An assessment of juvenile Atlantic cod *Gadus morhua* distribution and growth using diver operated stereo-video surveys

S. A. M. Elliott*†, P. A. Ahti*, M. R. Heath‡, W. R. Turrell§ and D. M. Bailey*

*Institute of Biodiversity, Animal Health and Comparative Medicine, University of Glasgow, Glasgow G12 8QQ, U.K., ‡Department of Mathematics and Statistics, University of Strathclyde, 16 Richmond Street, Glasgow G1 1XQ, U.K. and §Marine Scotland Science, Marine Laboratory, P. O. Box 101, 375 Victoria Road, Aberdeen AB11 9DB, U.K.

(Received 22 December 2015, Accepted 7 April 2016)

Stereo-video scuba transects were conducted during daylight hours from June to September 2013 within a proposed marine protected area (MPA) in the Firth of Clyde, west of Scotland. More juvenile Atlantic cod *Gadus morhua* of fork length (*L*<sub>f</sub>) range 6–11 cm were observed in substrata containing mixed gravel, including maerl, than in boulder-cobble substrata with high algal cover, or sand with low density seagrass. Community composition was significantly different between substratum types. A decrease in *G. morhua* abundance was observed over the period of data collection. Over time, mean and variance in *G. morhua* *L*<sub>f</sub> increased, indicating multiple recruitment events. Protecting mixed gravel substrata could be a beneficial management measure to support the survival and recruitment of juvenile *G. morhua*; other substrata might be important at night given their diel migratory behaviour. Stereo-video cameras provide a useful non-destructive fisheries-independent method to monitor species abundance and length measurements.

© 2016 The Authors. *Journal of Fish Biology* published by John Wiley & Sons Ltd on behalf of The Fisheries Society of the British Isles.

Key words: coastal; habitat; marine protected area; scuba; stereo-video cameras.

INTRODUCTION

With increasing concern over the state of the marine environment, much attention has been paid to the development of marine protected areas (MPAs) as an ecosystem-based approach to protect vulnerable substrata and restore species and their habitats (Roberts *et al.*, 2005; Seitz *et al.*, 2014). In many cases, however, factors affecting the survival of temperate marine fishes are not well understood (Langton *et al.*, 1996). This is of particular relevance within European waters where measures to restore fish stocks have focused primarily on reducing fishing effort, fishing gear adaptations to reduce by-catch and fisheries closures (Fernandes & Cook, 2013; Hilborn, 2011). While improvements in some stocks have been observed in the European Union [e.g. European anchovy *Engraulis encrasicolus* (L. 1758) and whiting *Merlangius merlangus* (L. 1758)], West
of Scotland Atlantic cod *Gadus morhua* L. 1758 stocks remain depleted (Fernandes & Cook, 2013; ICES, 2014).

The Firth of Clyde was once a productive fishery. Commercially important *G. morhua* stocks, however, declined sharply around the 1980s (Thurstan & Roberts, 2010; Heath & Speirs, 2012). Since the first phase of the *G. morhua* recovery plan was introduced (early 2000s) (Anon, 2001; Kraak et al., 2013), measures have been implemented to try and restore stocks, including the prohibition of targeted fishing and a seasonal spawning area closure implemented in the outer Firth of Clyde (Anon, 2001, 2002; Clarke et al., 2015). Today, the predominant fishery occurring in the Firth of Clyde is the Norway lobster *Nephrops norvegicus* fishery, with smaller amounts of scallop dredging and creel fishing occurring (Thurstan & Roberts, 2010; McIntyre et al., 2012). There are various possible reasons for the lack of recovery in *G. morhua* stocks. In the U.K., little attention has been paid to key habitat requirements for juveniles in comparison to Canada, the U.S.A. and Scandinavian countries (Bailey et al., 2011).

To avoid confusion, within the present paper, habitat refers to resources and conditions required by a species to live in during a particular stage of its ontogeny (Hall et al., 1997). Habitat therefore includes the types of substrata (e.g. sediment and algae type), physiochemical parameters and biological characteristics required by a species (Gaillard et al., 2010; Elliott et al., 2016). A substratum type is considered important where a change in its conditions or availability has the ability to directly affect the survival of fishes (Langton et al., 1996; Able, 1999). All terminology used in this paper is in line with Elliott et al. (2016).

Age-0 year *G. morhua* are known to migrate into and inhabit shallow (<20 m) nearshore waters between June and October following pelagic larval stages (Magill & Sayer, 2004; Gibb et al., 2007). It is particularly important to understand the habitats of juveniles since cohort size of marine fishes may be determined during their first year (Campana et al., 1989; Myers & Cadigan, 1993; Able, 1999). Juvenile demersal fishes are also thought to occupy a narrower range of substrata than adults (Gibson, 1994; Able, 1999). Higher densities of *G. morhua* have been observed around rocky reefs and eelgrass substrata (Tupper & Boutilier, 1995; Bertelli & Unsworth, 2014), as well as in more exposed areas (Lekve et al., 2006).

Monitoring of fishes in shallow coastal areas containing rocky reefs and boulders is not possible using fisheries-dependent mechanisms such as demersal trawling gear. Fishing and gear restrictions may also inhibit access in managed areas. Scuba transect methods can be advantageous, reducing damage and mortality to benthos and fishes, and being able to provide greater detail about the association of individual fish with the morphology of the seabed (Gregory & Anderson, 1997). To produce accurate comparative surveys, undertaking standardized diver surveys and minimizing disturbance to fauna can improve precision and reduce bias (Sayer & Poonian, 2007). Stereo-video cameras are particularly advantageous as they enable accurate measurements to be made (Harvey et al., 2002). Stereo-video systems have previously been used in tropical and deep sea environments (Cappo et al., 2006; Fitzpatrick et al., 2012) but their application to identify fish substratum association in the U.K. has only recently been trialled through baited camera techniques (Unsworth et al., 2014). Such methods might be a valuable means of collecting information for spatial planning and for monitoring whether management is effective.

The aims of this study were two-fold: first, to determine the effectiveness of stereo-video scuba belt transects to assess species abundance and length in U.K.
waters and second, to assess abiotic and biotic variables influencing the distribution and abundance of juvenile *G. morhua* in shallow subtidal waters. Data were collected between June and September 2013 around the south of the Isle of Arran, Firth of Clyde. All study sites fell within the South Arran nature conservation MPA (NCMPA) (SNH, 2014), but took place before designation and any new management measures were implemented. By understanding abiotic and biotic variables affecting age-0 year *G. morhua* abundance and distribution, targeted management measures within the South Arran NCMPA could be implemented to support their survival and apply a more ecosystem-based management.

**MATERIALS AND METHODS**

**STUDY LOCATION**

Data were collected at depths of 4.5–23.0 m around South Arran NCMPA (Fig. 1). South Arran NCMPA encompasses an area of 250 km² and was designated in 2014 for its internationally important seagrass and maerl beds in addition to other substrata (burrowed mud, kelp and seaweed communities) and epibenthic fauna (SNH, 2014). The MPA contains within its boundaries the Lamlash Bay no take zone (NTZ), designated in 2008 and prohibiting all fishing within its boundaries under the Inshore Fishing (Scotland) Act of 1984 (Axelsson *et al.*, 2009).

**CAMERA SET-UP**

A SeaGIS underwater stereo-video camera system (SeaGIS, 2013) which consisted of two high-definition (HF G25, Canon; www.canon.co.uk) video cameras in waterproof housings, attached to a custom-made diver-portable steel frame (Fig. 2) was used. The system was set up similar to the prototype described in Harvey & Shortis (1995, 1998); however, this system...
Fig. 2. Image of stereo-video camera and line set-up showing (i) float for frame buoyancy, (ii) stereo-video cameras in housing, (iii) custom-made bar to attach LED lights and (iv) leaded line.

was optimized for smaller bodied fishes. Distances between cameras were therefore configured with a base separation of 66 cm and an inward calculated angle of view of c. 10° in seawater with a visibility of <6 m distance. Each camera was set to manual mode with the focal length set to infinity (∞). Two underwater LED W38VR Archonlight (1400 lumen; www.archonlight.co.uk) torches were mounted on the frame, facing at an angle to the middle of the stereo-camera field of view. Prior to in-field data collection, the mounted cameras were calibrated within a controlled environment using methods outlined within Harvey & Shortis (1998) and using the programme and user guide CAL (SeaGIS, 2013). A calibration cube (1 m × 1 m × 0.5 m) containing 85 targets was filmed with the stereo-video camera system in 20 different orientations (SeaGIS, 2013). Individual camera calibrations were produced using the CAL software and physical camera parameters, camera separation and orientation parameters were computed to allow accurate photographic measurements to be taken (SeaGIS, 2013).

DATA COLLECTION

Deployment locations were determined according to existing information collected on substratum types around the pre-designated MPA (COAST, 2012; SNH, 2014). Stratified random points were identified within five zones (Fig. 1). The zones were created according to prior information on substratum type and wave fetch, using Generate Stratified Random Points with Geospatial Modelling Environment software (Spatial Ecology, 2013) in Arc geographic information system (GIS) version 10.1. These zones were created to provide independent replicates of each substratum type and collect data across a representative range of substrata, depths and wave fetch values. Repeat transects within the same location were not undertaken. Survey work was not conducted in strong tides (measured using tide timetables) and bad weather (heavy rain and wind speed and gusts >15 km h⁻¹), because of difficulties in equipment and rigid inflatable boat handling. It has been previously observed that tidal conditions can cause variability in G. morhua counts (Sayer & Poonian, 2007).

The abundance of G. morhua around south Arran NCMPA was recorded along 100 m strip transects between 5 June and 20 September 2013 (Fig. 1). Since juvenile G. morhua had not yet arrived during data collection days in June (5–13), data analysis used 31 transect videos, taken after the first observation of G. morhua. Strip transects were chosen as a standard and accurate technique for assessing fish abundance (Kimmel, 1985; Hunter & Sayer, 2009). A leaded line
Table I. Substratum type characterized according to dominant sediment type and macrophyte type and density

| Substratum type          | Sediment composition                                                                 | Algae and seagrass type and density                      |
|--------------------------|--------------------------------------------------------------------------------------|---------------------------------------------------------|
| Algal-boulder-cobble (ABC) | Sediments composed of mixed boulders and cobbles (particles > 6-4 cm)                | Sediment covered in a mixture of kelp and red algae (>60% algae cover). Examples of algae species include *Laminaria* spp. and *Ceramium* spp. |
| Algal-gravel-pebble (AGP) | Mixed gravel (stone, shell and maerl), *Phymatolithon calcareum* and pebble (particles 0-4–6-4 cm) | Between 20 and 50% of sediment covered by algae         |
| Sand                     | Sandy sediments which may contain some gravel (consisting of broken shell) (particles < 0-4 cm) | <25% algae or seagrass *Zostera marina* cover           |

TRANSECT

transect was laid perpendicular to the shore line to keep survey depth consistent within the transect. Following a 10 min wait for any disturbance to the seabed or fauna to dissipate (Dickens *et al.*, 2011), the divers descended and swam at a slow constant speed along the transect. Transects were carried out by scuba divers swimming c. 1 m above the seabed with cameras held at a slight downward angle to capture fauna in front of the field of view and the substratum. An index of maximum horizontal visibility was measured using a Secchi disc attached to the end of the leaded line. The maximum distance at which it could be distinguished was measured in the stereo-video recordings. An LED diode was used to synchronize the video footage prior to surveys and following transect completion (Harvey & Shortis, 1995). To reduce diel effects on species, data collection took place between 0800 and 1500 hours (GMT), a minimum of 3 h after sunrise and before sunset. As a result of logistical complications, night sampling did not take place.

VIDEO ANALYSIS

Each transect video was analysed twice by two observers using Event Measure software (SeaGIS, 2013) to reduce observer bias. The first analysis focused on substratum characterization, the second on fauna identification, abundance and length measurements. In the absence of acoustically mapped substrata around south Arran, substratum categories were visually classified according to the most abundant combination of sediment grain sizes and macrophyte types observed together (Table I), similar to Gregory & Anderson (1997) and Cote *et al.* (2001, 2003). As transects had a uniform combination of sediment and algae type, transects were assigned a single overall transect substratum type using the two most common divisions on the Wentworth scale sediment (Wentworth, 1922; Connor *et al.*, 2004) and broad algae type and density (estimated by percentage cover; Table I). Seagrass was not treated separately to sand because of the low density and spatial extent within the area, and the small sample size of the dataset. Equally, maerl was not treated separately from gravel-pebble substratum type because of its gravel-pebble sized form around south of Arran. In addition impacted maerl has been demonstrated to be more similar to gravel than live maerl (Kamenos *et al.*, 2003). As a result of insufficient prior knowledge of the substratum types of the area, the experimental design was unbalanced. Fourteen algal-boulder-cobble substratum type transects were carried out compared with 12 algal-gravel-pebble transects and five for the sand substratum category.

© 2016 The Authors. *Journal of Fish Biology* published by John Wiley & Sons Ltd on behalf of The Fisheries Society of the British Isles. 2016, 89, 1190–1207
Sections of the video recordings where the camera angle was incorrect and the substratum was not visible were removed and the transect length was adjusted in subsequent calculations. Any further distance lost from transect length caused by large boulders or slack line was deducted from the total length of the transect. One entire transect was removed from the analysis because of inappropriate field of view. For each transect, the width of the field of view of the video camera was measured by identifying recognizable points on the seabed on both cameras. Horizontal visibility along the transect was measured in the video recordings as the greatest distance at which the Secchi disc was visible.

Fauna were identified to the lowest taxonomic level possible, usually to species. The fish fork length ($L_F$) measurements were taken (measuring from the nose to the fork). To undertake $L_F$ measurements, each individual observed had to be visible in both cameras. $L_F$ measurements of all 	extit{G. morhua} observed were therefore not possible. All $L_F$ measurements with a root mean square (RMS) error above 2 cm and with a precision of $L_F$ measurement >0.5 cm were removed from the analysis (SeaGIS, 2013).

### DATA ANALYSIS

To understand community composition differences between substratum types, permutation analysis of variance (PERMANOVA) in PERMANOVA 6 software as described in Anderson et al. (2008) was undertaken. PERMANOVA was used in order to overcome distributional and homoscedasticity restrictions of ANOVA. The standardized abundance of species was square root transformed to reduce the influence of dominant species. A Bray–Curtis similarity coefficient was used prior to applying PERMANOVA. Posterior pair-wise tests were used to compare the difference between the groups of samples. The PERMANOVA was run with 9999 permutations to draw inferences at the $P_{(perm)} < 0.001$ level. Visualization of the matrices was achieved using non-metric multi-dimensional scaling (nMDS) plots which provide values of stress (stress increases with reduced dimensionality or the ordination). Similarity percentages (SIMPER) analysis was used to determine which species contributed most to the dissimilarity between the different substratum types (Clarke & Warwick, 2001).

The effect of abiotic habitat variables on age-0 year 	extit{G. morhua} abundance included: substratum type, depth (m), distance from coast (m), Julian date ($J_D$, days) and wave fetch (km). Wave fetch values for a 200 m coastline grid (downloaded from www.sams.ac.uk/michael-burrows) were used as described in Burrows et al. (2008). For each transect location, wave fetch for the closest grid was obtained. Distance from coast was calculated using Arc GIS version 10.1. Biotic variables explored included: Hill diversity $N_2$ (reciprocal of Simpson’s index) and $N_{\infty}$ (reciprocal of the proportional abundance of the commonest species) (Hill, 1973) for epibenthic fauna (e.g. tunicates, echinoderms and crustaceans). Difficult to identify fauna, e.g. hydroid, bryozoan and 	extit{Majidae} spp., could not always be identified to species level. For continuity of analysis, such fauna were quantified in total visible hydroid and bryozoan or 	extit{Majidae} abundance (Unsworth et al., 2014).

To condense multivariate variability into fewer dimensions and identify habitat variables affecting the distribution of 	extit{G. morhua}, a principal component analysis (PCA) was performed using R software (version 3.03; R Core Team; www.r-project.org). Explanatory variables observed to have a stronger effect on 	extit{G. morhua} abundance from the PCA were used in a generalized linear model (GLM) to understand 	extit{G. morhua} abundance, removing collinear variables. An offset for transect area (m$^2$) was incorporated into the GLM. A negative binomial distribution was used to account for over dispersion. Explanatory variables included substratum type (three levels), Hill diversity index for epibenthic fauna (continuous), wave fetch (continuous) and $J_D$ (treated as a continuous variable to reduce the number of parameters used in the model). The model of best fit was log $Y_i = \beta_0 + \beta_1 S_{ij} + \beta_2 J_D + \text{offset(transect area)}$, where $Y_i$ is 	extit{G. morhua} abundance, $\beta$ the coefficient, $S_{ij}$ substratum type and, $J_D$ is the Julian date. A random effect for zone using R package ‘glmmADMD’ (Skaug et al., 2014) was tested for but was not significant. Tukey tests using R package ‘multcomp’ (Hothorn et al., 2008) were used to test the difference between categorical variables. Backwards stepwise model selection was implemented (Bolker et al., 2009; Zuur et al., 2009) and a log likelihood ratio test was used to test model significance against the null hypothesis in addition to checking residual plots.
A general linear mixed model (GLMM) using R package ‘nlme’ (Pinheiro et al., 2014) was used to model length measurements. The best model fit included $J_D$ as a fixed effect with an offset for the transect area, and a random effect for zone: $Y_i = \beta_0 + \beta_1 J_D + \text{offset(transect area)} + b_{ij}$, where $Y_i$ is $G. \text{morhua}$, $\beta$ the coefficient are the coefficients, $J_D$ the Julian date and $b_{ij}$ is the random effect for zone. A large outlier identified by Cleveland dotplot was removed from analysis since it was considered that the individual could have been of age 1 year.

RESULTS

Thirty-one stereo-video scuba transects were analysed, covering an area of 4093.14 m$^2$ (mean ± s.d. transect length = 95.56 ± 10.23 m and mean ± s.d. transect width = 1.38 ± 0.18 m) (Fig. 1). A total of 496 $G. \text{morhua}$ were identified with a mean ± s.d. of 11.41 ± 19.47 per transect and within four of the 31 (13%) transects no $G. \text{morhua}$ were observed. Forty-five taxonomic groups were identified from 34 different families. Ninety per cent (9327) of the fauna identified were classed as epibenthic fauna. The maximum distance $G. \text{morhua}$ were able to be identified and measured accurately was 2.86 m from the cameras (mean ± s.d. = 1.52 ± 0.39 m) and the minimum distance objects were measured was 0.85 m. The maximum distance the Secchi disc was seen from the cameras varied between 4 and 5.5 m. It is therefore unlikely that varying underwater visibility affected identification and measurement analysis.

Differences in community composition between substratum types were observed (pseudo-$F = 2.33$, $P_{(\text{perm})} < 0.001$). Pair-wise tests between substratum type showed significant differences between algal-gravel-pebble (AGP) and algal-boulder-cobble (ABC) ($t = 1.63$, $P_{(\text{perm})} < 0.001$) and ABC and sand substratum type ($t = 1.99$, $P_{(\text{perm})} < 0.001$). No significant difference between AGP and sand substratum type was observed ($t = 0.91$, $P_{(\text{perm})} > 0.05$). The nMDS plot (Fig. 3) shows relatively good ordination (stress 0.16), with some overlap between substratum types. SIMPER analysis showed 22 species were required to explain dissimilarity between substratum types with 80% dissimilarity between AGP and sand, 79% between AGP and ABC and 94% between ABC and sand. Hydroids and poor cod Trisopterus minutus (L. 1758) featured in the top species causing the largest dissimilarity between AGP and sand and AGP and ABC. Burrowing anemones Ceriantheopsis lloydii and the common sea urchins Echinus esculentus led to greatest dissimilarity between ABC and sand (cumulative dissimilarity of 19%).

ABIOTIC AND BIOTIC EFFECTS ON $G. \text{MORHUA}$ ABUNDANCE

The PCA was conducted on seven variables. Two components had eigenvalues over Kaiser’s (1960) criterion of 1, and in combination explained 57% (PC1 55%, PC2 22%) of the variance. PC1 was most negatively correlated with Hill diversity indices followed by substratum type and positively correlated with wave fetch. PC2 correlated most strongly with distance from coast with a negative correlation with substratum type (Table II). These results indicate that $N_2$, substratum type, distance from coast and wave fetch had stronger trends than other variables and were therefore used as explanatory variables to understand the abundance and distribution of $G. \text{morhua}$.

Analysis of the explanatory variables independently, only substratum type and $J_D$ had an effect on the abundance of juvenile $G. \text{morhua}$ [$L = 95.32$ (d.f. = 5, theta = 0.48, © 2016 The Authors. *Journal of Fish Biology* published by John Wiley & Sons Ltd on behalf of The Fisheries Society of the British Isles. 2016, 89, 1190–1207}
The highest abundance of juvenile *G. morhua* was observed within AGP substratum type, and the lowest abundance was observed in sand substratum type. Intermediate values were observed in ABC (Fig. 4 and Appendices I and II). A decrease in the abundance of *G. morhua* was observed over the period of data collection (Fig. 5 and Appendix I).

**LENGTH ANALYSIS**

One hundred and twenty-one *G. morhua* *L*<sub>f</sub> measurements were made with a mean ± s.d. of 6.3 ± 1.4 cm. The largest *G. morhua* observed was 11.4 cm and the smallest 3.2 cm. The largest individual (2 cm larger than the second largest individual) was excluded from analysis as it could have been a small age 1 year individual.

| Variable                  | PC1   | PC2   |
|---------------------------|-------|-------|
| Depth                     | 0.240 | 0.268 |
| Distance from coast       | 0.258 | 0.568 |
| *J*<sub>D</sub>           | −0.175| 0.265 |
| *N*<sub>2</sub>           | −0.539| 0.360 |
| *N*<sub>∞</sub>           | −0.512| 0.410 |
| Substratum type           | −0.448| −0.261|
| Wave fetch                | 0.301 | 0.409 |

*J*<sub>D</sub>, Julian date; *N*<sub>2</sub>, Hill diversity *N*<sub>2</sub> (reciprocal of Simpson’s index); *N*<sub>∞</sub>, reciprocal of the proportional abundance of the commonest species.
Fig. 4. Substratum type association of age-0 year group *Gadus morhua* observed around south Arran nature conservation marine protected area (NCMPA). More juveniles were found in relation to substratum type algal-gravel-pebble than algal-boulder-cobble or sand. No significant difference was observed between algal-boulder-cobble and sand. The varied width boxplots, proportional to the square root of the sample sizes, indicate the 25th and 75th percentiles of the total number of *G. morhua* observed within the different substrata. The upper bars indicate the 10th and the lower bars the 90th percentiles. The —— indicates the median size. ◯ indicate the outliers. ———- between substratum types with * refers to Tukey test P-value significance (*, *P* < 0·05; **, *P* < 0·01).
1997). The combination of colouration and substrata of sufficient rugosity to seek refuge within suggests that age-0 year *G. morhua*, of the size ranges observed, may choose to spend a greater proportion of their time on algal-gravel-pebble substratum type. Similarly, Lough *et al.* (1989) observed juvenile *G. morhua* in high abundance on pebble-gravel substrata. The high variability associated with these observations (Fig. 4) is likely to be a consequence of the small sample size and some variability in juvenile *G. morhua* substratum selection.

![Figure 5](image)

**Fig. 5.** *Gadus morhua* abundance for each substratum type over the course of data collection. ○, abundance of *G. morhua* from 22 July to 20 September 2013. ---, algal-boulder-cobble; ----, algal-gravel-pebble; ~~~~~, sand GLM fitted lines; shaded area indicates ±95% c.i. A decline in *G. morhua* abundance was observed over the course of data collection ($P < 0.01$).

![Figure 6](image)

**Fig. 6.** *Gadus morhua* fork length ($L_F$) over the course of data collection. Data points represent $L_F$ of *G. morhua* measured from 22 July to 20 September 2013. ---, the GLMM fitted line; □, ±95% c.i. An increase in age-0 year *G. morhua* $L_F$ was observed over the course of data collection ($P < 0.01$).

© 2016 The Authors. *Journal of Fish Biology* published by John Wiley & Sons Ltd on behalf of The Fisheries Society of the British Isles. 2016, 89, 1190–1207
Transects within Lamlash Bay NTZ were algal-gravel-pebble substratum types. The effect of the NTZ on juvenile *G. morhua* abundance was not explored as data on juvenile gadoid abundance were not available prior to its establishment to perform a before-after control impact study (Sale et al., 2005). A study undertaken by Howarth et al. (2015) found no difference in fish abundance within and out-with Lamlash Bay NTZ. The latter may be a result of the reserve’s small size (2.67 km²) and its young age (Howarth et al., 2015). Previous research on juvenile *G. morhua* does, however, show limited movement (Grant & Brown, 1998) but this may vary depending on substratum type (Laurel et al., 2004).

Seagrass beds have previously been observed to be nursery grounds for age-0 year *G. morhua* (Linehan et al., 2001; Bertelli & Unsworth, 2014; Lilley & Unsworth, 2014) with some studies showing increased nocturnal association (Anderson et al., 2007; Bertelli & Unsworth, 2014). Because of the sample size and low density of *Z. marina* sampled within the area, this substratum was merged with sand. Low-density seagrass areas have been related to be more similar to sandy sites (Jackson et al., 2001; McCloskey & Unsworth, 2015), particularly when patchy with low shoot density and area coverage (Jackson et al., 2001; Gorman et al., 2009). Mixed diurnal behaviour has also been observed with age-0 year *G. morhua*, with some experiments showing more active behaviour during daylight hours (Keats & Steele, 1992; Sayer & Poonian, 2007). Differential aggregation behaviour has also been observed depending on light levels, predator presence and seagrass patch size (Laurel et al., 2003, 2004; Anderson et al., 2007).

Gotceitas & Brown (1993) observed that juvenile *G. morhua* within an experimental tank selected cobble substrata in the presence of predators whilst selecting sand and gravel-pebble substrata in the absence of predators. It is possible that the juveniles identified during data collection did not feel threatened by the diver, and the low abundance of larger piscivores (Heath & Speirs, 2012) may have led to higher abundances on algal-gravel-pebble substratum type. In this study, no predator–prey interactions were observed. It is thought that some gravel substrata, specifically containing maerl, may contribute to higher species diversity, structural rugosity (relative to the size of *G. morhua*) and heterogeneity, and that these factors are of importance to the survival of juvenile *G. morhua* (Hall-Spencer et al., 2003; Kamenos, 2004; Lough, 2010).

A decline in *G. morhua* abundance and an increase in juvenile size and size variation were detected over the course of data collection. *Gadus morhua* have been observed to arrive in recruitment pulses to coastal areas during downwelling events (Ings et al., 2008). The increase in size variation is most likely caused by pulse recruitment occurring over this time period, or one continued long pulse recruitment (Bastrikin et al., 2014) from July to August 2013. The decline in abundance is unlikely to have been caused by fish moving into deeper waters within such a narrow time span since previous studies show that this migration occurs after their first winter or first year (Magill & Sayer, 2004).

Fewer $L_F$ measurements than counts were made (24% of the total number of *G. morhua*) owing to a combination of not being able to distinguish individual juveniles within schools in both cameras and a blind spot between the cameras where the *G. morhua* were too close to the cameras to be measured (Unsworth et al., 2014). This latter problem could have been reduced by having the cameras closer together, but at the expense of reduced accuracy at distance (Boutros et al., 2015). Precision in the Z direction (towards and away from camera) is affected by the distance between
cameras, affecting all measurements of objects which are not angled normal to the camera axis (SeaGIS, 2013; Boutros et al., 2015).

Future temperate water studies should take water visibility and fish size into account in order to maximize the number of fish measured. Stereo-video scuba transects can provide detailed and valuable information on fish assemblage and population structure in rocky and sensitive substrata which would otherwise be inaccessible. Use of semi-closed or closed circuit rebreather apparatus, or autonomous underwater vehicles (AUV) may further reduce observer bias (Sayer & Poonian, 2007; Clarke et al., 2009). With the rise in MPAs and spatial restrictions to manage substrata and species around the U.K., this technique provides important information for fisheries management and information for possible future monitoring.

Despite measures in place to recover stocks, the already low numbers of *G. morhua*, small length index and isolation of the Firth of Clyde in comparison to neighbouring areas are likely to cause it to be more susceptible to local fishing impact (Heath & Speirs, 2012). Much debate exists on the value of MPAs for the protection of fishes, particularly in temperate environments (Roberts et al., 2005; Takashina & Mougi, 2014; Fernández-Chacón et al., 2015). If an MPA can protect important substrata of value to juvenile *G. morhua*, bottle neck recruitment may be avoided, thus increasing the survival of individuals at this critical stage in their life cycle (Lough, 2010). Management measures have recently (December 2015) been established to recover maerl beds found within the NCMPA (Scottish Government, 2015). On the basis of the data presented here, it appears that such management measures could have benefits for juvenile *G. morhua*. In the meantime, further investigations are recommended to strengthen habitat-related observations of juvenile *G. morhua* abundance and distribution. Better understanding and protection of important habitat components could support juvenile *G. morhua* survival and recruitment.

The authors would like to thank the two independent reviewers for their helpful feedback on this manuscript. Thanks to J. Clarke, C. Willmott, C. Hopkins and D. McNeil for dive technical assistance and H. Wood and R. Cheshire for the boat handling expertise and use of their RIBs to collect data. We also thank H. Wood and Scottish Natural Heritage for information and data on benthic substrata within the area around south Arran, and H. Wood for the many other types of logistical support he provided. Thanks to P. Johnson for statistical advice. Finally, the first author would like to give a special thanks to Marine Scotland (Clyde 2020) and the ClimateXChange centre student support and NERC National facility for Scientific Diving (Grant NFSD/13/01) for scientific diving training without which collection of the data would not have been possible.

**References**

Able, K. W. (1999). Measures of juvenile fish habitat quality: examples from a National estuarine research reserve. In *Fish Habitat: Essential Fish Habitat and Habitat Rehabilitation* (Beneka, L. R., ed.), pp. 134–147. *American Fisheries Society Symposium 22.*

Anderson, J. L., Laurel, B. J. & Brown, J. A. (2007). Diel changes in behaviour and habitat use by age-0 Atlantic cod (*Gadus morhua* L.) in the laboratory and field. *Journal of Experimental Marine Biology and Ecology* 351, 267–275. doi: 10.1016/j.jembe.2007.07.001

Anderson, M., Gorley, R. & Clarke, K. (2008). PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. Plymouth: PRIMER-E.

Bastrikin, D. K., Gallego, A., Millar, C. P., Priede, I. G. & Jones, E. G. (2014). Settlement length and temporal patterns of juvenile cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), and whiting (*Merlangius merlangus*) in a northern North Sea coastal nursery area. *ICES Journal of Marine Science* 71, 2101–2113. doi: 10.1093/icesjms/fsu029
Bertelli, C. M. & Unsworth, R. K. F. (2014). Protecting the hand that feeds us: seagrass (Zostera marina) serves as commercial juvenile fish habitat. Marine Pollution Bulletin 83, 425–429. doi: 10.1016/j.marpolbul.2013.08.011

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H. & White, J. S. S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution 24, 127–135. doi: 10.1016/j.tree.2008.10.008

Boutros, N., Shortis, M. R. & Harvey, E. S. (2015). A comparison of calibration methods and system configurations of underwater stereo-video systems for applications in marine ecology. Limnology and Oceanography: Methods 13, 1–13. doi: 10.1002/lom3.10020

Burrows, M. T., Harvey, R. & Robb, L. (2008). Wave exposure indices from digital coastlines and the prediction of rocky shore community structure. Marine Ecology Progress Series 353, 1–12. doi: 10.3354/meps07284

Campana, S. E., Frank, K. T., Hurley, P. C., Koeller, P. A., Page, F. H. & Smith, P. C. (1989). Survival and abundance of young Atlantic cod (Gadus morhua) and haddock (Melanogrammus aeglefinus) as indicators of year-class strength. Canadian Journal of Fisheries and Aquatic Sciences 46, 171–182. doi: 10.1139/f89-287

Cappo, M., Harvey, E. & Shortis, M. (2006). Counting and measuring fish with baited video techniques—an overview. In Cutting-Edge Technologies in Fish and Fisheries Science (Lyle, J. M., Furlani, D. M. & Buxton, C. D., eds), pp. 101–114. Hobart: Australian Society for Fish Biology.

Clarke, K. R. & Warwick, R. M. (2001). Change in Marine Communities, An Approach to Statistical Analysis and Interpretation, 2nd edn. Plymouth: PRIMER-E.

Clarke, M. E., Tolimieri, N. & Singh, H. (2009). Using the seabed AUV to assess populations of groundfish in untrawlable areas. In The Future of Fisheries Science in North America (Beamish, R. J. & Rothschild, B. J., eds), pp. 357–372. Dordrecht: Springer. doi: 10.1007/978-1-4020-9210-7_20

Clarke, J., Bailey, D. M. & Wright, P. J. (2015). Evaluating the effectiveness of a seasonal spawning area closure. ICES Journal of Marine Science 72, 2627–2637. doi: 10.1093/icesjms/fsv144

Cote, D., Moulton, S., Scruton, D. A. & McKinley, R. S. (2001). Microhabitat use of juvenile Atlantic cod in a coastal area of Bonavista Bay, Newfoundland. Transactions of the American Fisheries Society 130, 1217–1223. doi: 10.1577/1548-8659

Cote, D., Ollerhead, L., Scruton, D. & McKinley, R. (2003). Microhabitat use of juvenile Atlantic cod in a coastal area of Newfoundland determined by 2D telemetry. Marine Ecology Progress Series 265, 227–234. doi: 10.3354/meps265227

Dalley, E. L. & Anderson, J. T. (1997). Age-dependent distribution of demersal juvenile Atlantic cod (Gadus morhua) in inshore/offshore northeast Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences 54, 168–176. doi: 10.1139/f96-171

Dickens, L. C., Goatley, C. H. R., Tanner, J. K. & Bellwood, D. R. (2011). Quantifying relative diver effects in underwater visual censuses. PLoS One 6, e18965. doi: 10.1371/journal.pone.0018965

Elliott, S. A. M., Milligan, R. J., Heath, M. R., Turrell, W. R. & Bailey, D. B. (2016). Disentangling habitat concepts for demersal marine fish management. Oceanography and Marine Biology: Annual Review.

Fernandes, P. G. & Cook, R. M. (2013). Reversal of fish stock decline in the Northeast Atlantic. Current Biology 23, 1432–1437. doi: 10.1016/j.cub.2013.06.016

Fernández-Chacón, A., Moland, E., Espeland, S. H. & Olsen, E. M. (2015). Demographic effects of full vs. partial protection from harvesting: inference from an empirical before-after control-impact study on Atlantic cod. Journal of Applied Ecology 52, 1206–1215. doi: 10.1111/1365-2664.12477

Fitzpatrick, B. M., Harvey, E. S., Heyward, A. J., Twiggs, E. J. & Colquhoun, J. (2012). Habitat specialization in tropical continental shelf demersal fish assemblages. PLoS One 7, e39634. doi: 10.1371/journal.pone.0039634

Gaillard, J.-M., Hebblewhite, M., Loison, A., Fuller, M., Powell, R., Basille, M. & Van Moorter, B. (2010). Habitat-performance relationships: finding the right metric at a given spatial scale. Philosophical Transactions of the Royal Society B 365, 2255–2265. doi: 10.1098/rstb.2010.0085
Gibb, F. M., Gibb, I. M. & Wright, P. J. (2007). Isolation of Atlantic cod (Gadus morhua) nursery areas. *Marine Biology* 151, 1185–1194. doi: 10.1007/s00227-006-0565-0

Gibson, R. N. (1994). Impact of habitat quality and quantity on the recruitment of juvenile flatfishes. *Netherlands Journal of Sea Research* 32, 191–206. doi: 10.1016/0077-7579(94)90040-X

Gorman, A. M., Gregory, R. S. & Schneider, D. C. (2009). Eelgrass patch size and proximity to the patch edge affect predation risk of recently settled age 0 cod (Gadus). *Journal of Experimental Marine Biology and Ecology* 371, 1–9. doi: 10.1016/j.jembe.2008.12.008

Gotceitas, V. & Brown, J. A. (1993). Substrate selection by juvenile Atlantic cod (Gadus morhua): effects of predation risk. *Oecologia* 93, 31–37. doi: 10.1007/BF00321187

Grant, S. M. & Brown, J. A. (1998). Nearshore settlement and localized populations of age 0 Atlantic cod (Gadus morhua) in shallow coastal waters of Newfoundland. *Canadian Journal of Fisheries and Aquatic Sciences* 55, 1317–1327. doi: 10.1139/cjfas-55-6-1317

Gregory, R. S. & Anderson, J. (1997). Substrate selection and use of protective cover by juvenile Atlantic cod Gadus morhua in inshore waters of Newfoundland. *Marine Ecology Progress Series* 146, 9–20. doi: 10.3354/meps146009

Hall, L. S., Krausman, P. R. & Morrison, M. L. (1997). The habitat concept and a plea for standard terminology. *Wildlife Society Bulletin* 25, 173–182.

Hall-Spencer, J. M., Grall, J., Moore, P. G. & Atkinson, R. J. (2003). Bivalve fishing and maerl-bed conservation in France and the UK - retrospect and prospect. *Aquatic Conservation: Marine and Freshwater Ecosystems* 13, S33–S41. doi: 10.1002/aqc.566

Harvey, E. S. & Shortis, M. R. (1995). A system for stereo-video measurement of sub-tidal organisms. *Marine Technology Society Journal* 29, 10–22. doi: 10.1007/s00227-010-1404-x

Harvey, E. S. & Shortis, M. R. (1998). Calibration stability of an underwater stereo video system: implications for measurement accuracy and precision. *Marine Technology Society Journal* 32, 3–17.

Harvey, E. S., Fletcher, D. & Shortis, M. R. (2002). Estimation of reef fish length by divers and by stereo-video: a first comparison of the accuracy and precision in the field on living fish under operational conditions. *Fisheries Research* 57, 255–265. doi: 10.1016/S0165-7836(01)00356-3

Heath, M. R. & Speirs, D. C. (2012). Changes in species diversity and size composition in the Firth of Clyde demersal fish community (1927-2009). *Proceedings of the Royal Society B* 279, 543–552. doi: 10.1098/rspb.2011.1015

Hill, M. O. (1973). Diversity and evenness: a unifying notation and its consequences. *Ecology* 54, 427–432. doi: 10.2307/1934352

Hilborn, R. (2011). Future directions in ecosystem based fisheries management: A personal perspective. *Fisheries Research* 108, 235–239. doi: 10.1016/j.fishres.2010.12.030

Howarth, L. M., Pickup, S. E., Evans, L. E., Cross, T. J., Hawkins, J. P., Roberts, C. M. & Stewart, B. D. (2015). Sessile and mobile components of a benthic ecosystem display mixed trends within a temperate marine reserve. *Marine Environmental Research* 107, 8–23. doi: 10.1016/j.marenvres.2015.03.009

Hunter, W. R. & Sayer, M. D. J. (2009). The comparative effects of habitat complexity on faunal assemblages of northern temperate artificial and natural reefs. *ICES Journal of Marine Science* 66, 691–698. doi: 10.1093/icesjms/fsp058

Ings, D. W., Gregory, R. S. & Schneider, D. C. (2008). Episodic downwelling predicts recruitment of Atlantic cod, Greenland cod and white hake to Newfoundland coastal waters. *Journal of Marine Research* 66, 529–561. doi: 10.1357/002224008787157476

Jackson, E. L., Rowden, A. A., Atrill, M. A., Bossey, S. J. & Jones, M. B. (2001). The importance of seagrass beds as a habitat for fishery species. *Oceanography and Marine Biology* 39, 269–304.

Kaiser, H. F. (1960). The application of electronic computers to factor analysis. *Educational and Psychological Measurement* 20, 141–151. doi: 10.1177/00131644600200116

Kamenos, N. A., Moore, P. G., & Hall–Spencer, J. M. (2003). Substratum heterogeneity of dredged vs un–dredged maerl grounds. *Journal of the Marine Biological Association of the UK* 83, 411–413. doi: 10.1017/S0025315403007264h
Kamenos, N. (2004). Small-scale distribution of juvenile gadoids in shallow inshore waters; what role does maerl play? *ICES Journal of Marine Science* **61**, 422–429. doi: 10.1016/j.icesjms.2004.02.004

Keats, D. W. & Steele, D. H. (1992). Diurnal feeding of juvenile cod (*Gadus morhua*) which migrate into shallow water at night in eastern Newfoundland. *Journal of Northwest Atlantic Fishery Science* **13**, 7–14. doi: 10.2960/J.v13.a1

Kimmel, J. J. (1985). A new species-time method for visual assessment of fishes and its comparison with established methods. *Environmental Biology of Fishes* **12**, 23–32. doi: 10.1007/BF00007707

Kraak, S. B. M., Bailey, N., Cardinale, M., Darby, C., De Oliveira, J. A. A., Eero, M., Graham, N., Holmes, S., Jakobsen, T., Kempf, A., Kirkegaard, E., Powell, J., Scott, R. D., Simmonds, E. J., Ulrich, C., Vanhee, W. & Vintner, M. (2013). Lessons for fisheries management from the EU cod recovery plan. *Marine Policy* **37**, 200–213. doi: 10.1016/j.marpol.2012.05.002

Langton, R. W., Steneck, R. S., Gotceitas, V., Juanes, F. & Lawton, P. (1996). The interface between fisheries research and habitat management. *North American Journal of Fisheries Management* **16**, 1–7. doi: 10.1577/1548-8675(1996)016<0001

Laurel, B. J., Gregory, R. S. & Brown, J. A. (2004). Behavioural consequences of density-dependent habitat use in juvenile cod (*Gadus morhua*) and *G. ogac*: the role of movement and aggregation. *Marine Ecology Progress Series* **272**, 257–270. doi: 10.3354/meps272257

Lekve, K., Enersen, K., Enersen, S. E., Gjosaeter, J. & Stenseth, N. C. (2006). Interannual variability in abundance and length of young coastal cod in the subtidal zone. *Journal of Fish Biology* **68**, 734–746. doi: 10.1111/j.1095-8649.2005.00953.x

Lilley, R. J. & Unsworth, R. K. F. (2014). Atlantic cod (*Gadus morhua*) benefits from the availability of seagrass (*Zostera marina*) nursery habitat. *Global Ecology and Conservation* **2**, 367–377. doi: 10.1016/j.gecco.2014.10.002

Linehan, J. E., Gregory, R. S. & Schneider, D. S. (2001). Predation risk of age-0 cod (*Gadus*) relative to depth and substrate in coastal waters. *Journal of Experimental Marine Biology and Ecology* **263**, 25–44. doi: 10.1016/S0022-0981(01)00287-8

Lough, R. G. (2010). Juvenile cod (*Gadus morhua*) mortality and the importance of bottom sediment type to recruitment on Georges Bank. *Fisheries Oceanography* **19**, 159–181. doi: 10.1111/j.1365-2419.2010.00535.x

Lough, R. G., Valentine, P. C. & Potter, D. C. (1989). Ecology and distribution of juvenile cod and haddock in relation to sediment type and bottom currents on eastern Georges Bank. *Marine Ecology Progress Series* **56**, 1–12. doi: 10.3354/meps056001

Magill, S. H. & Sayer, M. D. J. (2004). Abundance of juvenile Atlantic cod (*Gadus morhua*) in the shallow rocky subtidal and the relationship to winter seawater temperature. *Journal of the Marine Biological Association of the United Kingdom* **84**, 439442. doi: 10.1017/S0025315404009415h

Marty, L., Rochet, M. J. & Ernande, B. (2014). Temporal trends in age and size at maturation of four North Sea gadid species: cod, haddock, whiting and Norway pout. *Marine Ecology Progress Series* **497**, 179–197. doi: 10.3354/meps10580

McCloskey, R. M. & Unsworth, R. K. F. (2015). Decreasing seagrass density negatively influences associated fauna. *PeerJ* **3**, e1053. doi: 10.7717/peerj.1053

Myers, R. A. & Cadigan, N. G. (1993). Density dependent juvenile mortality in marine demersal fish. *Canadian Journal of Fisheries and Aquatic Sciences* **50**, 1576–1590. doi: 10.1139/f93-179

Roberts, C. M., Hawkins, J. P. & Gell, F. R. (2005). The role of marine reserves in achieving sustainable fisheries. *Philosophical Transactions of the Royal Society B* **360**, 123–132. doi: 10.1098/rstb.2004.1578

Sale, P. F., Cowen, R. K., Danilowicz, B. S., Jones, G. P., Kritzer, J. P., Lindeman, K. C., Planes, S., Polumin, N. V. C., Russ, G. R., Sadovy, Y. J. & Steneck, R. S. (2005). Critical science gaps impede use of no-take fishery reserves. *Trends in Ecology & Evolution* **20**, 74–80. doi: 10.1016/j.tree.2004.11.007
Sayer, M. D. J. & Poonian, C. (2007). The influences of census technique on estimating indices of macrofaunal population density in the temperate rocky subtidal zone. *Underwater Technology* 27, 119–139. doi: 10.3723/175605407783360053

Schneider, D. C., Norris, M. J. & Gregory, R. S. (2008). Predictive analysis of scale-dependent habitat association: juvenile cod (*Gadus* spp.) in eastern Newfoundland. *Estuarine, Coastal and Shelf Science* 79, 71–78. doi: 10.1016/j.ecss.2008.03.005

Seitz, R. D., Wennhage, H., Bergström, U., Lipcius, R. N. & Ysebaert, T. (2014). Ecological value of coastal habitats for commercially and ecologically important species. *ICES Journal of Marine Science* 71, 648–655. doi: 10.1093/icesjms/fst152

Takashina, N. & Mougi, A. (2014). Effects of marine protected areas on overfished fishing stocks with multiple stable states. *Journal of Theoretical Biology* 341, 64–70. doi: 10.1016/j.jtbi.2013.09.027

Thurstan, R. H. & Roberts, C. M. (2010). Ecological meltdown in the Firth of Clyde, Scotland: two centuries of change in a coastal marine ecosystem. *PLoS One* 5, e11767. doi: 10.1371/journal.pone.0011767

Tupper, M. & Boutillier, R. G. (1995). Effects of habitat on settlement, growth, and post-settlement survival of Atlantic cod *Gadus morhua*. *Canadian Journal of Fisheries and Aquatic Sciences* 52, 1834–1841. doi: 10.1139/f95-176

Unsworth, R. K. F., Peters, J. R., McCloskey, R. M. & Hinder, S. L. (2014). Optimising stereo baited underwater video for sampling fish and invertebrates in temperate coastal habitats. *Estuarine, Coastal and Shelf Science* 150, 281–287. doi: 10.1016/j.ecss.2014.03.020

Wentworth, C. K. (1922). A scale of grade and class terms for clastic sediments. *Journal of Geology* 30, 377–392. doi: 10.1086/207555

Zuur, A. F., Leno, E. N., Walker, N. J., Saveliev, A. A. & Smith, G. M. (2009). *Mixed Effects Models and Extensions in Ecology with R*. New York, NY: Springer Science and Business Media.

**Electronic References**

Anon (2001). Commission Regulation (EC) No. 456/2001 of 6 March 2001 Establishing measures for the recovery of the stock of cod to the west of Scotland (ICES Division VIa) and associated conditions for the control of activities of fishing vessels. *Official Journal of the European Communities*, L65/13. Available at http://stecf.jrc.ec.europa.eu/documents/43805/44876/07-09_SG-MOS+07-03+-+Evaluation+of+closed+areas+II.pdf/ (last accessed 23 February 2015).

Anon (2002). The sea fish (prohibited methods of fishing) (Firth of Clyde) order 2002. Scottish statutory instrument 2002. *HMSO, No. 58*. Available at http://faolex.fao.org/docs/html/uk36239.htm/ (last accessed 23 February 2015).

Axelsson, M., Dewey, S., Plastow, L. & Doran, J. (2009). Mapping of marine habitats and species within the Community Marine Conservation Area at Lamlash Bay. *Scottish Natural Heritage Commissioned Report No. 346*. Available at http://www.snh.gov.uk/publications-data-and-research/publications/search-the-catalogue/publication-detail/?id=1508/ (last accessed 23 June 2014).

Bailey, N., Bailey, D. M., Bellini, L., Fernandes, P. G., Fox, C., Heymans, S., Holmes, S., Howe, J., Hughes, S., Magill, S., McIntyre, F., McKee, D., Ryan, M. R., Smith, I., Tyldesley, G., Watret, R. & Turrell, W. R. (2011). The west of Scotland marine ecosystem: a review of scientific knowledge. *Marine Scotland Science Report 911*, 1–292. Available at http://www.gov.scot/resource/doc/295194/0123085.pdf/ (last accessed 3 March 2014).

COAST (Community of Arran Seabed Trust) (2012). Proposed marine protected area south coasts of Arran. Community of Arran Seabed Trust. Available at http://arrancoast.com/website_pdf/COAST_Arran_South_MPA_proposal_9May_FinalP.pdf/ (last accessed 19 May 2015).

Connor, D. W., Allen, J. H., Golding, N., Lieberknecht, L. M., Northen, K. O. & Reker, J. B. (2004). *The Marine Habitat Classification for Britain and Ireland Version 04.05*. JNCC, Peterborough. Available at http://jncc.defra.gov.uk/marinehabitatclassification/ (last accessed 15 April 2015).
ICES (2014). *Celtic and West of Scotland. Cod in Division VIa (West of Scotland). Advice June 2014*. Available at [http://www.ices.dk/sites/pub/Publication%20Reports/Advice/2014/2014/cod-scw.pdf](http://www.ices.dk/sites/pub/Publication%20Reports/Advice/2014/2014/cod-scw.pdf) (last accessed 15 April 2015).

McIntyre, F., Fernandes, P. G. & Turrell, W. R. (2012). Scottish Marine and Freshwater Science Report Volume 3 Number 3: Clyde Ecosystem Review, Scottish Marine and Freshwater Science Report. Marine Scotland Science, 1–123. Available at [http://www.gov.scot/Publications/2012/06/7562/](http://www.gov.scot/Publications/2012/06/7562/) (last accessed 3 March 2014).

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team. (2014). *Linear and Nonlinear Mixed Effects Models. R Package Version 3.1-118*. Available at [http://CRAN.R-project.org/package=nlme/](http://CRAN.R-project.org/package=nlme/) (last accessed 10 February 2015).

Scottish Government (2015). *South Arran Marine Conservation Order*. Available at [http://www.gov.scot/Topics/marine/marine-environment/mpanetwork/MPAMGT/protectedareasmsgt/](http://www.gov.scot/Topics/marine/marine-environment/mpanetwork/MPAMGT/protectedareasmsgt/) (last accessed 22 December 2015).

SeaGIS (2013). *Measurement Science*. Available at [http://www.seagis.com.au/index.html/](http://www.seagis.com.au/index.html/) (last accessed 19 December 2015).

Skaug, H., Fournier, D., Bolker, B., Magnusson, A. & Nielsen, A. (2014). *Generalized Linear Mixed Models Using AD Model Builder. R Package Version 0.8. 0*. Available at [http://glmmadmb.r-forge.r-project.org/glmmADMB.pdf/](http://glmmadmb.r-forge.r-project.org/glmmADMB.pdf/) (last accessed 18 December 2015).

SNH (Scottish Natural Heritage) (2014). *South Arran Protected Area*. Available at [http://www.snh.gov.uk/protecting-scotlands-nature/protected-areas/national-designations/mpas/mpa-ar/](http://www.snh.gov.uk/protecting-scotlands-nature/protected-areas/national-designations/mpas/mpa-ar/) (last accessed 15 April 2015).

Spatial Ecology (2013). *Geospatial Modelling Environment*. Available at [http://spatialecology.com/](http://spatialecology.com/) (last accessed 21 May 2013).

**APPENDIX**

APPENDIX I. Results from the model of best fit for the response variable *Gadus morhua* abundance. Explanatory variables show substratum type and Julian date ($J_D$) with an offset of transect area (m$^2$). Coefficients and diagnostics ($Z$- and $P$-values) indicate the effect of each parameter level on the reference level, denoted as intercept. The reference level is substratum type, algal-boulder-cobble (ABC).

| Variables | Estimate | s.e. | Z-value | P-value |
|-----------|----------|-----|---------|---------|
| Intercept | 3·1028   | 1·6938 | 1·8320 | >0·05 |
| AGP       | 1·1524   | 0·4721 | 2·4410 | <0·05 |
| Sand      | −1·2494  | 0·7448 | −1·6780 | >0·05 |
| $J_D$     | −0·0280  | 0·0079 | −3·5370 | <0·001 |

AGP, algal-gravel-pebble.

APPENDIX II. Results from the Tukey test performed between substratum type categories for the response variable *Gadus morhua* abundance.

| Variables | Estimate | s.e. | Z-value | P-value |
|-----------|----------|-----|---------|---------|
| AGP-ABC   | 1·1386   | 0·4757 | 2·393  | <0·05 |
| Sand-ABC  | −1·2227  | 0·7547 | −1·620 | >0·05 |
| Sand-AGP  | −2·3613  | 0·7595 | −3·109 | <0·01 |

AGP, algal-gravel-pebble; ABC, algal-boulder-cobble.
APPENDIX III. Results from the model of best fit for the response variable *Gadus morhua* fork length ($L_F$). Fixed effects show Julian day ($J_D$) with an offset of transect area (m²)

| Variables | Estimate  | s.e.   | t-value | P-value |
|-----------|-----------|--------|---------|---------|
| Intercept | 23.30671  | 12.51339 | 1.862542 | >0.05   |
| $J_D$     | 0.182449  | 0.059287 | 3.077398 | <0.01   |

APPENDIX IV. Results from the model of best fit for the response variable *Gadus morhua* fork length ($L_F$) variation over the period of data collection

| Variables | Estimate  | s.e.   | t-value | P-value |
|-----------|-----------|--------|---------|---------|
| Intercept | -9.6035   | 20.48846 | -0.469  | >0.05   |
| $J_D$     | 0.2948    | 0.09732 | 3.030   | <0.01   |

$J_D$, Julian day.