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Small-scale distribution of juvenile gadoids in shallow inshore waters; what role does maerl play?

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The indirect effects of demersal fisheries, such as habitat degradation, are currently thought to be impacting gadoid stocks. Maerl fulfils nursery area prerequisites for several invertebrate species, so its role in similar ecosystem service provision for gadoids has been addressed. Juvenile cod (*Gadus morhua*), saithe (*Pollachius virens*), and pollack (*Pollachius pollachius*) in shallow (<7 m) inshore waters were surveyed with fykenets and scuba off western Scotland over a period of 12 months. Juvenile densities were highest from September to November, and at that time, significantly more were present during the day and associated with maerl (that lacked macroalgal cover) than with heavily vegetated rocky and gravel substrata. Juvenile cod were present throughout the year, whereas saithe appeared in July, and pollack from September to January. With its abundance of food, maerl probably has a high holding capacity for juvenile gadoids, and thus is an important part of the inshore nursery system.

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Introduction

Maerl grounds, which vary in size from tens to thousands of square metres, consist of loose-lying, coralline red algae (Giraud and Cabioch, 1976), and are in areas characterized by extensive water movement (tidal and/or wave action) in the photic zone (Woelkerling, 1988). Live maerl grounds are highly biodiverse (BIOMAERL team, 2003; Steller *et al.*, 2003), and have significantly greater heterogeneity than common adjacent substrata, including gravel, sand, and impacted dead maerl (Kamenos *et al.*, 2003). A single physical impact event may significantly reduce the heterogeneity of maerl thalli to that of a gravel substratum, by breakage, and may lead to subsequent death of the maerl (Hall-Spencer and Moore, 2000b; Kamenos *et al.*, 2003). To date, no data are available on the effects of maerl on juvenile gadoid distributions, a topic addressed herein.

Recently, owing to realization that fishing pressure is exceeding sustainable limits on a global scale, there has been mounting pressure to reduce fishing capacity (Pauly *et al.*, 2002; Schiermeier, 2002). Traditional controls such as reduction of quotas have been implemented in an effort to curb such pressures and to conserve spawning stocks.

However, the indirect effects of demersal fisheries, such as habitat degradation, are now thought also to be affecting gadoid stocks (Lindholm *et al.*, 1999).

To survive, pelagic populations of most gadoids are dependent on the recruitment of juvenile fish to shallow coastal areas that offer physical refuge and protection from predation (Pihl, 1982). Recruitment of 0-group cod, for example, occurs over a short period (2−4 months) following metamorphosis from the larval stage, prior to settling on demersal habitats (Campana *et al.*, 1994). Cod settlement begins in early summer (Tupper and Boutilier, 1995a) and, in western Scottish waters, peaks in July and declines to nothing in late November (Magill and Sayer, 2004). Newly settled cod inhabiting rocky reefs establish and defend territories in a size-specific social hierarchy. 0-Group fish, however, lose their site fidelity before their first winter, when they move offshore. During that interval, survival of 0-group cod is habitat-dependent (Tupper and Boutilier, 1995b).

In the absence of predators, juvenile gadoids forage over less complex substrata, including sand and gravel, but also over more complex maerl (Hall-Spencer and Moore, 2002). However, when predators threaten, they utilize more

complex substrata and vegetation for protection including: interstitial spaces of cobble substrata (Gotceitas and Brown, 1993; Gotceitas et al., 1995; Fraser et al., 1996; Lindholm et al., 1999); camouflage against pebble substrata (Lough et al., 1989); and hiding in unnamed vegetation (Wheeler, 1980; Gregory et al., 1997; Rangeley and Kramer, 1998; Lindholm et al., 1999), or in stands of Desmarestia sp. (Keats et al., 1987), kelp (Gotceitas et al., 1995), eelgrass (Borg et al., 1997; Gotceitas et al., 1997; Linehan et al., 2001), Fucus sp. (Borg et al., 1997), or Cladophora sp. (Borg et al., 1997).

Distribution, foraging activity, and predator avoidance are also reflected in diel changes of fish location. More 0-group cod are caught at night, independent of the sampling gear used (Methven and Bajdik, 1994; Methven and Schneider, 1998; Pihl and Wennhage, 2002), which Methven and Schneider (1998) attribute to inshore movement at night (or dusk) rather than to increased catchability then. Juvenile gadoids undertake such inshore migrations, either as they shoal, forage, and feed during the day, then disperse at night to protective inshore bottom cover, so avoiding predation by older conspecifics, which takes place mainly at night (Pihl, 1982; Keats and Steele, 1992; Grant and Brown, 1998a, b; Pihl and Wennhage, 2002), or as they feed nocturnally in shallow waters, but aggregate on the bottom by day in deeper water, seeking protection during times of higher predation (Lough et al., 1989; Olsen and Soldal, 1989; Linehan et al., 2001). Keats and Steele (1992) suggest that, because there are so many conflicting reports of feeding times, juvenile cod exhibit great flexibility in diel activity patterns.

This study aims to investigate the diel, shallow-water (<10 m Chart Datum, CD) distribution of juvenile cod (Gadus morhua), saithe (Pollachius virens), and pollack (Pollachius pollachius) in relation to live maerl and adjacent common substrata.

Material and methods

Investigations were carried out in Caol Scotnish, Loch Sween (56°01.99′N 05°36.13′W) southwest Scotland. Caol Scotnish is characterized by three key sites/substrata, live Lithothamnion glaciale maerl, rocky substrata with ~95% Halidrys siliquosa cover, and gravel covered with Chorda filum from June to November. All sites were in depths of 4–7 m CD, and subject to moderate tidal flows (max: 0.29–0.45 m s^{-1}). The substrata were mapped using scuba, and gadoids were sampled on five occasions between April 2002 and February 2003, with non-uniform absolute temporal differences between each successive bi-monthly survey, so avoiding temporal pseudo-replication (Underwood, 1997), i.e. sampling events coinciding with behavioural cycles in the organisms being sampled.

Maerl grounds are slow-growing and easily damaged (Hall-Spencer and Moore, 2000a; BIOMAERL team, 2003; Kamenos et al., 2003) and are protected under the EC Habitats Directive, so mobile gears were not used for sampling purposes. Static gear trials have shown that fykenets are successful at catching juvenile gadoids (Nostvik and Pedersen, 1999). They also have the advantage of not becoming entangled in loose-lying surface maerl, which tangles gill and trammel nets within a few hours of deployment.

Eight double-ended, square-otter-guarded fykenets (mesh size: 14 mm [leader], 10 mm [net]; height: 53 cm; leader length: 6 m) were deployed by hand from a 5-m dory. Nets were deployed during daylight, and emptied and redeployed at night. Dusk and dawn are here defined as falling within the hours of night/darkness. All nets were deployed with the same orientation, placing the leader perpendicular to the tidal flow and >150 m from the nearest net. Each of the five sampling periods lasted for 4 days, during which 12× night and 8× daylight samples were obtained from maerl and gravel, and 9× night and 6× daylight samples from rock. After each day/night cycle, nets were moved to another site/substratum to minimize net effects. Catch number and species, and length measurements were recorded each time the nets were hauled. All fish were retained for further analysis. Larger size classes of gadoid stomach content were determined as described in Bowen (1996) within 1 h of the fish being caught.

Additionally, visual estimates of gadoid numbers were made using scuba. Transects were swum by two divers at 9–10 m min^{-1} for 5 min (n varied between 7 and 21). All transects were surveyed at slack water (±2 h) to minimize current effects on the divers' swimming distances, and in randomly selected directions. Shoals, or individual fish, observed crossing or in a strip 2-m wide (transect volume = 100 m^3) were recorded along each 50-m transect. At the size/age at which fish or shoals (e.g. cod) were observed, they do not exhibit territoriality (Tupper and Boutilier, 1995b), so the same fish or shoal may have been encountered more than once on the same transect.

Data analysis

Fyke-net catches were adjusted to catch h^{-1} assuming a linear relationship, because catch rate relationships only become non-linear after extended (>1 day) net deployment (Austin, 1977; Hamley and Howley, 1985; Nostvik and Pedersen, 1999).

Reciprocally (x′ = 1/(x + 0.5)) transformed data (to fit parametric assumptions) were analysed as a repeated measure ANCOVA because, although the nets were deployed in different locations during each repetitive sample, and gadoids are highly mobile, the size of the population was not known. Therefore, depletion may have been taking place during the sampling period (i.e. successive days during the 4-day sampling session). Numbers of fish of larger size classes in each net were used as a covariate, because adult and larger conspecific presence affects juvenile abundance either through predation or local juvenile

181 avoidance (Helfman, 1989; Rangeley and Kramer, 1998).
182 *Post hoc* comparisons were investigated with a Tukey test.
183 Univariate comparisons of catch composition within each
184 substratum/diel period were made using six *a priori* multiple
185 comparison Kruskal–Wallis tests with Dunn–Šidák ad-
186 justed p values. Additionally, an individual Kruskal–Wallis
187 test was used to compare the numbers of larger size classes
188 of gadoids during each diel period.
189 Although there were only a few species and size classes
190 of fish present, multivariate analyses were used to aid in the
191 differentiation of species/size compositions associated with
192 each substratum and month. Multivariate analyses were
193 performed using PRIMER® (Clarke and Warwick, 1994;
194 Clarke and Gorley, 2001). Multivariate data analysis was
195 by non-metric multi-dimensional scaling ordination (MDS),
196 using the Bray–Curtis similarity matrix. Analyses used
197 untransformed data, because only a few species/size com-
198 binations were present. Two-way crossed pairwise analyses
199 of similarity, ANOSIMs (assumptions met), were carried
200 out to test for significant differences ($R > 0.15$) in assem-
201 blage composition between substrata. Similarity percentage
202 (SIMPER) analyses were used to examine the contribution
203 of individual species towards the dissimilarity between the
204 different substrata. This analysis was selected because the
205 samples were in well-defined groups (substrata), and not
206 described by more continuous distributions. SIMPER anal-
207 ysis also examined the contribution each species made to
208 the average similarity within a group.

209 Results

210 Temporal abundance

211 Juvenile gadoids (< 12 cm (the upper size limit of juveniles
212 caught)) were found at Caol Scotnish during all months
213 sampled. However, there were significantly bigger catch
214 rates in September and November, which did not differ
215 significantly from each other ($H_4 = 32.30$, $p > 0.0001$;
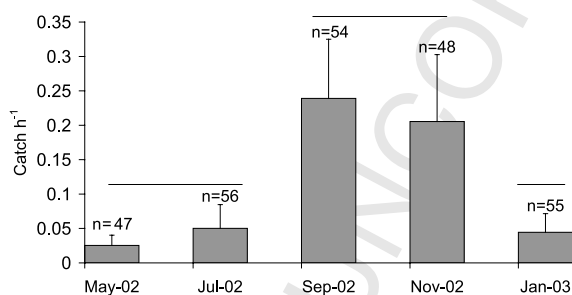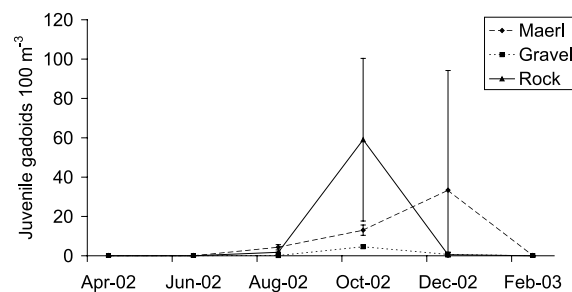216 Figure 1). Visual observations using scuba also indicated

Figure 2. Mean number of juvenile gadoids observed associated with maerl, gravel, and rocky substrata in Caol Scotnish using scuba during bi-monthly sampling events. Error bars = s.d. Straight lines do not indicate linear progressions between data points, but are given to aid trend determination.

increased numbers of juvenile gadoids during the period 217
September–November, with highest densities over maerl 218
and rocky substrata (Figure 2). 219
Large size class fish (all cod > 32 cm, the lower size 220
limit of large size class fish caught) were present only from 221
May to November, and were significantly more numerous 222
in September than in all months other than November 223
($H_4 = 15.07$, $p = 0.005$; Figure 3). All larger size class cod 224
had empty stomachs. Further analysis was therefore 225
concentrated on the period September–November, which 226
appears to be the period when juvenile gadoids utilize the 227
shallow waters of Loch Sween. 228

Juvenile density, September–November 229

Interaction effects between substratum and diel period were 230
not significant ($F_2 = 2.78$, $p = 0.068$). Significantly more 231
juvenile gadoids were caught over maerl than over rock and 232
gravel, and significantly more over rock than over gravel 233
($F_2 = 35.41$, $p < 0.0001$; Figure 4). Significantly more 234
juvenile gadoids were caught during daylight than during 235
darkness ($F_1 = 15.42$, $p < 0.0001$; Figure 4). The presence 236
of larger gadoids had no effect on the numbers of juvenile 237

Figure 1. Mean number of juvenile gadoids (< 12 cm) caught per hour at Caol Scotnish (data combined for maerl, rocky, and gravel substrata) using fykenets at bi-monthly sampling events. Error bars = s.d. Horizontal lines at the same level indicate substrata that did not differ significantly from each other.
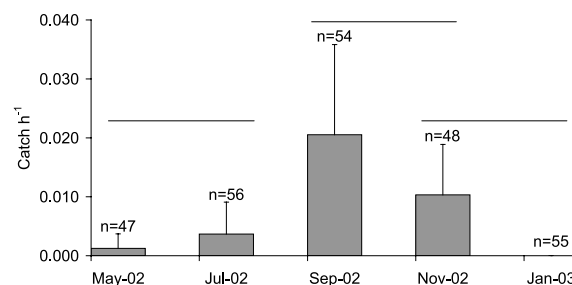

Figure 3. Mean number of gadoids of the larger size classes (> 32 cm) caught per hour at Caol Scotnish (data combined for maerl, rocky, and gravel substrata) using fykenets at bi-monthly sampling events. Error bars = s.d. Horizontal lines at the same level indicate substrata that did not differ significantly from each other.
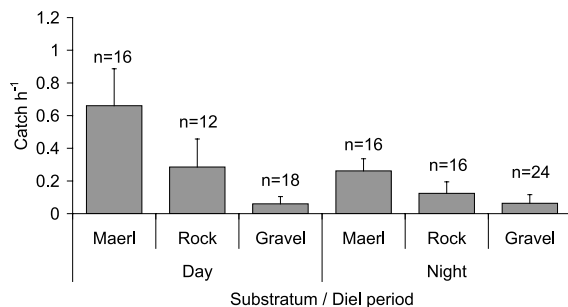
Figure 4. Mean number of juvenile gadoids (<12 cm) caught over maerl, rock, and gravel using fykenets by day and by night, September–November. Error bars $=$ 95% C.I.

238 gadoids caught ($F_1 = 3.45$, p $= 0.067$). Gadoids of the
239 larger size classes were caught over rocky and gravel areas
240 only during daylight, and over maerl and rock only at night
241 during the period September–November. Similar numbers
242 of gadoids in the larger size classes were caught during both
243 diel periods ($H_1 = 4.14$, p $= 0.127$; Figure 5).
244   Similar numbers of juvenile cod, saithe, and pollack were
245 caught over all substrata during each diel period (H_2 all
246 <6.46, p all >0.0085; the Dunn–Šidák adjusted p value)
247 apart from significantly more juvenile pollack than cod or
248 saithe over maerl by day ($H_2 = 15.92$, p <0.0001; Figure 6).

249 Community structure

250 Significant differences in assemblage composition associat-
251 ed with substrata (global R $= 0.24$, p $= 0.001$) and month
252 (global R $= 0.234$, p $= 0.001$) were detected with a two-
253 way crossed ANOSIM. Pairwise comparisons indicated
254 "gravel and maerl" and "rock and maerl" assemblages to
255 be slightly separable (R >0.25), whereas "gravel and rock"
256 assemblages were indistinguishable (R <0.25; Table 1). No
257 2 months had well-separated (R >0.75) assemblage compo-
258 sitions, though "May and January" and "July and January"
259 had overlapping but clearly different assemblage composi-
260 tion. "May and July", "May and September", "May and
261 November", "July and November", "July and September",
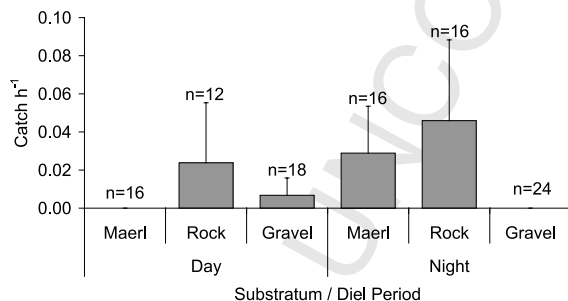262 and "September and January" were all slightly separable

Figure 5. Mean number of gadoids of the larger size classes (>32 cm) caught over maerl, rock, and gravel using fykenets by day and by night, September–November. Error bars $=$ s.d.

(R >0.25), whereas "September and November", and 263
"November and January" were not separable (R <0.25) in 264
terms of assemblage composition (Table 1). 265

As indicated by the low global R statistic (ANOSIM), no 266
substrata were typified by any particular species or age 267
group. However, maerl and gravel were discriminated from 268
each other (1.13 (dissimilarity/s.d.)) by higher abundances 269
of juvenile pollack on maerl (0.18 (average abundance)) 270
than on gravel (0.02), and similarly maerl and rock were 271
discriminated (1.09) by higher abundances of juvenile 272
pollack on maerl (0.18) than on rock (0.05). 273

Only May could be typified by great abundance (0.09) of 274
juvenile cod (1.94 (similarity/s.d.)). All other months were 275
not typified by any particular species or size class. Abun- 276
dances of juvenile cod in May (0.09 (average abundance) 277
contributed to its dissimilarity with September (0.06, 1.17 278
(average abundance, dissimilarity/s.d.)), and January (0.04, 279
1.77). High densities of juvenile pollack in January (0.08) 280
contributed to its dissimilarity with May (0.00, 1.45) and 281
July (0.00, 1.26), and high densities in September (0.18) 282
contributed to its dissimilarity with January (0.08, 1.43). 283
Enhanced abundance of saithe in July (0.13) contributed to 284
its dissimilarity with November (0.11, 1.05) and January 285
(0.03, 1.07). 286

Discussion 287

Gadoid densities were highest in Caol Scotnish during late 288
summer and autumn. Recruitment of post-settlement juve- 289
nile gadoids to shallow inshore waters is well documented 290
(Carr, 1991; Gibson *et al.*, 1996; Pihl and Wennhage, 291
2002), and to a lesser extent seasonal migrations of larger 292
fish into the shallows (Pihl and Wennhage, 2002), probably 293
in search of food, does take place. Although our fyke-net 294
catches were quite low during the period of high density of 295
juveniles (owing to the static nature of the gear and the use 296
of otter guards, that reduce catch rates; Jeffries *et al.*, 1984, 297
1988), direct observations confirmed abundant juvenile fish 298
(up to 201 juvenile gadoids 100 m^{-3}). High variability 299
associated with these observations was most likely attribut- 300
able to the non-territoriality, high mobility, shoaling, and 301
diver-avoidance behaviour of the species being monitored. 302

Juvenile gadoids were in greater densities over maerl 303
than over heavily vegetated rock and gravel substrata. As 304
juveniles were caught on all substrata it is possible that, 305
considering the static nature of the sampling gear, they 306
were less active while in vegetated areas, possibly seeking 307
refuge, and actively foraging while over the less heteroge- 308
neous substrata (Eklov and Persson, 1996), such as the 309
macroalgae-devoid maerl, so increasing their catchability. 310
Unlike the current findings, a comparison of coralline algal 311
sites, so-called "barrens", with dense macroalgal stands in 312
Newfoundland by Keats *et al.* (1987), revealed significantly 313
more 1- and 2-group cod in fleshy macroalgal beds 314
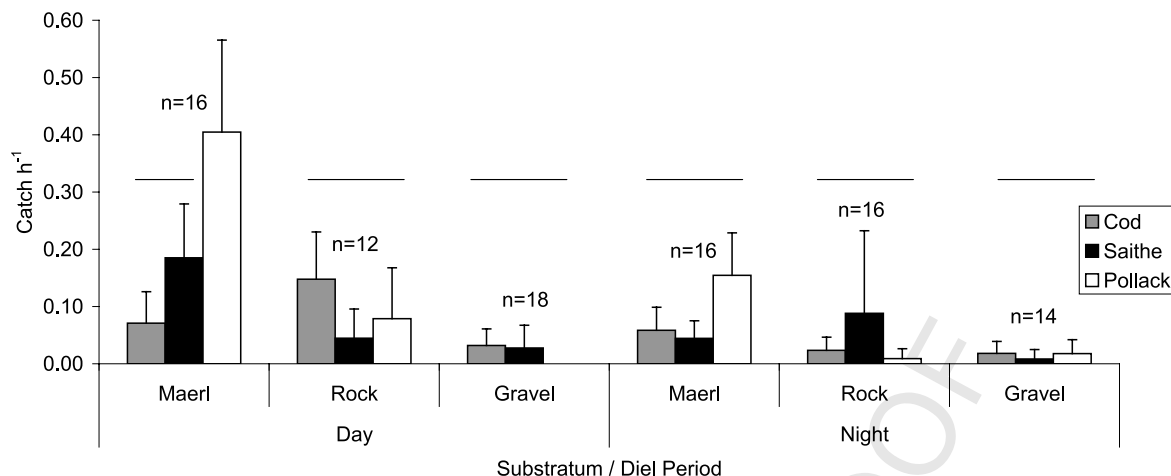(*Desmarestia* sp.) than on barrens (all 8–10 m CD) 315

Figure 6. Mean number of juvenile cod, saithe, and pollack (<12 cm) caught over maerl, rock, and gravel using fykenets by day and by night, September–November. Error bars = s.d. Horizontal lines indicate fish densities that did not differ significantly within each substratum/diel period group.

surveyed using scuba. These authors concluded that the juvenile cod were using the macroalgal stands for protection.

During the period September–November, significantly more juvenile gadoids were present by day than by night over maerl, whereas numbers remained lower over rock and gravel by both day and night. Perhaps the juveniles were more active, probably foraging, during daylight (i.e. increasing their catchability) than at night in the shallow waters of Loch Sween. However, Methven and Schneider (1998) observed more juvenile cod in shallow water by night than by day, which they considered as being either to feed or to avoid predation. It is unlikely that fish caught by day were migrating to or from deeper water, because juvenile gadoids make such migrations at dusk and dawn (Methven and Schneider, 1998; Pihl and Wennhage, 2002), both of which periods are here defined as night/darkness.

The numbers of juveniles on each substratum and diel period were not affected by the presence of larger, predatory gadoids, nor did the numbers of gadoids of larger size class differ between diel periods. This was unexpected, because juvenile cod avoid predators and larger conspecifics (Methven and Schneider, 1998). It is possible, therefore, that the densities of larger size classes were so low that impacts on juvenile distributions remained very localized and were not picked up by our sampling regime, that juveniles and larger size classes were temporally segregated within each sampling session, so we could not determine the presence of any relationships, and that the otter guards we used only allowed capture of the smallest of the large size classes of gadoids. Although we found no effect of predator presence on juvenile densities (possibly an artefact of the sampling technique), higher densities of larger size classes (i.e. potential predators) occurred at night on maerl during late summer and early autumn, supporting our suggestion that juvenile gadoids do prefer to forage in daylight over maerl.

Olsen and Soldal (1989) observed that the so-called holding capacity of coastal locations suitable for 0-group cod is most likely restricted primarily by food capacity. Therefore, considering the high organic biomass (e.g. polychaetes) associated with maerl grounds than the other substrata (BIOMAERL team, 1999, 2003), and that juvenile gadoids do forage over maerl grounds (through unpublished stomach content analysis), such grounds may provide higher holding capacities of juvenile gadoids per unit area than the sand and gravel areas traditionally associated with

Table 1. Pairwise comparisons of untransformed month and substratum pairs using a two-way crossed ANOSIM (analysis of similarity). Where global R significance ∼ 0, the null hypothesis is accepted and the compared assemblages are indistinguishable; where R = 1, similarities within substrata (all replicates) are greater than any similarities between substrata.

Pairwise comparison	Global R significance statistic	Global R significance level (%)
Gravel and maerl	0.312	0.1
Gravel and rock	0.015	34.6
Maerl and rock	0.272	0.1
May and July	0.283	1.3
May and September	0.375	0.2
May and November	0.240	0.5
May and January	0.500	0.2
July and September	0.215	0.6
July and November	0.325	0.1
July and January	0.566	0.1
September and November	0.011	37.5
September and January	0.258	0.6
November and January	0.139	3.3

foraging juvenile gadoids such as pollack (Rangeley and Kramer, 1998). Gadoids that forage on gravel exhibit better survival, partly because of greater food availability (Lough *et al.*, 1989), because survival of overwintering young-of-year fish is generally higher in larger fish, and the rapid growth of newly settled individuals is physiologically and ecologically selectively advantageous in terms of lowering predation risk (Walsh, 1987). Maerl grounds may therefore increase such survival further.

Nursery areas are defined by their high population densities of juveniles, fast somatic growth rates, and characteristically good survival, as well as by their ability to supply recruits to adult populations (Beck *et al.*, 2001). Considering our findings and the difficulty of testing recruitment success, we conclude that juvenile gadoids are using Caol Scotnish as a nursery area during late summer and autumn, partly sustained by the abundant food biomass of live maerl matrix.

No months had well-separated gadoid assemblages, though May was typified by abundance of juvenile cod, probably the previous year's late-spawned cohort. Of note, though, was the sequential appearance of other gadoid juveniles around and during the months of greater juvenile density, with abundance of saithe in July followed by similar abundance of pollack from September to January. This separation was likely coincidental, because juvenile cod were present from July to January. However, it may demonstrate temporal niche separation of nursery area usage by the different species within the gadoid guild, to reduce interspecific competition for food and/or refugia. Although site-specific, juvenile (5–15 cm) saithe and pollack utilize similar benthopelagic food sources, which differ from those utilized by the more benthic-tending cod (Bromley *et al.*, 1997; Høines and Bergstad, 1999), allowing cod, and either saithe or pollack, to co-exist. Older saithe and pollack have less dietary overlap (Sarno *et al.*, 1994). Unlike the current result, Pihl and Wennhage (2002) demonstrated clear separation of fish assemblages during summer, when considering 25 adult and juvenile fish species, including gadoids.

Densities of juvenile pollack were greatest over maerl than were those of other gadoids. Of course, this may indicate increased catchability of pollack by fykenets when foraging over maerl during daylight, and/or lesser catchability at night when in vegetated areas. It is therefore possible that pollack are less active nocturnally than other juvenile gadoids, or that they are more active foragers than other species during daylight, so increasing their catchability by static fykenets. However, adult pollack are less active foragers than adult saithe (Sarno *et al.*, 1994).

We conclude that maerl grounds may increase the holding capacity of localized inshore shallow-water nursery areas, with gadoids consistently preferring to forage over maerl than over gravel, despite the extra vegetative cover provided by the latter (at least in Caol Scotnish). Considering that anthropogenic damage can kill maerl and reduce its heterogeneity to areas resembling a gravel substratum (Hall-Spencer and Moore, 2000a; Kamenos *et al.*, 2003), it is clear that if maerl areas are helping to increase the localized juvenile gadoid holding capacities of inshore waters, destruction of such habitats may lead to significant reduction of the holding capacity of inshore areas.

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