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3 **1 Survival of the fittest: explanations for gadoid**
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6 **2 imbalance in heavily fished seas**
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ABSTRACT

1. Anthropogenic activities have caused degradation of the world's ecosystems, accelerating loss of biodiversity. In marine ecosystems, fishing has had strong impacts on fish populations and their habitats. However, not all species have responded equally to fishing pressure.
2. Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*) and whiting (*Merlangius merlangus*) are of high commercial value throughout the North Atlantic. Despite having relatively similar life cycles, the state of stocks of these three species varies enormously, with whiting faring better than cod. Within the Firth of Clyde (southwest Scotland) this imbalance is especially accentuated, where small whiting now make up the greater proportion of the biomass.
3. In this study, cod, haddock and whiting recruitment to coastal areas, growth and bait attraction were explored within a marine protected area (MPA) in the Firth of Clyde. Over the course of summer 2013 and 2014, whiting and haddock arrived at coastal areas earlier than cod and grew faster. Cod were on average the smallest gadoid observed and whiting the largest. Whiting also had more predominant scavenging behaviour.
4. These results in combination with other life history and behaviour traits indicate that whiting may be at a competitive advantage over cod, and this may partly explain the imbalance of gadoids in the Firth of Clyde. This study highlights the importance of considering life history differences in multi-species fisheries management and how appropriately managed MPAs could help restore fish population and assemblage structure.

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3 36 **KEY WORDS:** behaviour, fisheries management, gadoid, growth, life-history traits,
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5 37 marine protected areas, recruitment, scavenging, stereo-video cameras.
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39 1. INTRODUCTION

40 Growing demands on the world's resources are affecting wildlife populations
41 through direct mortality of target species and the transformation of their habitats
42 (Foley et al., 2005; Sanderson et al., 2002). Reductions in population sizes from
43 hunting or harvesting, or habitat transformation can also cause imbalances in
44 community structures and ecosystem functioning, exacerbating extinction rates
45 (Dobson, Bradshaw & Baker, 1997; Hammer, Jansson & Jansson, 1993). Particular
46 life-history traits and habitat preferences can cause certain species to be more
47 vulnerable than others (Bastrikin, Gallego, Millar, Priede & Jones, 2014; Higginson,
48 2017). Understanding competition between species can therefore be critical to
49 ecosystem-based management.
50

51 Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*) and whiting
52 (*Merlangius merlangus*) are all species of high commercial value and have suffered
53 declines and alterations in population structure (Cote, Ollerhead, Scruton &
54 McKinley, 2003; Fernandes & Cook, 2013; Holmes, Millar, Fryer & Wright, 2014). In
55 recent years, following strict management measures, improvements have been
56 observed in North Sea stocks of these species (Fernandes & Cook 2013; ICES,
57 2017a). However, along the west coast of Scotland, recruitment and spawning
58 stock biomass remains relatively low, particularly for cod (Fernandes & Cook 2013;
59 ICES 2017b; 2017c; 2017d). Cod is also listed as vulnerable on IUCN redlist and is
60 listed as an OSPAR threatened and declining species (Sobel, 1996; OSPAR 2014).

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4
5 62 The Firth of Clyde (south-west Scotland) was an important fishing location for a
6
7 63 variety of demersal species (Heath & Speirs, 2012; Thurstan & Roberts, 2010).
8
9 64 Heavy fishing pressure during the twentieth century led to a steep decline in
10
11 65 landings of demersal fish (Thurstan & Roberts, 2010). As a result, a prohibition on
12
13 66 trawl fishing within three nautical miles of the shoreline was introduced (1989)
14
15 67 (Thurstan & Roberts, 2010). However, this was repealed in 1984 due to widespread
16
17 68 infringements and to allow access for *Nephrops norvegicus* fishing (Thurstan &
18
19 69 Roberts, 2010). Since the late 1990s, the Firth of Clyde demersal trawl fishery
20
21 70 primarily targets *Nephrops*, but with a significant by-catch of fish (Thurstan &
22
23 71 Roberts, 2010). A study by Heath and Speirs (2012) showed that since the
24
25 72 expansion of demersal trawling peaked in 1984, species richness of the Firth of
26
27 73 Clyde has remained almost unchanged, but the evenness has declined sharply. By
28
29 74 around 2000, 87% of the demersal fish biomass was composed of whiting, whereas
30
31 75 this species had comprised only 7% of the biomass between 1920 and 1959.
32
33 76 Furthermore, the mean body length in the fish community had halved since the
34
35 77 1960. Recent studies within the Firth of Clyde by Hunter, Speirs and Heath, (2015,
36
37 78 2016), demonstrated declining age at maturation and growth in cod, haddock and
38
39 79 whiting, during the period of heavy fishing pressure. These observations do not,
40
41 80 however, explain the imbalance of whiting within this semi-enclosed sea.
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48 82 Cod, haddock and whiting in this region are all members of the family *Gadidae* and
49
50 83 are known to have relatively similar life cycles. Spawning aggregations occur from
51
52 84 late winter to spring (Demain, Gallego, Jaworski, Priede & Jones, 2011; Olsen et
53
54 85 al., 2010; Wright, Tobin, Gibb & Gibb, 2010). Pelagic larval eggs are produced in
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3 86 batches which drift to coastal areas from late April to June where the juveniles
4
5 87 live for the first few months (Gibb, Gibb & Wright, 2007; Olsen et al., 2010).
6
7 88 Important food sources for juvenile gadoids include crustaceans and polychaetes,
8
9 89 and small fish such as plaice (*Pleuronectes platessa*) (Bastrikin et al., 2014;
10
11 90 Demain et al., 2011). Scavenging behaviour has been observed in all three species
12
13 91 (Groenewold & Fonds, 2000; Jenkins, Mullen & Brand, 2004), in addition to
14
15 92 predation between gadoids (Köster, Stephenson & Trippel, 2014; Temming, Floeter
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17 93 & Ehrich, 2007).
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22 94
23 95 This study aimed to determine the competitive interactions between gadoid
24
25 96 species during the post-settlement phase of their life in the Firth of Clyde.
26
27 97 Comparative analysis of gadoid recruitment, growth and scavenging behaviour was
28
29 98 undertaken using Stereo Baited Remote Underwater Video (SBRUV) systems within
30
31 99 a Marine Protected Area (MPA). Recruitment to coastal areas was explored by
32
33 100 measuring relative abundance variations, size and growth over the course of the
34
35 101 summer. Scavenging behaviour was investigated by measuring attraction to the
36
37 102 bait. The motivation for the study was to better understand why whiting has
38
39 103 become so dominant in the demersal fish community of the region.
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44 105 2. METHODS

46 106 2.1. Data collection

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49 107 Data were collected within south Arran nature conservation MPA, the Firth of
50
51 108 Clyde, south-west Scotland at depths of 4.0 m - 47.2 m, between June and
52
53 109 September 2013 and 2014 (Figure 1). Gadoid sampling took place using three
54
55 110 SBRUV frames as described in Elliott, Turrell, Heath and Bailey (2017a). From 5
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3 111 June to 29 September 2013, 80 camera deployments were carried out from a 6.5 m
4
5 112 RIB. However, data were used from 15th July (74 deployments), as before this date
6
7 113 no gadoids were observed. The following year, a further 185 deployments were
8
9 114 carried out between 30 June to 18 September 2014, from a 10.8 m research vessel
10
11 115 (RV Actinia) (Table 1). During 2014, data were not collected around the south-west
12
13 116 side of the island due to the slower steaming speed of the vessel used. As a result
14
15 117 of resource and logistical reasons, data were not collected continuously through
16
17 118 the periods of data collection. In the sampling design, the area of data collection
18
19 119 was divided into five zones, with samples collected within each zone to facilitate
20
21 120 replication. For logistic reasons and because of the long summer day length at the
22
23 121 study latitude, all deployments took place during daylight hours.
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29 123 Throughout data collection, Atlantic mackerel (*Scomber scombrus*) was used as
30
31 124 bait since it is oily and so produces a down current bait plume, and is relatively
32
33 125 inexpensive. The bait was held suspended 91 cm in front of the cameras and at a
34
35 126 height of 46 cm above the seabed to ensure visibility between the stereo-video
36
37 127 cameras and to minimise macro-algae hindering fish measurements. Calibration of
38
39 128 the cameras took place prior to and over the course of field data collection within
40
41 129 a controlled environment using methods outlined within Harvey and Shortis (1998)
42
43 130 and CAL software manual (version 2.11, www.seagis.com.au/event.html).
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50 132 **2.2. Video analysis**

51 133 EventMeasure software (version 3.61, www.seagis.com.au/event.html) was used to
52
53 134 analyse videos. Gadoid recruitment and growth were estimated from changes in
54
55 135 relative abundance and length measurements. Relative abundances were measured
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3 136 using the maximum number of individuals of the same species appearing in a single
4
5 137 frame at the same time during each separate video deployment (MaxN) as
6
7 138 described by Priede, Bagley, Smith, Creasey and Merrett (1994) and Watson,
8
9 139 Harvey, Anderson and Kendrick (2005). Fish fork length and position measurements
10
11 140 were taken at one time point per deployment, when the maximum number of
12
13 141 measurable fish was present. Length measurements with a precision > 0.5 cm and
14
15 142 a root mean square error > 2 cm were removed from analysis as recommended in
16
17 143 the SeaGIS software manual (version 2.11, www.seagis.com.au/event.html).
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21
22 145 Gadoid scavenging behaviour was quantified using water column positions relative
23
24 146 to the bait box and by an index of bait attraction or indifference. Gadoid water
25
26 147 column position was estimated using stereo-video Y and Z measurements (relative
27
28 148 to the mid-point of the camera system). Y values are approximate to height above
29
30 149 and below the cameras and Z values are the distance from the camera system
31
32 150 (Shortis, Harvey & Abdo, 2009). A subsample of 48 camera deployments (from 28
33
34 151 July to 1 August 2014) was used to assess gadoid bait attraction, since this
35
36 152 behaviour took longer to record. Gadoid bait attraction was classified as attracted
37
38 153 when the fish swam directly towards the bait with a maximum distance of ~20 cm
39
40 154 from the bait box. Indifference behaviour was classified when the fish swam
41
42 155 directly past the frame and did not approach.
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46 157 **2.3. Data analysis**

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49 158 All statistical analysis was performed with R software (version 3.2.2). A log
50
51 159 likelihood ratio test was used to test model significance against the null
52
53 160 hypothesis. Tukey tests were performed to test for differences between
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3 161 explanatory categorical variables (grouped day of data collection for 2014 and
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5 162 gadoid species where relevant). Random effects for grouped time period and zone
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7 163 were included in the model where relevant and significant, to account for
8
9 164 temporal and spatial variation (referred to by lowercase letters in Equations 1 to
10
11 165 4).

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16 167 MaxN was used to analyse gadoid recruitment to coastal areas over the period of
17
18 168 data collection (Equation 1). MaxN was analysed using negative binomial
19
20 169 generalized linear mixed models (GLMM) (Equation 1). A negative binomial
21
22 170 distribution was used to account for over dispersion of gadoid MaxN. Equations 1
23
24 171 and 2 were modelled on each gadoid species separately.

25
26
27 172 $\log(Y_i) = \beta_0 + \beta_1 T_{i(j)} + z_{ij}$ (1)

28
29 173 where Y_i is gadoid MaxN fitted with a logarithmic link, β are the coefficients, $T_{i(j)}$,
30
31 174 day (2013) or week (2014) of data collection, and z_{ij} the random effect (zone).

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34 175 Subscript i refers to the number of samples and j refers to categorical explanatory
35
36 176 variables.

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40 178 To explore gadoid arrival and growth over the period of data collection, gadoid
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42 179 length measurements were used (Equation 2 and 3). Equation 3, was modelled
43
44 180 separately to identify whether there were significant differences in gadoid growth
45
46 181 between the three species. Following analysis of DAtabase of TRAwl Surveys
47
48 182 (DATRAS) Age Length Key (product for standard species only) quarter 4 (October -
49
50 183 December) for the Firth of Clyde area, all individuals larger than 15 cm were
51
52 184 removed from the analysis to reduce the likelihood of observing age-1 individuals.
53
54
55 185 In total eight out of 9 length measurements greater than 15 cm were removed

186 from the cod length dataset prior to the analysis (max size measured 21.18 cm,
 187 total mean length 8.20 cm ± Standard Error (SE) 0.19 cm). Whereas 27 out of 208
 188 haddock measurements were removed (max size measured 21.69 cm, total mean
 189 length 12.02 cm ± SE 0.21 cm) and 60 out of 152 whiting measurements removed
 190 (max size measured 35.53 cm, total mean length 14.00 cm ± SE 0.35 cm). Refer to
 191 supporting information Table 1 for gadoid length measurements after removal of
 192 these larger individuals.

193

194 Length and gadoid Y and Z measurements were analysed using linear and linear
 195 mixed models (LMM), (Equation 2 to 4).

$$196 \quad Y_i = \beta_0 + \beta_1 T_{i(j)} \quad (2)$$

$$197 \quad Y_i = \beta_0 + \beta_1 G_{ij} + t_{ij} \quad (3)$$

198 Where Y_i is the individual gadoid fork length, G_{ij} , gadoid species and t_{ij} the
 199 random effect, grouped day of data collection. To explore age-0 cohorts, model
 200 distributions were identified using the Bhattacharya (1967) method. This method
 201 involves the decomposition of 0+ year length frequency distributions by visual
 202 identification of frequencies perceived to belong to one cohort.

203

204 Differences in gadoid scavenging behaviour were resolved by exploring the
 205 positions of the gadoid relative to the bait box (Y and Z positions; Equation 4), in
 206 addition to gadoid bait attraction.

$$207 \quad Y_i = \beta_0 + \beta_1 G_{ij} + t_{ij} + z_{ij} \quad (4)$$

208 Where Y_i is the gadoid Y or Z position, t_{ij} and z_{ij} are the random effects to account
 209 for spatial and temporal variations. A Wilcoxon Signed Rank test was used to
 210 estimate the significance of gadoids bait attraction differences.

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3. RESULTS

3.1. Gadoid recruitment and growth

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10 214 Over the course of summer 2013, a decline in cod MaxN was observed (Log
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12 215 likelihood (L) = -157.18, degrees of freedom (d.f.) = 4, dispersion (theta) = 0.93, P
13
14 216 value (P) < 0.05; Table 1) and a 1.98 cm increase in average length (L = -233.56,
15
16 217 d.f. = 3, P < 0.001; Figure 2; Supporting information Table 1). During summer 2014,
17
18 218 an increase in MaxN was observed in the second (28 July-01 August) and third week
19
20 219 (26 August - 2 September) of data collection (Tukey test P < 0.05 and P < 0.01),
21
22 220 followed by a decline in cod MaxN in the fourth week (15 to 18 September) (L = -
23
24 221 164.80, d.f. = 6, theta = 1.09, P < 0.001; Table 1). A growth of 2.71 cm was also
25
26 222 detected (L = -188.33, d.f. = 5, P < 0.05; Figure 2; Supporting information Table
27
28 223 1).

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33
34 225 Haddock MaxN did not significantly increase or decrease over the course of the
35
36 226 summer 2013 (L = -59.11, d.f. = 4, theta = 0.76, P > 0.05; Table 1). However, in
37
38 227 2014, an increase in MaxN was observed following the first week of data collection
39
40 228 (Tukey test P < 0.001) (L = -236.76, d.f. = 6, theta = 0.91, P < 0.01; Table 1). The
41
42 229 latter indicates a possible recruitment pulse shortly after the first week of July.
43
44 230 Growth was also observed over the course of data collection during 2013 (3.95 cm)
45
46 231 and 2014 (3.22 cm) (L = -88.19, d.f. = 3, P < 0.001 and L = -228.43, d.f. = 5, P <
47
48 232 0.001 respectively; Figure 2; Supporting information Table 1).

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54 234 Over the course of data collection 2013 there was no difference in whiting MaxN (L
55
56 235 = -54.41, d.f. = 4, P > 0.05; Table 1). However, a 5.75 cm increase in average

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3 236 length of age-0 individuals was observed ($L = -17.29$, d.f. = 3, $P < 0.05$; Figure 2;
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5 237 Supporting information Table 1). During 2014 whiting MaxN varied over the course
6
7 238 of data collection with a decrease in in the third week (26 August - 2 September)
8
9 239 of data collection (Tukey test $P < 0.05$) ($L = -2236.73$, d.f. = 6, $\theta = 1.09$, $P <$
10
11 240 0.01 ; Table 1). An increase in growth of 1.39 cm, $SE \pm 0.07$ cm was also detected
12
13 241 ($L = -185.11$, d.f. = 4, $P < 0.05$; Figure 2; Supporting information Table 1).
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17
18 243 Over the course of both years cod were smaller than haddock and whiting ($L = -$
19
20 244 1003.89 , d.f. = 5, $P < 0.001$) with haddock and whiting being of more similar sizes
21
22 245 (Table 2; Figure 2). For both years, more cod (mean MaxN = 3.62, \pm standard
23
24 246 error=0.26) were observed than haddock (mean MaxN = 0.98, \pm se = 0.15) or
25
26 247 whiting (mean MaxN = 0.86, \pm se = 0.13) (Table 1). Two age-0 cohorts were
27
28 248 identified using Bhattacharya's (1967) method for whiting whereas only one cohort
29
30 249 was identified for haddock and cod (Supplementary information Figure 1). The
31
32 250 latter provides evidence of pulse recruitment for whiting.
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36 252 **3.2. Gadoid scavenging behaviour**

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38 253 Significant differences between gadoids were observed with respect to their
39
40 254 positioning relative to the seabed, cameras and bait. Cod positioned themselves on
41
42 255 average closer to the sea bed and further from the cameras than haddock or
43
44 256 whiting. Whiting average position was closest to the cameras in terms of height
45
46 257 and distance off the sea bed (for Y $L = -1961.405$, d.f. = 6, $P < 0.001$ and for Z $L =$
47
48 258 -2441.08 , d.f. = 6, $P < 0.001$; Table 2; Figure 3).
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3 260 Whiting were the most attracted to the bait (94%, 68 out of 74 individuals),
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5 261 followed by haddock (57%, 54 out of 95 individuals). Only one out of 141 cod was
6
7 262 attracted to the bait box (Figure 4), resulting in cod being significantly less
8
9 263 attracted to the bait than haddock and whiting (Tukey test $P < 0.001$) ($L = -$
10
11 264 105.967 , d.f. = 5, $P < 0.001$). There was a significant size difference between the
12
13 265 cod and whiting attracted to the bait compared to those that were not (cod:
14
15 266 Wilcoxon (W) = 347, $P < 0.001$, haddock: $W = 268$, $P > 0.05$, whiting: $W = 57$, $P <$
16
17 267 0.001). Cod larger than 15 cm were more attracted to the bait.
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4. DISCUSSION

25 270 Rapid environmental changes provide challenges to which species need to adapt.
26
27 271 Intensive fishing activities over the last few centuries have not only had profound
28
29 272 impacts on targeted species but also the wider marine ecosystem (Holmlund &
30
31 273 Hammer, 1999). Here, cod, haddock and whiting recruitment, growth and
32
33 274 scavenging behaviour in a nursery area were compared to understand why whiting
34
35 275 has become so dominant in the demersal fish community of the Firth of Clyde.
36
37 276 Although cod, haddock and whiting are all members of the same family, and have
38
39 277 apparently similar life histories, the detailed observations described here
40
41 278 demonstrated differences in behaviours during their juvenile stages. Because there
42
43 279 has been no systematic protection of gadoid nursery areas in the study region,
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45 280 these behavioural and life history differences may partly explain the documented
46
47 281 (Heath & Speirs, 2012) biomass imbalance between these species.
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53 283 Cod recruited to coastal areas later than haddock and whiting (evidenced by their
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55 284 smaller size at the start of data collection). Over the course of data collection,
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3 285 haddock and whiting grew faster than that of cod. Cod relative abundance was
4
5 286 observed to be on average higher than that of haddock and whiting. However, this
6
7 287 may have been due to the shallow depths which the deployments took place (< 48
8
9 288 m). Cod have been observed to occupy shallower waters than haddock and whiting
10
11 289 (Elliott et al., 2017a). During both years, a decline in juvenile cod relative
12
13 290 abundance was observed at the end of the data collection. Whereas, haddock and
14
15 291 whiting relative abundance were variable, demonstrating either stronger pulse
16
17 292 recruitment than cod, or better survival.
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20 293

21
22 294 Bastrikin et al. (2014), undertook a similar study, observing the diet, growth and
23
24 295 recruitment of pelagic to demersal age-0 gadoids from mid-May to the end of
25
26 296 August in the North Sea. They observed declines in cod over the course of data
27
28 297 collection, with haddock recruiting to coastal areas earliest and whiting having the
29
30 298 most protracted recruitment which is in line with the observations in this study.
31
32 299 The size ranges of juvenile gadoids observed by Bastrikin et al. (2014), were
33
34 300 similar to those seen in this study. Spawning earlier, multiple times throughout the
35
36 301 season, the faster growth rates and on average larger size of whiting and haddock
37
38 302 gives them a competitive advantage over cod (Hislop, 1975; McEvoy & McEvoy
39
40 303 1992; Wright & Trippel, 2009), and potentially makes cod more vulnerable to
41
42 304 predation (Demain et al., 2011; Werner & Gilliam, 1984).
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48 306 From the combined position, and bait attraction results, whiting were observed to
49
50 307 be more attracted to the bait than haddock and cod. In a bait attraction
51
52 308 investigation in the North Sea by Martinez et al. (2011), whiting were also observed
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54 309 to be more attracted to baited camera systems than haddock. This greater
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3 310 tendency to scavenge may be advantageous in a system exposed to high levels of
4
5 311 trawling, with resultant discards and mortality of benthic fauna. It is not clear why
6
7 312 cod may have been less attracted to the bait. They may have a lower preference
8
9 313 for carrion or, being smaller than whiting, more driven by predator avoidance (Biro
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11 314 & Stamps, 2008).

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15
16 316 Studies by Demain et al. (2011), showed that as these three gadoids mature and
17
18 317 grow, they adapt their feeding strategy to an increasingly pisivorous diet (Demain
19
20 318 et al., 2011). The larger (older) cod were observed to be more attracted to the
21
22 319 bait, strengthening the argument, that the on average smaller size of cod places
23
24 320 them at a disadvantage to whiting and haddock in exploiting carrion. Gadoids are
25
26 321 also known to predate on one another (Hislop, Robb, Bell, & Armstrong, 1991;
27
28 322 Köster et al., 2014), and whiting have been found to be particularly voracious
29
30 323 predators wiping out entire cod populations (Temming et al., 2007).

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34
35 325 Another factor to take into consideration when considering the Firth of Clyde
36
37 326 gadoid imbalance, is that the habitats occupied by juvenile haddock and whiting
38
39 327 (deeper sand and mud seabed types) (Elliott et al., 2017a), are less vulnerable to
40
41 328 damage by mobile demersal gear than that of cod (Collie, Hall, Kaiser & Poiner,
42
43 329 2000; Kaiser et al., 2006). Juvenile haddock and whiting are found over sand and
44
45 330 mud substrata which are also found in large quantities throughout the Firth of
46
47 331 Clyde (Elliott, Sabatino, Heath, Turrell & Bailey, 2017b; McIntyre, Fernandes &
48
49 332 Turrell, 2012). Cod have been observed in higher relative abundance over fragile
50
51 333 maerl and seagrass seabed types and more heterogeneous landscapes within the
52
53 334 Firth of Clyde, with ontogenetic shifts in seabed type with increasing size (Elliott,

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3 335 Ahti, Heath, Turrell & Bailey, 2016; Elliott et al., 2017a; Elliott et al., 2017b). The
4
5 336 secondary impacts of seabed homogenisation from fishing activities (Jennings &
6
7 337 Kaiser, 1998), and cod having more specific habitat requirements puts them yet
8
9 338 again at a survival disadvantage to haddock and whiting.

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13 340 From 1889 to 1962 trawling was restricted to areas further than three nautical
14
15 341 miles from the coast (Thurstan & Roberts, 2010). As of 1962 a byelaw was
16
17 342 introduced to allow *Nephrops* trawlers throughout the Firth of Clyde (Thurstan &
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19 343 Roberts, 2010). Today, *Nephrops* trawling and scallop dredging still continues and
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21 344 results in fish mortality through bycatch (Bergmann, Wieczorek, Moore & Atkinson,
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23 345 2002). The continued mobile demersal activity is of particular importance given
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25 346 much of the maerl found to occur around the South of Arran has been observed to
26
27 347 be in a degraded state (Elliott et al, 2017a). Reduced substratum diversity and
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29 348 quality from decades of demersal mobile gears may therefore be having a negative
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31 349 impact on cod populations (Elliott et al., 2017a; 2017b).

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37 351 Studies undertaken in North America and in Norway have shown that settlement
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39 352 and post-settlement survival of gadoid may be the best means to improve gadoid
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41 353 population regulation (e.g. Laurel, Knoth & Ryer, 2016; Myers & Cadigan, 1993;
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43 354 Olsen & Moland, 2011). Moland et al., (2013) and Murawski, Brown, Lai, Rago and
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45 355 Hendrickson (2000), studied the effect of demersal fish habitat protection
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47 356 measures on Georges Bank (Southern New England, USA) and along the Norwegian
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49 357 Skageerak coast. In both cases improved recruit survival was observed in cod and
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51 358 haddock (Moland et al., 2013; Murawski et al., 2000).

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3 360 The imbalance in the Firth of Clyde may be partly explained by compensatory
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5 361 effects from fishing activities (Heino & Godø, 2002), where initially trawlers
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7 362 heavily targeted cod (Thurstan & Roberts, 2010), enabling the less commercially
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9 363 desirable whiting to become more abundant. However, as fisheries began targeting
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11 364 other species, such as whiting and plaice (Thurstan & Roberts, 2010), fisheries
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13 365 induced pressures may have led to the removal of larger individuals and the more
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15 366 adaptive species (such as whiting) becoming mature at a younger age (Hunter et
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17 367 al., 2015; 2016). Furthermore, since cod were so heavily targeted and for such a
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19 368 long period of time (from the 19th to early 21st century) (Thurstan & Roberts,
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21 369 2010), stock levels may have fallen below critical levels, prohibiting any self-
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23 370 regeneration despite recover management measures put in place (Frank &
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25 371 Brickman, 2000; Myers, Hutchings & Barrowman, 1997). Such compensatory effects
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27 372 have been found in a wide range of fisheries throughout the world (e.g. codfish,
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29 373 flatfish, skates and rays, tuna, swordfish, etc.) (Myers & Worm, 2003).
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35 375 **Implications for fisheries and conservation management**

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38 376 Whiting and haddock have exhibited better survival strategies during their juvenile
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40 377 stages than cod. Whiting were observed to recruit to coastal areas earlier than
41
42 378 haddock and cod, they were observed to have the fastest growth rates and were
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44 379 behaviourally more dominant in bait attraction. Separate studies by Elliott et al.
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46 380 (2017a; 2017b) show that recently settled cod seek out very different habitats to
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48 381 whiting (and haddock), favouring heterogeneous substrates dominated by maerl
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50 382 and seagrass. These seabed types are predominantly in shallow water, so the
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52 383 exposure to demersal trawling in inshore waters post-1984 may have had a
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54 384 particularly detrimental effect on cod.
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386 Nature conservation MPAs were not initially designated to protect gadoid stocks
387 due to the high mobility of adults. However, given the vulnerable nature of cod
388 stocks, protecting juvenile habitat may need to be a priority to help give them a
389 fighting chance. This paper highlights how, insights from behavioural and life-
390 history analyses could help understand why certain stocks seem to be faring better
391 than others and could help inform fisheries and conservation management
392 measures to support the recovery of depleted and vulnerable populations.

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577 **Tables and figures**

578 Table 1: Juvenile gadoid mean MaxN over the course of data collection (SE = standard error)

Year	Grouped day of data collection	Number of days data collected	Number of deployments	Mean MaxN ± SE		
				Cod	Haddock	Whiting
2013	15 - 31 July	4	26	6.54 ± 0.74	0.12 ± 0.19	0.62 ± 0.28
	12 - 26 August	3	20	1.40 ± 0.33	1.30 ± 0.94	0.40 ± 0.49
	25 - 28 September	4	28	2.50 ± 0.77	1.25 ± 0.46	0.21 ± 0.32
2014	30 June - 07 July	4	41	0.07 ± 0.20	0.37 ± 0.23	1.32 ± 0.22
	28 July - 01 August	4	48	0.96 ± 0.50	1.85 ± 0.35	1.66 ± 0.31
	26 August - 2 September	4	48	1.33 ± 0.25	0.98 ± 0.22	0.30 ± 0.16
	15 - 18 September	4	48	0.50 ± 0.25	0.85 ± 0.22	0.96 ± 0.40

579

580 Table 2. Age-0 gadoid mean position and size and over the course of summer 2013
 581 and 2014 data collection period (Y = the height above and below the cameras; Z =
 582 distance from the cameras, SE = standard error)

Gadoid	Mean Y distance from the camera \pm SE (cm)	Mean Z distance from the camera \pm SE (cm)	Mean size \pm SE (cm)
Cod	-6.68 \pm -0.97	167.61 \pm 2.55	7.78 \pm 0.12
Haddock	-2.96 \pm -0.85	146.62 \pm 2.54	11.07 \pm 0.14
Whiting	-3.2 \pm -1.22	121.03 \pm 2.50	11.25 \pm 0.23

583

584 Figure 1. Data collection locations within South Arran marine protected area (red
 585 outline) over the course of summer 2013 (blue squares) and 2014 (purple squares).
 586 Purple triangles represent samples collected for gadoid bait attraction analysis.

587

588 Figure 2. Gadoid growth over the course of data collection period for 2013 (A) and
 589 2014 (B) with the model fitted lines and shaded area indicating \pm 95% confidence
 590 intervals. Symbols represent individual gadoid length measurements.

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592 Figure 3. Gadoid Y and Z positioning for 2013 and 2014. Measurements closer to
 593 the camera are shown in red and further from the camera in black (Y = the height
 594 above and below the cameras; Z = distance from the cameras).

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596 Figure 4. Gadoid mean bait attraction at MaxN with standard error bars. Shaded
 597 bars show gadoids attracted to the bait and clear bars show gadoid bait
 598 indifference.

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599 **Supporting information**

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601 Table 1. Age-0 gadoid seasonal size and growth

Gadoid	Year	Season mean length ± SE (cm)	Start of season		End of season		Gadoid mean growth (cm)
			Mean length ± SE (cm)	length range (cm)	Mean length ± SE (cm)	length range (cm)	
Cod	2013	7.39 ± 0.16	6.67 ± 0.17	4.20 - 10.83	8.66 ± 0.34	3.51 - 13.91	1.98 ± 0.17
	2014	8.27 ± 0.19	5.61*	5.61*	8.32 ± 0.58	3.01 - 11.88	2.71*
Haddock	2013	12.33 ± 0.25	9.10 ± 1.27	7.57 - 11.63	13.05 ± 0.27	8.30 - 14.81	3.95 ± 1.00
	2014	10.62 ± 0.15	9.02 ± 0.46	7.69 - 12.41	12.24 ± 0.26	10.12 - 14.69	3.22 ± 0.20
Whiting	2013	10.71 ± 0.73	9.20 ± 0.61	8.59 - 9.80	14.95*	14.95*	5.75*
	2014	11.34 ± 0.26	10.81 ± 0.35	6.30 - 14.98	12.20 ± 0.42	8.16 - 14.98	1.39 ± 0.07

602 * Indicates where too few length measurements were obtained to calculate a standard error

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3 603 Figure 1. Bhattacharya's method for decomposition and characterisation of
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5 604 Gaussian components for (A) cod, (B) haddock and (C) whiting. I) Histogram with
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7 605 determined Gaussian component II) Graph of the logarithmic differences in length.
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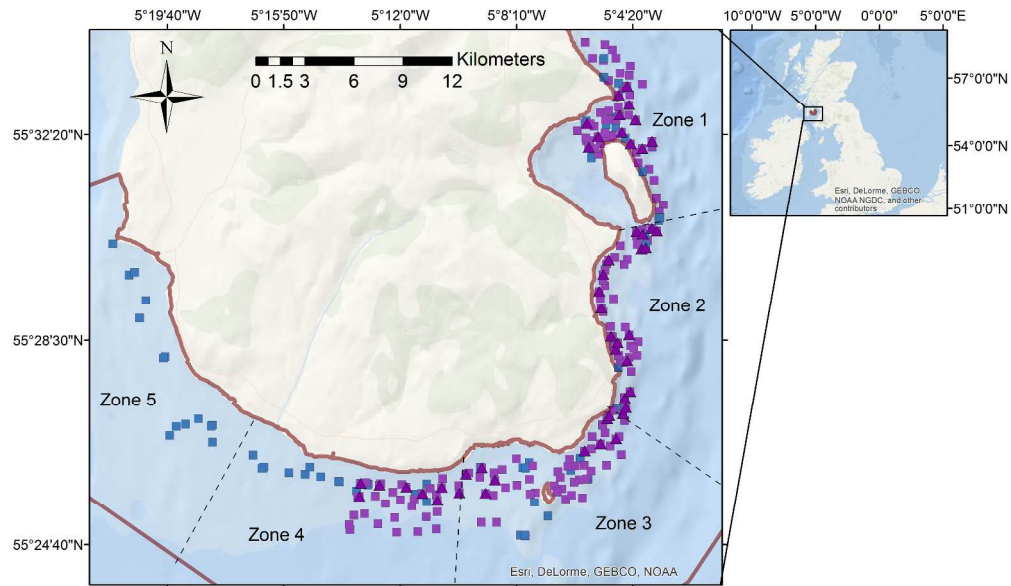


Figure 1. Data collection locations within South Arran marine protected area (red outline) over the course of summer 2013 (blue squares) and 2014 (purple squares). Purple triangles represent samples collected for gadoid bait attraction analysis.

350x209mm (300 x 300 DPI)

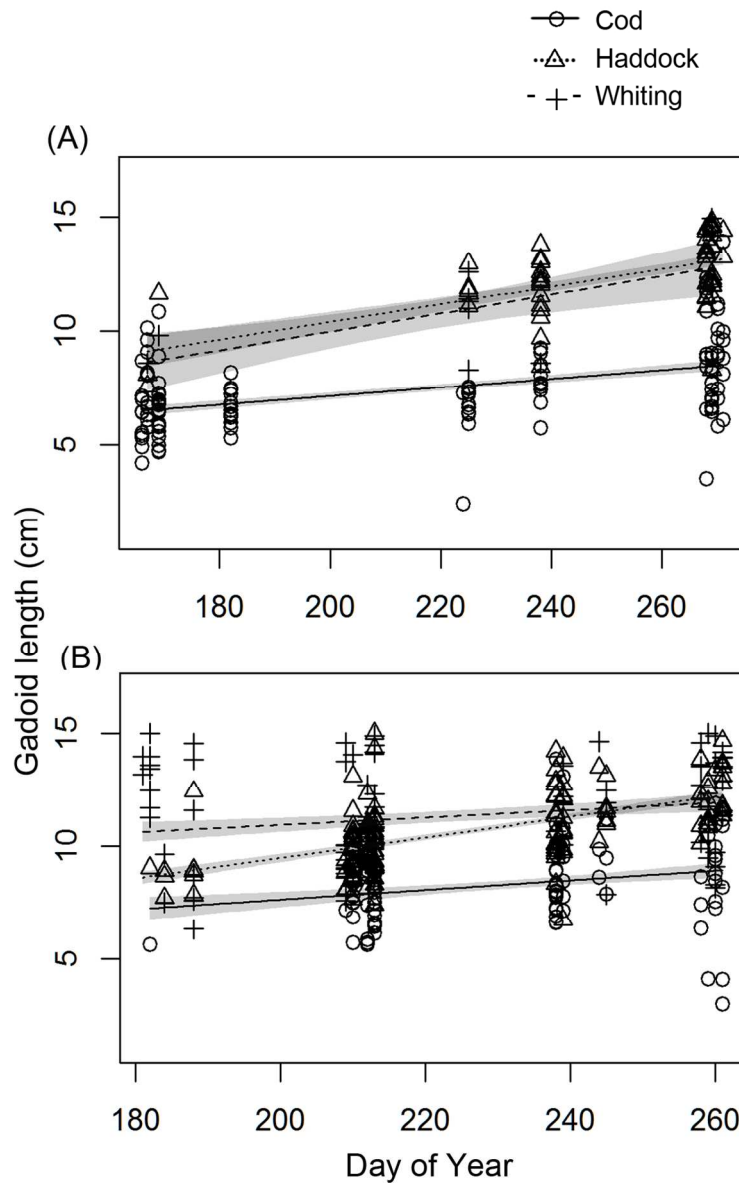


Figure 2. Gadoid growth over the course of data collection period for 2013 (A) and 2014 (B) with the model fitted lines and shaded area indicating $\pm 95\%$ confidence intervals. Symbols represent individual gadoid length measurements.

99x160mm (300 x 300 DPI)

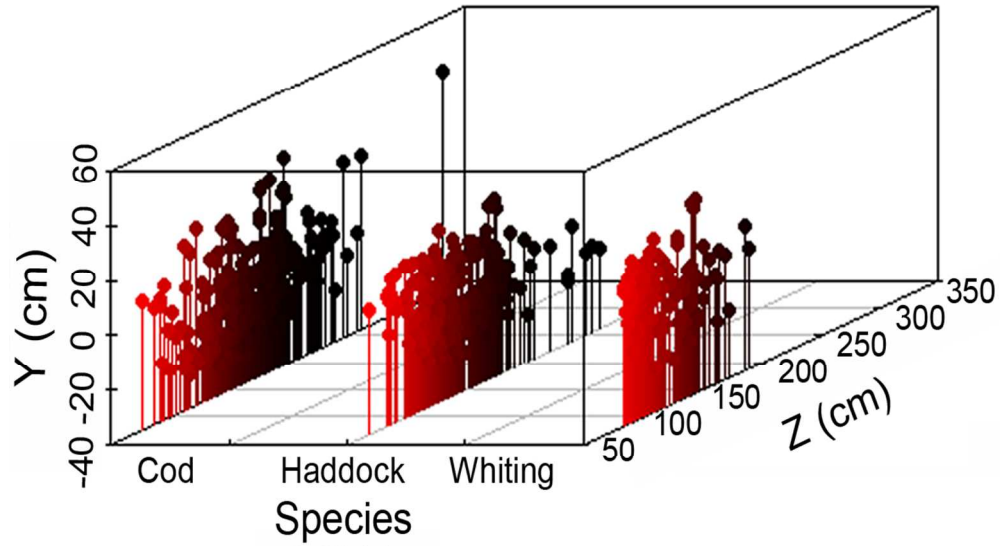


Figure 3. Gadoid Y and Z positioning for 2013 and 2014. Measurements closer to the camera are shown in red and further from the camera in black (Y = the height above and below the cameras; Z = distance from the cameras).

99x55mm (300 x 300 DPI)

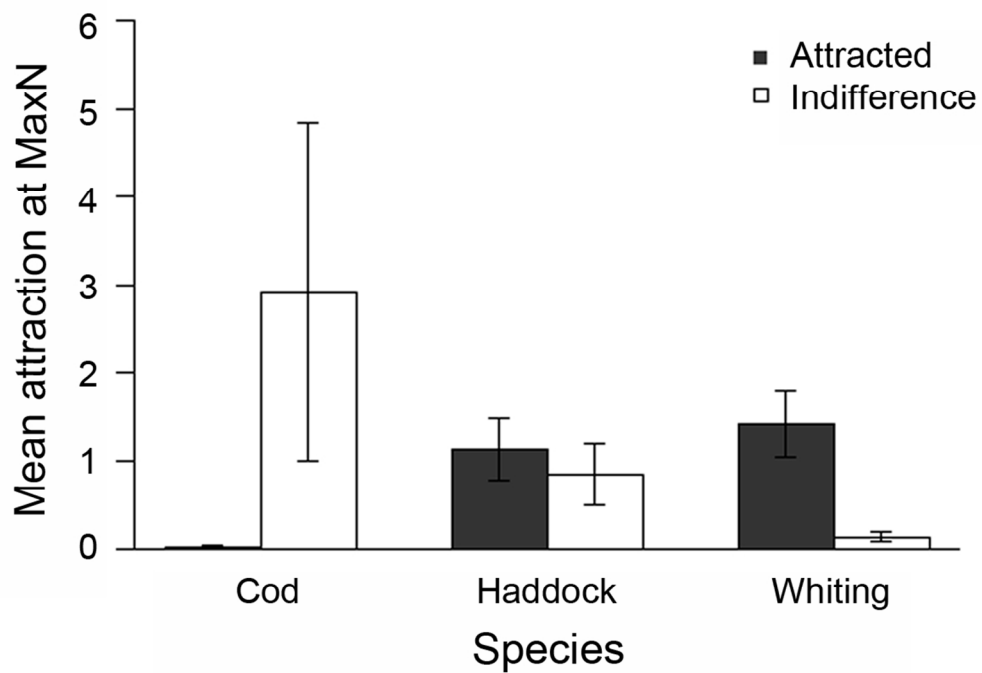


Figure 4. Gadoid mean attraction at MaxN with standard error bars. Shaded bars show gadoids attracted to the bait and clear bars show gadoid bait indifference.

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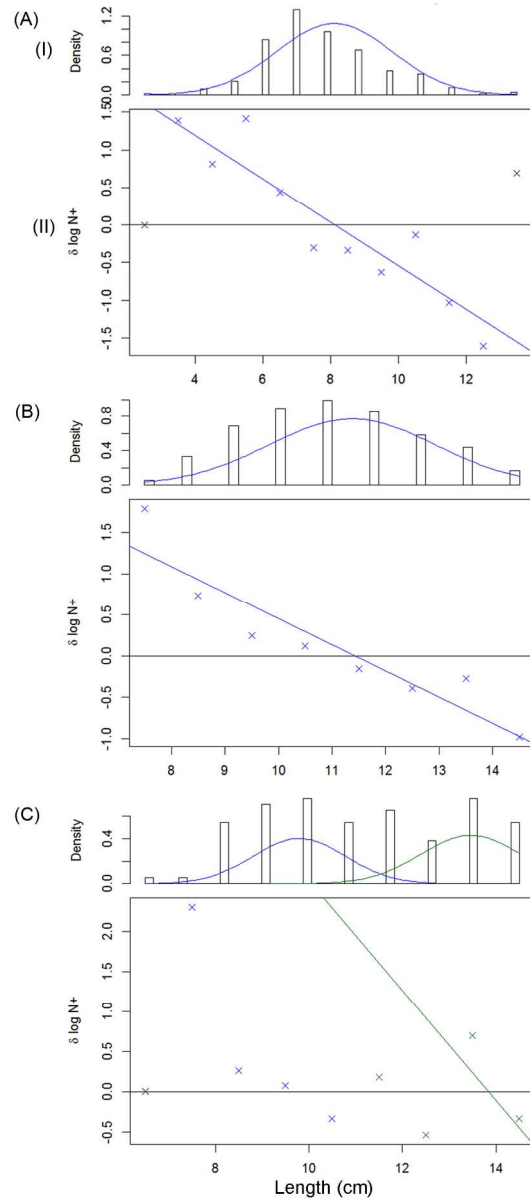


Figure 1. Bhattacharya's method for decomposition and characterisation of Gaussian components for (A) cod, (B) haddock and (C) whiting. I) Histogram with determined Gaussian component II) Graph of the logarithmic differences in length.

100x227mm (300 x 300 DPI)