al.*, 2015b) and Loch Linnhe respectively (Rees, 2009; Moore *et al.*,
269 2012). Conversely, the decreased abundance of juveniles in Scapa Flow maybe
270 caused by limited connectivity, due to reduced tidal flow and a lack of known
271 neighbouring reefs (Rees, 2009; Gormley *et al.*, 2015a). Furthermore, while the Scapa
272 Flow population had the largest L_{∞} , it also had a lower mussel density compared to the
273 Port Appin and North Lleyn reefs. Although gamete production is correlated with body
274 size, population density has been shown to be equally important to fertilisation success
275 and reproductive output (Levitan, 1991), and consequently could partially account for
276 lowered abundance of juveniles in the northern population. The higher structural
277 complexity found on reefs with higher densities might also afford more shelter to
278 juveniles from predation (Comely, 1978; Holt *et al.*, 1998). An increase in reef
279 complexity has been shown to increase post-settlement survival in other bivalves
280 (Gutierrez *et al.*, 2003; Nestlerode *et al.*, 2007).

281

282 The high mussel density and narrow-shaped shells of mussels from North Lleyn, and
283 low density and globular-shaped shells from Scapa Flow and Port Appin, support the
284 view that crowding leads to narrower shells (Alunno-Bruscia *et al.*, 2001; Lauzon-Guay
285 *et al.*, 2005; Caill-Milly *et al.*, 2012). However, the lower density at Port Appin does
286 not support this hypothesis. Moreover, given that flow rates were significantly higher
287 at North Lleyn than at Port Appin or Scapa Flow, flow rate, rather than density, may be
288 the stronger driver of shell morphology. The narrow-shaped shells from North Lleyn
289 are possibly a morphological adaptation to allow a better hold within the sediment and
290 reduce the risk of dislodgment in fast flowing currents (Seed, 1968; Seed, 1980; Steffani
291 & Branch, 2003; Fariñas-Franco *et al.*, 2014).

292

293 A significant positive relationship was observed between latitude and L_{∞} when
294 including data from the Anwar *et al.* (1990) study. Bergmann's rule, that a species will
295 demonstrate a larger body size at higher latitudes (i.e. lower temperatures), may explain
296 this relationship (Berke *et al.*, 2013). Oxygen concentration generally limits the size of
297 ectotherm species as surface area to volume ratios decrease with increased body size,
298 thereby reducing gas exchange capability. The increased solubility of oxygen at lower

299 seawater temperatures however, coupled with lowered metabolic demands under such
300 conditions, reduces these size constraints in animals at higher latitudes (Chapelle &
301 Peck, 2004; Makarieva *et al.*, 2005; Moran & Woods, 2012). However, Berke *et al.*
302 (2013) highlight that there is enormous diversity in size-latitude relationships for
303 marine bivalves. Body size is influenced by a complex interaction of physiological,
304 ecological and evolutionary drivers that effect growth rates, food availability,
305 reproductive output, predation pressure, longevity and various other factors. Under
306 increased thermal stress (e.g. at the edge of a biogeographic range), strain is placed on
307 internal physiological systems. The related costs of energy acquisition, conversion and
308 conservation, impact energy budgets with negative consequences for growth and
309 reproduction (Sokolova *et al.*, 2012). There are numerous studies that demonstrate
310 temperature-induced changes to various aspects of energetics including growth,
311 metabolism, reproductive output, and condition index in ectotherm species (Pörtner,
312 2002; Lesser & Kruse, 2004; Pörtner, 2012; Sokolova, 2013; Hofmann & Todgham,
313 2010). Additionally, given that shell formation and repair are energetically expensive
314 (Palmer, 1992), increasing temperature may have negative repercussions for shell
315 growth. Elevated temperature may also negatively affect shell biomineralisation,
316 particularly when coupled with limited food availability (Thomsen *et al.*, 2013;
317 Mackenzie *et al.*, 2013). Additionally, variation in depth between sites, particularly
318 with regard those deeper sites examined by Anwar *et al.* (1990), may influence the
319 growth of mussels at the same latitude but at different depths, especially as previous
320 research has shown that even small changes in temperature can influence bivalve
321 growth (Almada-Villela *et al.*, 1982). Likewise, there are additional abiotic (e.g.
322 photoperiod) and biotic (e.g. food availability) factors which vary with latitude and also
323 influence growth that future work could consider (Stromgren, 1976; Brodte *et al.*,
324 2006).

325

326 A significant negative relationship between flow rate and the maximum theoretical
327 length (L_{∞}) was also observed in *M. modiolus* when including data from Anwar *et al.*
328 (1990). Such findings could be an indication of the energetic demands of byssal thread
329 production under high flow conditions, reducing the risk of dislodgement, and reducing
330 scope for growth (Comely, 1978; Okamura, 1986; Anwar *et al.*, 1990; Fariñas-Franco
331 *et al.*, 2014). The findings could also possibly highlight an upper limit to flow
332 conditions that are conducive to efficient food uptake, as current velocity determines
333 the flux of material available for feeding (Lesser *et al.*, 1994).

334

335 An increase in global CO₂ concentration has caused sea temperatures to rise, especially
336 in the latter part of the last century and, under current climate change emission
337 scenarios, is predicted to continue to increase (3-5 °C by 2100) (IPCC, 2014). For
338 *M. modiolus* reefs at the limit of the species' thermal tolerance (e.g. the North Lleyn
339 reef), warming is likely to be a contributory factor to potential decline. Mean bottom
340 temperature at this southern aspect of the distribution was 11°C in 2009 (Gormley *et al.*,
341 2013) and regional summer seawater temperatures as high as 17-18°C have been
342 reported (CEFAS Coastal Temperature Network). Warming is likely to cause range
343 shifts in species and habitats as species align their distributions to match their
344 physiological tolerances (Doney *et al.*, 2012). Consequently, *M. modiolus* reefs may
345 respond to future climate change by shifting distribution further northward. Climate-
346 population models have indicated that changes in population demographics, abundance
347 and size may accompany such climate-driven range shifts (Hare *et al.*, 2010). Results
348 here provide baseline values against which changes in such factors may be monitored

349 thereby aiding detection of potential climate change impacts. Further, where
350 populations are genetically connected (Gormley *et al.* 2015) and thus may have similar
351 adaptive capacity, consideration of the effects of temperature in more southern region
352 may give some indication of effects to be expected in more northerly populations.
353 However, given both the longevity of *M. modiolus* and current acceleration in rates of
354 climate change, many reefs will have limited opportunity for adaptation.

355

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

384

385 Significant morphological and demographic variation between locations also gives
386 cause for consideration that, since body size is often linked to fecundity, and population
387 size is clearly linked to total reproductive output (and probably recruitment) some
388 populations may be a higher priority for conservation management than others.
389 Whether it is preferable to direct conservation management effort towards high
390 densities of smaller individuals such as off the North Llyn (mean length 56.04 mm,
391 30.8 ind.m²) or reefs with low densities of bigger animals such as in Scapa Flow (mean
392 length of 88.7 mm and 5.80 ind.m²) would require a more detailed analysis of total
393 reproductive outputs and vectors.

394

395 This study presents differences between *M. modiolus* populations in terms of their
396 demographics, morphology and growth. Overall the study highlights that conservation
397 management needs to carefully consider the demographics and morphology of
398 protected *M. modiolus* populations in the prioritisation of management effort, in

399 assessments of the future prospects of protected areas, and the consideration of
400 restoration. These implications are particularly relevant to planning for a changing
401 climate.

402

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413

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