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Survival of the fittest: Explanations for gadoid imbalance in heavily fished seas

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Abstract

1. Anthropogenic activities have caused the degradation of the world's ecosystems, accelerating the 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 (south-west 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 the summers of 2013 and 2014, whiting and haddock arrived at coastal areas earlier than cod, and grew more quickly. 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 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 to restore fish population and assemblage structure.

KEYWORDS

behaviour, fisheries management, gadoid, growth, life-history traits, marine protected areas, recruitment, scavenging, stereo video cameras

1 | INTRODUCTION

Growing demands on the world's resources are affecting wildlife populations through direct mortality of target species and the transformation of their habitats (Foley et al., 2005; Sanderson et al., 2002). Reductions in population sizes from hunting or harvesting, or habitat transformation, can also cause imbalances in community structures and ecosystem functioning, exacerbating extinction rates (Dobson, Bradshaw, & Baker, 1997; Hammer, Jansson, & Jansson, 1993). Particular life-history traits and habitat preferences can cause

certain species to be more vulnerable than others (Bastrikin, Gallego, Millar, Priede, & Jones, 2014; Higginson, 2017). Understanding competition between species can therefore be critical to ecosystem-based management.

Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), and whiting (*Merlangius merlangus*) are all species of high commercial value, and have all suffered declines and alterations in population structure (Cote, Ollerhead, Scruton, & McKinley, 2003; Fernandes & Cook, 2013; Holmes, Millar, Fryer, & Wright, 2014). In recent years, following strict management measures, improvements have been observed in North Sea stocks of these species (Fernandes & Cook, 2013; International Council for the Exploration of the Sea, ICES, 2017a); however, along the west coast of Scotland, recruitment and spawning stock biomass remains relatively low, particularly for cod (Fernandes & Cook, 2013; ICES, 2017b, 2017c, 2017d). Cod is also listed as 'vulnerable' on the International Union for Conservation of Nature (IUCN) red list, and is listed as a threatened and declining species by the Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR, 2014; Sobel, 1996).

The Firth of Clyde (south-west Scotland) has been an important fishing location for a variety of demersal species (Heath & Speirs, 2012; Thurstan & Roberts, 2010). Heavy fishing pressure during the 20th century led to a steep decline in landings of demersal fish (Thurstan & Roberts, 2010). As a result, a prohibition on trawl fishing within three nautical miles of the shoreline was introduced in 1889 (Thurstan & Roberts, 2010); however, this was repealed in 1984 because of widespread infringements and to allow access for *Nephrops norvegicus* fishing (Thurstan & Roberts, 2010). Since the late 1990s, the Firth of Clyde demersal trawl fishery primarily targets *Nephrops*, but with a significant by-catch of other fish (Thurstan & Roberts, 2010). A study by Heath and Speirs (2012) showed that since the peak expansion of demersal trawling in 1984, the species richness of the Firth of Clyde has remained almost unchanged, but the evenness has declined sharply. By around 2000, 87% of the demersal fish biomass was composed of whiting, whereas this species had comprised only 7% of the biomass between 1920 and 1959. Furthermore, the mean body length in the fish community had halved since the 1960s. Recent studies within the Firth of Clyde by Hunter, Speirs, and Heath (2015; 2016), demonstrated a declining age at maturation and growth in cod, haddock, and whiting during the period of heavy fishing pressure. These observations do not, however, explain the imbalance of whiting within this semi-enclosed sea.

Cod, haddock, and whiting in this region are all members of the family *Gadidae*, and are known to have relatively similar life cycles. Spawning aggregations occur from late winter to spring (Demain, Gallego, Jaworski, Priede, & Jones, 2011; Olsen et al., 2010; Wright, Tobin, Gibb, & Gibb, 2010). Pelagic larval eggs are produced in batches, which drift to coastal areas from late April to June where the juveniles live for the first few months (Gibb, Gibb, & Wright, 2007; Olsen et al., 2010). Important food sources for juvenile gadoids include crustaceans and polychaetes, and small fish such as plaice (*Pleuronectes platessa*; Bastrikin et al., 2014; Demain et al., 2011). Scavenging behaviour has been observed in all three species (Groenewold & Fonds, 2000; Jenkins, Mullen, & Brand, 2004), in

addition to predation between gadoids (Köster, Stephenson, & Trippel, 2014; Temming, Floeter, & Ehrich, 2007).

This study aimed to determine the competitive interactions between gadoid species during the post-settlement phase of their life in the Firth of Clyde. Comparative analysis of gadoid recruitment, growth, and scavenging behaviour was undertaken using stereo baited remote underwater video (SBRUV) systems within a marine protected area (MPA). Recruitment to coastal areas was explored by measuring relative abundance variations, size, and growth over the course of the summer. Scavenging behaviour was investigated by measuring attraction to the bait. The motivation for the study was to better understand why whiting has become so dominant in the demersal fish community of the region.

2 | METHODS

2.1 | Data collection

Data were collected within South Arran nature conservation MPA, the Firth of Clyde, south-west Scotland, at depths of 4.0–47.2 m, between June and September 2013 and 2014 (Figure 1). Gadoid sampling took place using three SBRUV frames, as described in Elliott, Turrell, Heath, and Bailey (2017). From 5 June to 29 September 2013, 80 camera deployments were carried out from a 6.5-m Rigid Inflatable Boat; however, data were used from 15 July (74 deployments), as before this date no gadoids were observed. The following year, a further 185 deployments were carried out between 30 June and 18 September 2014, from a 10.8-m research vessel (RV *Actinia*) (Table 1). During 2014, data were not collected around the south-west side of the island because of the slower cruising speed of the vessel used. As a result of resources and logistics, data were not collected continuously through the periods of data collection. In the sampling design, the area of data collection was divided into five zones, with samples collected within each zone to facilitate replication. For logistical reasons and because of the long summer day length at the study latitude, all deployments took place during daylight hours.

Throughout data collection, Atlantic mackerel (*Scomber scombrus*) was used as bait because it is oily, and therefore produces a down-current bait plume, and is relatively inexpensive. The bait was held suspended 91 cm in front of the cameras and at a height of 46 cm above the sea bed to ensure visibility between the stereo-video cameras, and to minimize macroalgae hindering fish measurements. Calibration of the cameras took place prior to and over the course of field data collection within a controlled environment using the methods outlined by Harvey and Shortis (1998) with CAL 2.11 (https://www.seagis.com.au/bundle.html).

2.2 | Video analysis

EVENTMEASURE 3.61 (https://www.seagis.com.au/event.html) was used to analyse the videos. Gadoid recruitment and growth were estimated from changes in relative abundance and length measurements. Relative abundances were measured using the maximum number of individuals of the same species appearing in a single frame at the same time during each separate video deployment (*MaxN*) as described by
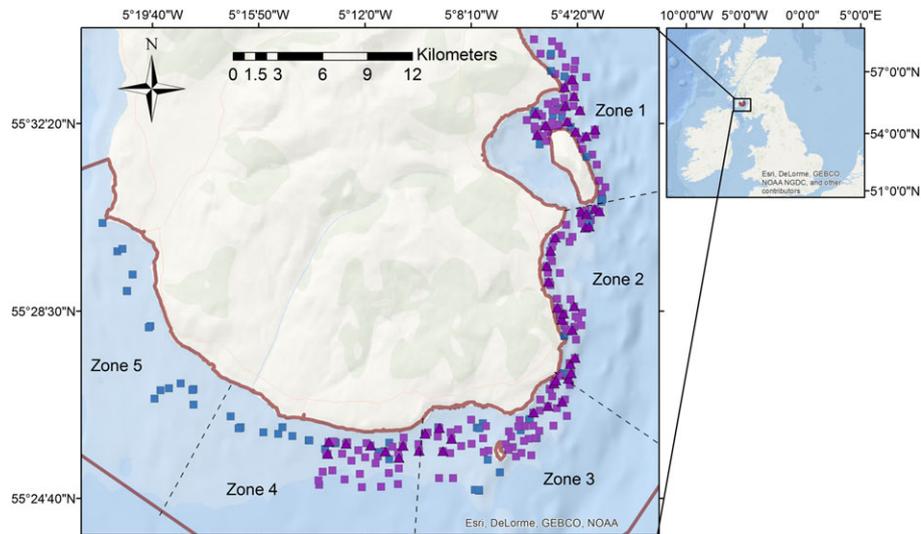
FIGURE 1 Data collection locations within South Arran marine protected area (red outline) over the course of summer 2013 (blue squares) and summer 2014 (purple squares). Purple triangles represent samples collected for gadoid bait attraction analysis

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–7 July	4	41	0.07 ± 0.20	0.37 ± 0.23	1.32 ± 0.22
	28 July–1 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

Priede, Bagley, Smith, Creasey, and Merrett (1994) and Watson, Harvey, Anderson, and Kendrick (2005). Fish fork length and position measurements were taken at one time point per deployment, when the maximum number of measurable fish was present. Length measurements with a precision of >0.5 cm and a root mean square error of >2 cm were removed from the analysis, as recommended in the SEAGIS 2.11 software manual (http://www.seagis.com.au/event.html).

Gadoid scavenging behaviour was quantified using water column positions relative to the bait box, and by an index of bait attraction or indifference. Gadoid water column position was estimated using stereo-video y and z measurements (relative to the mid-point of the camera system). The y values approximate the height above and below the cameras, and the z values are the distance from the camera system (Shortis, Harvey, & Abdo, 2009). A subsample of 48 camera deployments (from 28 July to 1 August 2014) was used to assess gadoid bait attraction, as this behaviour took longer to record. Gadoid bait attraction was classified as 'attracted' when the fish swam directly towards the bait with a maximum distance of ~20 cm from the bait box. 'Indifference' behaviour was classified when the fish swam directly past the frame and did not approach.

2.3 | Data analysis

All statistical analysis was performed with R 3.2.2. A log-likelihood ratio test was used to test model significance against the null hypothesis. Tukey's tests were performed to test for differences between explanatory categorical variables (grouped day of data collection for 2014 and gadoid species, where relevant). Random effects for grouped day of data collection and zone were included in the model, where relevant and significant, to account for temporal and spatial variation (referred to by lowercase letters in Equations 1–4).

MaxN was used to analyse gadoid recruitment to coastal areas over the period of data collection (Equation 1). *MaxN* was analysed using negative binomial generalized linear mixed models (GLMMs; Equation 1). A negative binomial distribution was used to account for the overdispersion of gadoid *MaxN*. Equations 1 and 2 were modelled on each gadoid species separately.

$$\text{Log}(y_i) = \beta_0 + \beta_1, T_{i(j)} + z_{ij} \tag{1}$$

where y_i is gadoid *MaxN* fitted with a logarithmic link, β values are the coefficients, $T_{i(j)}$ is the day (2013) or week (2014) of data collection, and z_{ij} is the random effect (zone). The subscript i refers to the number of samples and the subscript j refers to categorical explanatory variables.

To explore gadoid arrival and growth over the period of data collection, gadoid length measurements were used (Equations 2 and 3). Equation 3 was modelled separately to identify whether there were significant differences in gadoid growth between the three species. Following analysis of the Database of Trawl Surveys (DATRAS) Age Length Key (product for standard species only) quarter 4 (October–December) for the Firth of Clyde area, all individuals larger than

15 cm were removed from the analysis to reduce the likelihood of observing age-1 individuals. The removal of individuals larger than 15 cm included eight out of 228 individuals from the cod length dataset (max size measured 21.18 cm; total mean length 8.20 ± 0.19 cm SE). A total of 27 out of 208 haddock measurements were removed (max size measured 21.69 cm; total mean length 12.02 ± 0.21 cm), and 60 out of 152 whiting measurements were removed (max size measured 35.53 cm; total mean length 14.00 ± 0.35 cm). For gadoid length measurements after the removal of these larger individuals, please see Table S1.

Length and gadoid y and z measurements were analysed using linear and linear mixed models (LMMs; Equations 2–4).

$$y_i = \beta_0 + \beta_1, T_{i(j)}, \tag{2}$$

$$y_i = \beta_0 + \beta_1, G_{ij} + t_{ij} \tag{3}$$

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

Differences in gadoid scavenging behaviour were resolved by exploring the positions of the gadoid relative to the bait box (y and z positions; Equation 4), in addition to gadoid bait attraction.

$$y_i = \beta_0 + \beta_1, G_{ij} + t_{ij} + z_{ij}, \tag{4}$$

where y_i is the gadoid y or z position, and t_{ij} and z_{ij} are random effects that account for spatial and temporal variations. A Wilcoxon signed rank test was used to estimate the significance of gadoid bait attraction differences.

3 | RESULTS

3.1 | Gadoid recruitment and growth

Over the course of summer 2013, a decline in cod MaxN was observed (log likelihood (L) = −157.18, degrees of freedom (df) = 4, dispersion (θ) = 0.93, $P < 0.05$; Table 1) and a 1.98-cm increase in average length (L = −233.56, df = 3, $P < 0.001$; Figure 2; Table S1). During summer 2014, an increase in MaxN was observed in the second (28 July–1 August) and third weeks (26 August–2 September) of data collection (Tukey's test $P < 0.05$ and $P < 0.01$, respectively), followed by a decline in cod MaxN in the fourth week (15–18 September) (L = −164.80, df = 6, θ = 1.09, $P < 0.001$; Table 1). A growth of 2.71 cm was also detected (L = −188.33, df = 5, $P < 0.05$; Figure 2; Table S1).

Haddock MaxN did not significantly increase or decrease over the course of the summer of 2013 (L = −59.11, df = 4, θ = 0.76, $P > 0.05$; Table 1); however, in 2014, an increase in MaxN was observed following the first week of data collection (Tukey's test $P < 0.001$) (L = −236.76, df = 6, θ = 0.91, $P < 0.01$; Table 1). The latter indicates a possible recruitment pulse shortly after the first week of July. Haddock growth was observed over the course of data collection during 2013
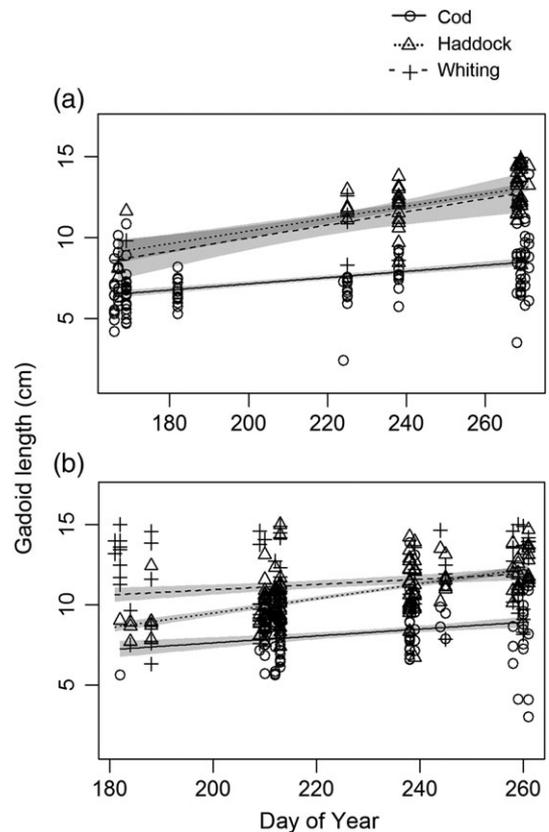

FIGURE 2 Gadoid growth over the course of data collection period for 2013 (a) and 2014 (b), with the model fitted lines and the shaded area indicating ±95% confidence intervals. Symbols represent individual gadoid length measurements

(3.95 cm) and 2014 (3.22 cm) (L = −88.19, df = 3, $P < 0.001$ and L = −228.43, df = 5, $P < 0.001$, respectively; Figure 2; Table S1).

Over the course of data collection in 2013 there was no difference in whiting MaxN (L = −54.41, df = 4, $P > 0.05$; Table 1); however, a 5.75-cm increase in average length of age-0 individuals was observed (L = −17.29, df = 3, $P < 0.05$; Figure 2; Table S1). During 2014, whiting MaxN varied over the course of data collection with a decrease in the third week (26 August–2 September) of data collection (Tukey's test $P < 0.05$) (L = −2236.73, df = 6, θ = 1.09, $P < 0.01$; Table 1). An increase in growth of 1.39 ± 0.07 cm was also detected (L = −185.11, df = 4, $P < 0.05$; Figure 2; Table S1).

Over the course of both years cod were smaller than haddock and whiting (L = −1003.89, df = 5, $P < 0.001$), with haddock and whiting being of more similar sizes (Figure 2; Table 2). For both years, more cod (mean MaxN = 3.62 ± 0.26) were observed than haddock (mean MaxN = 0.98 ± 0.15) or whiting (mean MaxN = 0.86 ± 0.13) (Table 1). Two age-0 cohorts were identified using Bhattacharya's (1967) method for whiting, whereas only one cohort was identified for haddock and cod (Figure S1). The latter provides evidence of pulse recruitment for whiting.

3.2 | Gadoid scavenging behaviour

Significant differences between gadoids were observed with respect to their positioning relative to the seabed, cameras, and bait. Cod positioned themselves on average closer to the sea bed and further from

TABLE 2 Age-0 gadoid mean position and size and over the course of the summer 2013 and 2014 data collection periods (y = the height above and below the cameras; z = the distance from the cameras; SE = standard error)

Gadoid	Mean y distance from the camera ± SE (cm)	Mean z distance from the camera ± SE (cm)	Mean size ± SE (cm)
Cod	−6.68 ± −0.97	167.61 ± 2.55	7.78 ± 0.12
Haddock	−2.96 ± −0.85	146.62 ± 2.54	11.07 ± 0.14
Whiting	−3.2 ± −1.22	121.03 ± 2.50	11.25 ± 0.23

the cameras than haddock or whiting. The average position of whiting was closest to the cameras in terms of height and distance off the sea bed (for y, L = −1961.405, df = 6, P < 0.001; for z, L = −2441.08, df = 6, P < 0.001; Figure 3; Table 2).

Whiting were the most attracted to the bait (92%, 68 out of 74 individuals), followed by haddock (57%, 54 out of 95 individuals). Only one out of 141 cod was attracted to the bait box (Figure 4), resulting in cod being significantly less attracted to the bait than haddock and whiting (Tukey's test P < 0.001) (L = −105.967, df = 5, P < 0.001). There was a significant difference between the cod and whiting attracted to the bait compared with those that were not attracted to the bait (cod, Wilcoxon (W) = 347, P < 0.001; whiting, W = 57, P < 0.001; haddock, W = 268, P > 0.05,). Cod larger than 15 cm were more attracted to the bait.
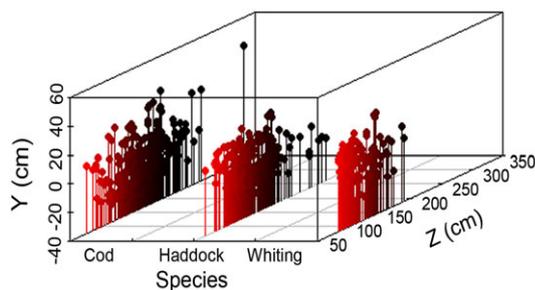

FIGURE 3 Gadoid y and z positioning for 2013 and 2014. Measurements closer to the camera are shown in red; measurements further from the camera are shown in black (y = the height above and below the cameras; z = distance from the cameras)
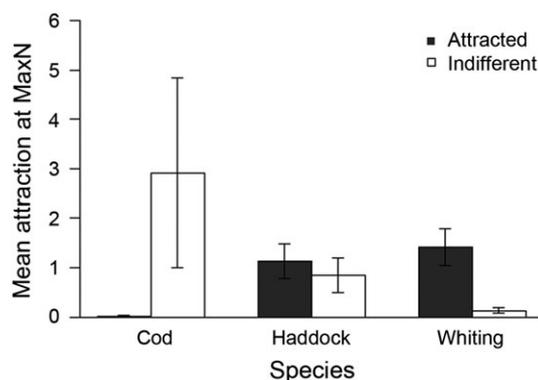

FIGURE 4 Gadoid mean bait attraction at MaxN with standard error bars. Shaded bars show gadoids attracted to the bait and clear bars show gadoid bait indifference

4 | DISCUSSION

Rapid environmental changes provide challenges to which species need to adapt. Intensive fishing activities over the last few centuries have not only had profound impacts on targeted species, but also on the wider marine ecosystem (Holmlund & Hammer, 1999). Here, the recruitment, growth, and scavenging behaviour of cod, haddock, and whiting in a nursery area were compared in order to understand why whiting have become so dominant in the demersal fish community of the Firth of Clyde. Although cod, haddock, and whiting are all members of the same family, and have apparently similar life histories, the detailed observations described here demonstrated differences in behaviours during their juvenile stages. Because there has been no systematic protection of gadoid nursery areas in the study region, these behavioural and life-history differences may partly explain the documented biomass imbalance between these species (Heath & Speirs, 2012).

Cod were recruited to coastal areas later than haddock and whiting (evidenced by their smaller size at the start of data collection). Over the course of data collection, haddock and whiting grew faster than cod. Cod relative abundance was observed to be on average higher than that of haddock and whiting; however, this may have been linked to the shallow depths at which the deployments took place (<48 m). Cod have been observed to occupy shallower waters than haddock and whiting (Elliott, Turrell, et al., 2017). During both years, a decline in the relative abundance of juvenile cod was observed at the end of data collection, whereas the relative abundances of haddock and whiting were variable, demonstrating either stronger pulse recruitment than cod, or better survival.

Bastrikin et al. (2014) undertook a similar study, observing the diet, growth, and recruitment of pelagic to demersal age-0 gadoids from mid-May to the end of August in the North Sea. They observed declines in cod over the course of data collection, with haddock recruiting to coastal areas earliest and whiting having the most protracted recruitment, which is in line with the observations in this study. The size ranges of juvenile gadoids observed by Bastrikin et al. (2014) were similar to those seen in this study. Spawning earlier, and multiple times throughout the season, the faster growth rates and on average larger size of whiting and haddock gives them a competitive advantage over cod (Hislop, 1975; McEvoy & McEvoy, 1992; Wright & Trippel, 2009), and potentially makes cod more vulnerable to predation (Demain et al., 2011; Werner & Gilliam, 1984).

From the combined position, and bait attraction results, whiting were observed to be more attracted to the bait than haddock and cod. In a bait attraction investigation in the North Sea conducted by Martinez et al. (2011), whiting were also observed to be more attracted to baited camera systems than haddock. This greater tendency to scavenge may be advantageous in a system exposed to high levels of trawling, with the resultant discards and mortality of benthic fauna. It is not clear why cod may have been less attracted to the bait. They may have a lower preference for carrion or, being smaller than whiting, are more driven by predator avoidance (Biro & Stamps, 2008).

Studies by Demain et al. (2011) showed that as these three gadoids mature and grow, they adapt their feeding strategy to an

increasingly piscivorous diet. The larger (older) cod were observed to be more attracted to the bait, strengthening the argument that the on-average smaller size of cod places them at a disadvantage to whiting and haddock in exploiting carrion. Gadoids are also known to predate on one another (Hislop, Robb, Bell, & Armstrong, 1991; Köster et al., 2014), and whiting have been found to be particularly voracious predators, wiping out entire cod populations (Temming et al., 2007).

Another factor to take into consideration when considering the gadoid imbalance in the Firth of Clyde, is that the habitats occupied by juvenile haddock and whiting (deeper sand and mud seabed types) (Elliott, Turrell, et al., 2017), are less vulnerable to damage by mobile demersal gear than that of cod (Collie, Hall, Kaiser, & Poiner, 2000; Kaiser et al., 2006). Juvenile haddock and whiting are found over sand and mud substrata, which are also found in large quantities throughout the Firth of Clyde (Elliott, Sabatino, Heath, Turrell, & Bailey, 2017; McIntyre, Fernandes, & Turrell, 2012). Cod have been observed in higher relative abundance over fragile maerl and seagrass seabed types, and over more heterogeneous landscapes, within the Firth of Clyde, with ontogenetic shifts in seabed type with increasing size (Elliott, Ahti, Heath, Turrell, & Bailey, 2016; Elliott, Sabatino, et al., 2017; Elliott, Turrell, et al., 2017). The secondary impacts of seabed homogenization from fishing activities (Jennings & Kaiser, 1998), with cod having more specific habitat requirements, put cod at a survival disadvantage to haddock and whiting.

From 1889 to 1962, trawling was restricted to areas further than three nautical miles from the coast (Thurstan & Roberts, 2010). As of 1962, a by-law was introduced to allow *Nephrops* trawlers access throughout the Firth of Clyde (Thurstan & Roberts, 2010). Today, *Nephrops* trawling and scallop dredging still continues, and results in fish mortality through by-catch (Bergmann, Wieczorek, Moore, & Atkinson, 2002). The continued mobile demersal activity is of particular importance given that much of the maerl found to occur around the south of Arran has been observed to be in a degraded state (Elliott, Turrell, et al., 2017). Reduced substratum diversity and quality from decades of demersal mobile gears may therefore be having a negative impact on cod populations (Elliott, Sabatino, et al., 2017; Elliott, Turrell, et al., 2017).

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

The imbalance in the Firth of Clyde may be partly explained by compensatory effects from fishing activities (Heino & Godø, 2002), where initially trawlers heavily targeted cod (Thurstan & Roberts, 2010), enabling the less commercially desirable whiting to become more abundant; however, as fisheries began targeting other species, such as whiting and plaice (Thurstan & Roberts, 2010), the fisheries-induced pressures may have led to the removal of larger individuals, and the more adaptive species (such as whiting) becoming mature at a younger age (Hunter et al., 2015, 2016). Furthermore, as cod were

so heavily targeted and for such a long period of time (from the 19th to early 21st century; Thurstan & Roberts, 2010), stock levels may have fallen below critical levels, prohibiting any self-regeneration despite recovery management measures being put in place (Frank & Brickman, 2000; Myers, Hutchings, & Barrowman, 1997). Such depensatory effects have been found in a wide range of fisheries throughout the world (e.g. codfish, flatfish, skates and rays, tuna, swordfish, etc.; Myers & Worm, 2003).

4.1 | Implications for fisheries and conservation management

Whiting and haddock have exhibited better survival strategies during their juvenile stages than cod. Whiting were observed to recruit to coastal areas earlier than haddock and cod, they were observed to have the fastest growth rates, and were behaviourally more dominant in bait attraction. Separate studies by Elliott, Turrell, et al. (2017) and Elliott, Sabatino, et al. (2017) show that recently settled cod seek out very different habitats to whiting (and haddock), favouring heterogeneous substrates dominated by maerl and seagrass. These seabed types are predominantly found in shallow water, so the exposure to demersal mobile gear in inshore waters post-1984 may have had a particularly detrimental effect on cod.

Nature conservation MPAs were not initially designated to protect gadoid stocks because of the high mobility of adults; however, given the vulnerable nature of cod stocks, protecting juvenile habitat may need to be a priority to help give them a fighting chance. This paper highlights how insights from behavioural and life-history analyses could help to understand why certain stocks seem to be faring better than others, and could help inform fisheries and conservation management measures to support the recovery of depleted and vulnerable populations.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.