



## Habitat associations of juvenile Atlantic cod (*Gadus morhua* L.) and sympatric demersal fish communities within shallow inshore nursery grounds

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### ABSTRACT

Resolving the relationship between demersal fish and sublittoral biotic habitats and substrates is a key element in the protection of important nursery grounds for strengthening fish recruitment. In Norway, coastal Atlantic cod (*Gadus morhua* L.) is a commercially and culturally important demersal fish for Norwegian coastal communities, and in recent decades the stock has declined to such an extent that a plan to rebuild the stock to biologically safe limits has been implemented. Yet, little is known about the specific biotic and abiotic habitat associations of the early-life stages of coastal cod, which is important for the management and protection of the species. The same shallow, sublittoral zones are inhabited by juveniles and adults of other commercial demersal gadoids and wrasses. This study presents novel findings on associations between juvenile coastal cod and other demersal fish species with seafloor substrates and biological habitats, inferred from five years of extensive fyke net surveys. Newly settled 0-group cod were typically associated with eel grass and red algae biotic habitats on sand and shell sand substrates. However, there was an ontogenic habitat shift amongst one year old (1-group) individuals that became more ubiquitous with their biotic habitat or substrate type choices. The juvenile gadoids saithe (*Pollachius virens*) and pollack (*Pollachius pollachius*), were most associated with hard bottom dominated sites with saithe being more abundant at exposed sites, compared to pollack. Goldsinny wrasse (*Ctenolabrus rupestris*) and corkwing wrasse (*Symphodus melops*) appeared to favor sugar kelp forests and red algae. Overall, the study identifies the specific sublittoral biotic habitats and substrates important to different early life stages of juvenile coastal cod and other commercially important demersal fish, providing critical information needed for identifying candidate coastal habitats for protection.

### 1. Introduction

Successful coastal zone management ultimately depends on a broad understanding of fish habitat dependencies (Peterson et al., 2000). For instance, vegetated areas such as eelgrass beds are identified as key nursery habitats in some northern regions and have been the focus of coastal conservation and restoration programs (Gotceitas et al., 1997; Warren et al., 2010). However, coastal ecosystems are highly diverse both in terms of available habitats and the associated communities of juvenile and mature demersal fish. A broader understanding of associations between fish and inshore habitats is often lacking, even for commercially important harvested species such as the Atlantic cod (*Gadus morhua* L.).

In Norway, Atlantic cod populations are divided into two distinct populations based on differences in life history characteristic and otolith

and genetic variation: Northeast Arctic cod and Norwegian coastal cod (Rollefson, 1933, 1934; Godø and Moksness, 1987; Stransky et al., 2008; Sarvas and Fevolden, 2005). Northeast Arctic cod is the larger oceanic stock, feeding offshore in the Barents Sea and migrating to spawning sites primarily in outer coastal areas around the Lofoten archipelago and further north (Bergstad et al., 1987; Marteinsdottir et al., 2005). Juvenile Northeast Arctic cod feeding, and nursery areas are mainly in the Barents Sea where larvae and young juveniles are transported by the Norwegian Coastal Current from the spawning grounds, but the yearlings may also be found in deeper parts of the fjords during autumn in northern Norway (Fevolden et al., 2012). In contrast, Norwegian coastal cod (NCC) reside in coastal areas and fjords throughout the whole Norwegian coast and utilize these areas for both spawning and nursery grounds (Jakobsen, 1987; Berg and Pedersen, 2001). The coastal cod is considered more sedentary than the highly migratory Northeast Arctic

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cod. Juveniles feed and grow in regions close to these spawning grounds (Knutsen et al., 2007; Rogers et al., 2014), although individuals may also show more pronounced movements, using less sheltered coastal areas for spawning and undertaking short feeding migrations into offshore banks or between coastal regions (Godø, 1984; Jakobsen, 1987; Michalsen et al., 2014; Johansen et al., 2020). Currently, the NCC is managed as two stocks: one North of 67° N latitude and one between 62 and 67° N (ICES, 2021).

Recent decades have seen a decline in NCC that has led to the development of a recovery plan to rebuild the stock to safe harvest limits (ICES, 2006; Kålås et al., 2006; Rogers et al., 2017; ICES, 2019). The current population recovery plan has involved the regulation of catches and technical gear restrictions to reduce fishing pressure, but a positive response has been absent. The survival of the stock is dependent on successful recruitment; therefore, the identification and protection of both spawning and nursery areas is an important element of a recovery strategy. The closure of coastal cod spawning grounds in Lofoten has been implemented to help stock recovery in the northern region (Dahle et al., 2018). The shallow sublittoral coastal areas that are of particular importance to the early life of coastal cod (Godø and Sunanå, 1984; Meager et al., 2012) are however relatively scarcely evaluated in management plans, and particularly vulnerable to environmental effects from coastal development and habitat degradation (Seitz et al., 2014; Ono et al., 2019).

The early-life survival of juvenile Atlantic cod is known to be a major factor influencing Atlantic cod recruitment and subsequent population size and structure (Tupper and Boutilier, 1995b). Several studies have shown that during the first 3 years Atlantic cod in Newfoundland remain relatively stationary where they utilize shallow vegetated coastal habitats (<30 m) for protection and feeding. These include macroalgal beds of erect brown and red macroalgae, such as kelps and fucoids (Cote et al., 2001), open sandy habitats (Cote et al., 2013) and seagrass meadows (Bradbury et al., 2008; Gotceitas et al., 1995, 1997). However, by mid-autumn many cod aged 2–3 years will leave coastal home ranges around Newfoundland and migrate seaward (Cote et al., 2004). In coastal Nova Scotia, the post-settlement survival and subsequent juvenile densities of Atlantic cod are known to be strongly influenced by habitat type (Tupper and Boutilier, 1995a; Lindholm et al., 1999). Shallow seafloor substrates, such as mud and sand bottoms and those containing cobbles and gravels, were critical to juvenile cod in the western Gulf of Maine (Grabowski et al., 2018). As a result of these studies, it is well known that small-scale changes in the availability of key coastal habitat types affect the spatial distribution of Atlantic coastal cod in eastern Canada and the USA. In comparison to the several decades of research on cod post-settlement survival, growth and habitat associations in eastern Canada summarized here, understanding of the effect of these factors on Northern European and NCC population dynamics and recruitment is limited (Sørensen, 2019). A similar understanding is required for the NCC to ensure that critical habitats remain protected against modifications from coastal development. It is however known that NCC fry in fjords may settle in shallow water (0–2 m) in the vicinity of spawning areas and continue to use these areas as nursery grounds (Jørstad et al., 2014). Further, the availability of vegetative cover from eel grass (*Zostera marina*) and coastal algae is important for juvenile cod on the Norwegian and Swedish west coast (Borg et al., 1997; Barceló et al., 2016). The long and diverse Norwegian coast offers a variety of substrates and biological habitats in shallow waters. However, it is not specifically known which sublittoral habitats are preferred by NCC, and if this changes with advancing year classes.

Aside from cod, the Norwegian coastal demersal fish community includes other gadoid species of commercial value, primarily saithe (*Pollachius virens*) and pollack (*Pollachius pollachius*). Similar to cod, first year-class saithe and pollack (0-group) also settle in shallow coastal waters (Nedreaas, 1986) where they live in schools feeding on planktonic crustaceans (Olsen et al., 2010). However, information relating to the habitat preferences of these demersal gadoids is also scarce. Other

important commercial fish in coastal Norway are wrasses, due to the relatively recent discovery of the utility of several species as cleaner fish to control sea lice infestations in sea-based farms for Atlantic salmon (*Salmo salar*). Wild capture of three target wrasse species (*Ctenolabrus rupestris*, *Symphodus melops*, and *Labrus bergylta*) has increased steadily since 2008 with over 20 million fish across the three species caught in 2017 (Blanco Gonzalez and de Boer, 2017). While some information exists regarding the habitat preferences of wrasse communities in an individual fjord (Skiftesvik et al., 2015), less is known about their habitat use in inshore island regions of Norway.

This general paucity of information about sub-littoral habitat preferences and utilization by juvenile resident NCC and other commercial coastal fish species is restricting the identification and potential protection of the most important shallow coastal habitats for juvenile recruitment. The main objective of this study was, therefore, to investigate the associations of juvenile Norwegian coastal cod (including sympatric coastal fish species) and life stages with seafloor substrates and biological habitats within shallow water nursery grounds.

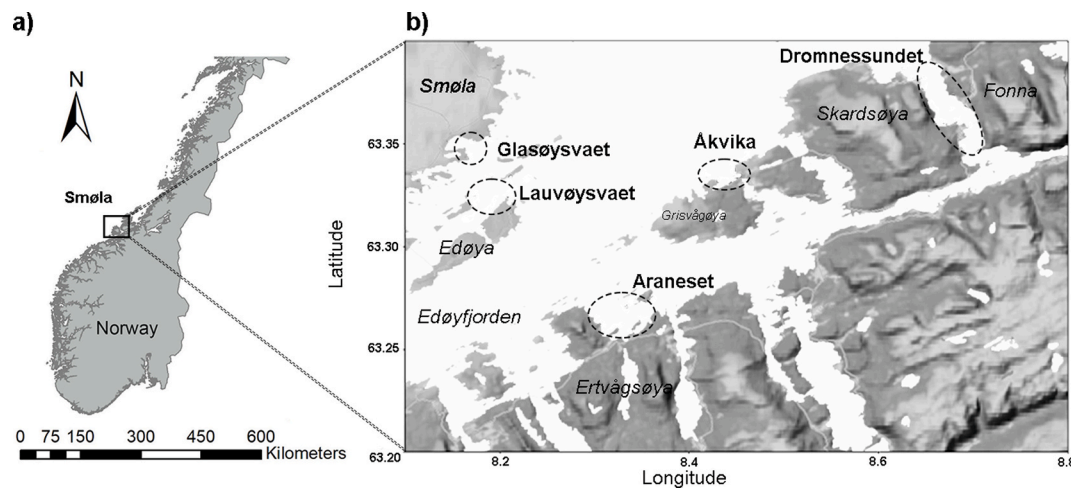
## 2. Material and methods

### 2.1. Site description

Examination of the habitat associations of juvenile cod and other coastal fish was conducted in sublittoral waters southeast of the island of Smøla (63.331°N, 8.19°E), in the county of Møre and Romsdal, western Norway (Fig. 1a). Sampling locations for juvenile cod and coastal fish communities were chosen to cover pre-identified cod spawning areas. Five spawning areas within the same region (Araneset, Åkvika, Dromnessundet, Glasøysvaet, and Lauvøysvaet) (Fig. 1b) were selected from the Norwegian Fisheries Directorate map based on fishers' identification of mature cod in a spawning state. Spawning areas were confirmed during egg mapping surveys conducted in March 2015 and 2016 (van der Meeren, 2016, 2017). Åkvika spawning area lies northeast of the island of Grisvågøya in an area of 0–30 m depth. (Supplementary Fig. 1a), while Araneset is in a bay protected by northern lying islands north of Ertvågøya island (water depth 0–60 m) (Supplementary Fig. 1b). Dromnessundet is a shallow (max ~ 50 m) sound between the Skardsøya island and Fonna mountain on the mainland (Supplementary Fig. 1c). Glasøysvaet and Lauvøysvaet are both located southeast of Smøla in water between 0 and ~80 m depth. Lauvøysvaet is between the islands of Storhaverøya and Lauvøya to the north and Edøya to the south, while Glasøysvaet is between the southeast point of Smøla and Glasøya island (Supplementary Fig. 1d). The shallow seafloor in these study regions primarily consisted of mixed sand, gravel, and cobbles between areas of hard bedrock substrates colonized by macroalgae (red algae, green algae, and kelp) and eelgrass.

### 2.2. Juvenile cod and demersal fish sampling

Double fyke nets were set in the sublittoral zone at depths between 2 and 8 m in mid-autumn, specifically late October and early November, to sample juvenile fish. The fyke nets were the Danish type 79/5, consisted of a 6 m long leading net with two connected cages at the ends, each with 5 rings and 3 funnels that create three cage chambers with progressively smaller mesh (17, 14, and 11 mm). Each gear setting consisted of two such double fyke nets linked together and weighted to the seafloor by 2 and 4 kg lead weights attached 1 m from the end of each of the outer cages, respectively (Supplementary Fig. 2a). Fyke nets were marked with a surface buoy and remained on the seafloor for a soak time between 1 and 5 days. Soak times over 2 days occurred occasionally when stormy weather prohibited collection. GPS position of the nets was registered by a Garmin echomap 52DV chart plotter. The weight ( $\pm 10$  g), and total length (cm) of each cod captured in each net were recorded, while for other demersal fish species only the number of individuals were recorded. All live fish were released in the vicinity of



**Fig. 1.** Map of sampling stations for juvenile cod and other coastal fish species at five sampling stations (Åkvika, Araneset, Dromnessundet, Glasøysvaet, and Lauvøysvaet) southeast of the island of Smøla. Panel a) shows the position of the island of Smøla on the west coast of Norway and b) the location of the sampling stations.

capture site after measurements were taken.

### 2.3. Cod otoliths for age determination

Individual cod that were dead in the fyke nets from injuries, caused for example by bird or crab attacks, were frozen to collect otoliths samples for aging. Otoliths were obtained from 14 cod between the lengths of 14 and 30 cm. Nine individuals measuring between 14 and 18 ( $\pm 0.5$ ) cm were assigned to 0-group, 4 cod between 22.5 and 30 cm to 1-group, and one cod at 28.5 cm length was assigned to 2-group, based on the otolith age reading.

### 2.4. Sampling design

Sampling sites within each spawning area were assigned unique position codes in the first year and revisited during subsequent years. Nineteen positions codes were defined in Åkvika, 23 in Araneset, 17 in Dromnessundet, 6 in Glasøysvaet, and 27 in Lauvøysvaet (Supplementary Figs. 1a–d). A total of 1189 fyke net gear settings were carried out in these 92 positions during yearly surveys from 2015 to 2019 in the 5 spawning areas, except in Dromnessundet where sampling was only conducted between 2016 and 2019. In total, there were 142 gear settings in 2015 and ~260 gear settings yearly between 2016 and 2019, with 1–7 fyke net gear deployed at each position annually (Table 1). The layout of these gear setting positions throughout each spawning area was designed to cover the majority of the shallow water habitat types. Fyke nets were positioned in nearshore water sites that contained the same habitat type within the general vicinity of fyke net (~20 m in all directions) and where gear retrieval was possible in prevailing wind conditions. Based on findings that tagged juvenile cod (1–3 years) around Smøla were recaptured at the exact same position (within 10–15 m) years later, it was assumed that cod caught in the fyke nets were

using the habitat assigned to that position. For full fyke net deployment information see Supplementary Tables 1a–e).

### 2.5. Substrate and habitat surveys via towed camera with video annotation

Substrate and habitat characteristics at 82 of the 92 fyke net positions were surveyed using a lightweight towed camera system deployed from the boat during the 2019 survey. This meant that substrate and biological habitat data was available for 1136 fyke net gear settings over the 5 year study. The towed camera consisted of a high-definition GoPro 7 Hero Black edition video camera in an underwater housing, mounted on a stainless-steel bar. An aerodynamic fin was attached to the end of the bar to automatically orientate the rig in the direction the boat was travelling while towed through the water using a surface line. The rig was weighted with a 5 kg iron weight suspended 1 m below the towed camera bar (Supplementary Fig. 2b). After deployment of a fyke net at each position, the towed camera was flown along the length of the gear (~20 m) at ~1 m above the seafloor to collect video of the substrate and habitat. Towed camera videos were analyzed by the VLC Media Player ([www.videolan.org](http://www.videolan.org)), and a main substrate and biotic habitat were assigned to each gear position, based on percentage cover. Substrate types were divided into four main categories: 1) solid bedrock, 2) sand and shell sand, 3) mixed sand substrates, and 4) stones and boulders (Table 2). Biotic type categories were based on the “Nature in Norway” (NiN) system from the national “Species data bank” and the University of Oslo (Rinde et al., 2021). The NiN system is designed for the national description and classification of terrestrial and marine biotic habitat types. (<https://www.artsdatabanken.no/NiN>). In this study, biotic habitat types were classified in five categories of main shallow water seabed vegetation types from the NiN system; 1) green algae, 2) red algae, 3) sugar kelp (*Saccharina latissima*), 4) *Laminaria hyperborea*




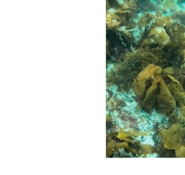




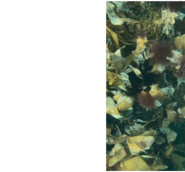
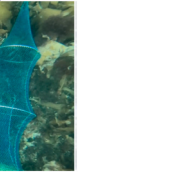
**Table 1**

Summary of fyke net deployments and cod catches at the five spawning sites in 2015, 2016, 2017, 2018, and 2019.

Spawning Site	2015		2016		2017		2018		2019	
	Gear	Cod	Gear	Cod	Gear	Cod	Gear	Cod	Gear	Cod
Araneset	45	93	54	101	54	129	54	71	54	114
Åkvika	32	87	48	127	48	107	48	165	48	79
Dromnessundet	0	0	45	191	44	187	45	252	45	211
Glasøysvaet	15	78	27	88	27	108	21	69	27	85
Lauvøysvaet	50	252	90	398	88	507	90	354	90	363
<b>Total</b>	<b>142</b>	<b>510</b>	<b>264</b>	<b>905</b>	<b>261</b>	<b>1038</b>	<b>258</b>	<b>911</b>	<b>264</b>	<b>852</b>

**Table 2**

Details of categories used to classify substrate and biotic habitat types at fyke net positions. Numbering in brackets are based on the “Nature in Norway” (NiN) system (<https://www.artsdatabanken.no/NiN>).

Substrate categories				
Solid bedrock	Sand and shell sand	Mixed Sands (Sand containing gravel and boulders, Gravel containing sand and boulders)		Stones and boulders
				
Nature habitat categories				
Green algae (M1-1)	Red algae (M1-2)	Sugar kelp ( <i>Saccharina latissima</i> ) forest (M1-3)	Laminaria kelp ( <i>Laminaria hyperborean</i> ) forest (M1-5)	Eelgrass beds (M7-4)
				

forest, and 5) eelgrass (*Zostera* spp.) beds (Table 2).

## 2.6. Statistical analysis

### 2.6.1. Identifying cod cohorts from length frequency analysis

Biotic and abiotic habitat selection is linked to cod size therefore length groups were identified and linked to corresponding year classes. Peaks in the length distributions of cod caught in each of the areas were estimated using the *mixdist* package in R (Macdonald et al., 2018). For initial data inspection, length distribution plots were produced for each year and area separately. In most cases, at least two separate peaks most likely attributable to 0- and 1- group cod, could be identified. Since the mean lengths of estimated peaks were very similar with a few exceptions, distributions based on all length data combined were produced. To attribute cod to different age cohorts based on length (1 cm intervals), the contribution of each length to each of the age cohort distributions was calculated. For length groups that represented more than one age group, we assigned all of the fish to the age group that had >50% of the lengths. The different length cohorts were then investigated with regards to their natural biotic habitat (NiN category) and abiotic substrate associations.

### 2.6.2. Catch rates

Cod catch per unit effort (CPUE) was defined as the number of fish caught per fyke net per day. Two separate analyses were conducted to explore variation in CPUE among and within spawning areas and years. First, a mixed effect model was used where CPUE was treated as the dependent variable and area as a categorical fixed variable. The position code was nested within year and treated as a random effect. This was followed by a Tukey post-hoc test that allowed for a group-wise comparison of all areas. Second, to analyze yearly variation in CPUE within spawning areas, a model was run with year included as the only fixed effect and position code as a random effect. As in the first analysis, the initial model run was followed by Tukey post-hoc tests for group-wise comparisons of yearly differences within each area. The *lme4* library of R (Bates et al., 2014) was used for all analyses, and models were run separately for all the different cohorts identified in the length-frequency

analysis.

### 2.6.3. Cod habitat- and substrate associations

Generalized linear mixed models (*lme4* package in R) (Bates et al., 2014) were applied to test to what extent habitat- and substrate type could explain variation in cod CPUE. First, cod catches by length cohort (response variable) were tested against a fixed categorical variable describing seafloor biotic habitat type, with an additional random term comprising year nested within position code. Second, a similar model structure was applied using substrate, rather than habitat type, as the fixed variable.

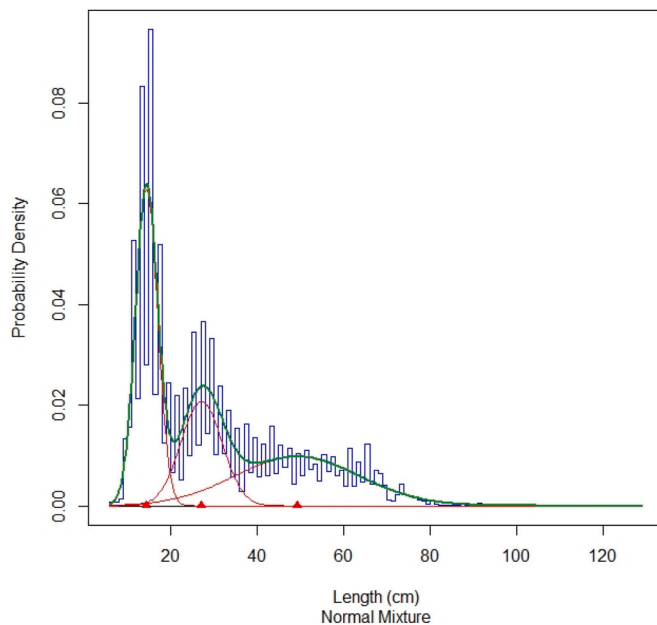
### 2.6.4. Multivariate analysis of fish community habitat associations

The *Adonis* function in the R package *Vegan* v.2.5–7 (Oksanen et al., 2020) was used to examine the relationship between the community structure of all demersal fish species, other than Atlantic cod, and substrate and biotic habitats. The analysis was conducted on fourth-root transformed mean CPUE data for each demersal species at each position code, to reduce the influence of high values of dominant species and ensure that rarer species were incorporated in the analysis. Position code was treated as a random factor nested within year. Pairwise post-hoc tests were conducted using the function *pairwise.adonis2* from the package *pairwise.adonis* (Martinez Arbizu, 2020). A similarity percentage (SIMPER) analysis was also conducted in the *Vegan* R package to examine the contribution of individual demersal fish species to the overall dissimilarity between species community composition from areas with different substrate and biotic habitats.

## 3. Results

### 3.1. Cod length cohorts

A total of 4216 cod were caught in 1189 fyke net gear settings over the whole study period (Table 1). Fitted length distributions revealed two clearly separate length cohorts made up of smaller cod (<35 cm), and a less well defined third cohort of bigger fish (Fig. 2). The estimated mean length of the first cohort (0-group) was 14.6 cm and 27.8 cm for



**Fig. 2.** Length distribution (blue bars) of all cod caught in the five study areas during the period 2015–2019. Red lines show individually fitted length cohorts, the green line the sum of all cohorts, and triangles the mean length of the estimated cohort. Intersects between the three individual cohorts were used to determine the length ranges for the first and second cohorts. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

the second cohort (1-group) for all cod caught across the five spawning sites and years. The length categories assigned to the 0-group and 1-group cohorts corresponded with the length and age of the 14 individual cod used for otolith age reading. Cod making up the 0-group cohort were caught in greater numbers than the cod from the second cohort (Fig. 2, Supplementary Table 2). Based on the mixdist model the 0-group cod were defined as fish of a length  $\leq 20$  cm, 1-group as cod  $> 20$  cm and  $\leq 35$  cm and 2+-group cod  $> 35$  cm.

### 3.2. Nursery area substrate and biotic habitats

Within the 82 fyke net positions surveyed for substrate and biotic habitat type, the Dromnessundet area was dominated by sand and shell sand substrate containing gravel and boulders, primarily covered by a red algae biotic habitat type. The most exposed nursery areas; Lauvøysvaet and Glasøysvaet, contained a mixture of sandy bottom containing gravel and boulders. The most bedrock substrate was

**Table 3**

Result of the model of between area differences in catch rate (CPUE) for i) 0-group ( $\leq 20$  cm), ii) 1-group ( $> 20$  cm and  $\leq 35$  cm) and iii) 2-group ( $> 35$  cm) cod. Given predictors are the effect of the categorical variable area. Estimates are the parameter estimate of the predictor, CI is the 95% confidence interval and p is the p-value. Significance (bold font) was assigned at  $p < 0.05$ . The treatment contrast of R was used with the intercept representing the value for Åkvika and the value for the other areas showing how they compare to this reference value. The letters show the results of Tukey post hoc tests, with different letters indicating significant between-area differences for each of the different size classes. Only the fixed effects are shown. The first letter shows the results of the post-hoc for the 0-group, the second letter the 1-group and the third letter the 2+ group. Marginal  $R^2$  is the amount of variation explained by the fixed effects whereas conditional  $R^2$  is the amount of variation explained by the fixed effects and the random effects Tukey post hoc test results are presented in Supplementary Tables 3a–e.

Predictors	0 - group catch			1 - group Catch			2+ - group Catch		
	Estimates	CI	p	Estimates	CI	p	Estimates	CI	p
Intercept <sup>a a a</sup>	0.45	0.24–0.66	<b>&lt;0.001</b>	0.27	0.14–0.39	<b>&lt;0.001</b>	0.40	0.25–0.54	<b>&lt;0.001</b>
[Araneset] <sup>a a a</sup>	–0.04	–0.29–0.22	0.774	–0.06	–0.19–0.06	0.306	–0.17	–0.28–0.06	<b>0.003</b>
[Dromnessundet] <sup>b b b</sup>	0.82	0.54–1.10	<b>&lt;0.001</b>	0.41	0.27–0.54	<b>&lt;0.001</b>	0.11	–0.01–0.24	0.071
[Glasøysvaet] <sup>a b b</sup>	–0.00	–0.37–0.36	0.980	0.32	0.15–0.49	<b>&lt;0.001</b>	0.32	0.18–0.47	<b>&lt;0.001</b>
[Lauvøysvaet] <sup>a b b</sup>	0.29	0.04–0.54	<b>0.022</b>	0.39	0.27–0.50	<b>&lt;0.001</b>	0.39	0.29–0.49	<b>&lt;0.001</b>
Observations	1198			1198			1198		
Marginal $R^2$ /Conditional $R^2$	0.069/0.507			0.108/0.336			0.128/0.270		

observed at Lauvøysvaet and Glasøysvaet. Glasøysvaet was completely covered in sugar kelp while the main biotic habitats at Lauvøysvaet were red algae and laminaria kelp on sand and shell sand containing boulders and bedrock. Substates at the Araneset and Åkvika were dominated by sand and shell sand containing gravel and boulders. The main biotic habitat type at Araneset was sugar kelp, and at Åkvika habitats primarily consisted of laminaria kelp and eel grass (Supplementary Figs. 3a and b).

### 3.3. Cod catch rates

For 0-group cod, the only statistically significant difference in CPUE was that more cod were caught in Dromnessundet than in all other spawning areas in 2016–2019 (Table 3, Fig. 3a). Dromnessundet is dominated by sand and shell sand substrate and red algae. Within areas, 0-group catches at Lauvøysvaet were higher in 2017 and 2016 than in all other years (Fig. 3a). Fewer 1-group cod were found in Araneset and Åkvika than in the other three areas. The latter result was generally consistent across all survey years, except that catches at Dromnessundet in 2016 were lower than in 2017 and 2019 and similar to those observed in Araneset and Åkvika (Fig. 3b, Table 3). As with 1-group cod, the lowest catches of 2+-group cod were in Araneset and Åkvika (Fig. 3c, Table 3). Within spawning areas, more 2+-group cod were caught in 2015 than all other years in both Lauvøysvaet and Glasøysvaet (Fig. 3c). Fewer 2+-group cod were caught in 2016 than in all other years in Lauvøysvaet (Fig. 3c). Summaries of the mixed effect models and their Tukey post-hoc tests examining cod catch rates within spawning areas are presented in Supplementary Tables 3a–e.

### 3.4. Cod cohort biotic habitat type associations

A total of 4062 cod were caught in 1136 fyke net gear settings with corresponding habitat information. The mean number of 0-group cod that were caught in stations covered with eel grass and red algae was significantly higher ( $p < 0.001$ ) than in stations characterized by sugar and laminaria kelp (Fig. 4a, Table 4). Though 0-group catches varied between years in eel grass and red algae areas, catches were consistently highest in these habitat types. In contrast, catches of 1-group and 2+-group cod were similar across the five biotic habitat categories (Fig. 4a, Supplementary Tables 4a and b). Across all areas and years, most cod, regardless of length group, were caught at stations covered with red algae, which was the main biotic habitat characteristic in only 29% of all stations (Supplementary Fig. 3a, Supplementary Fig. 4). Within individual spawning areas, only a few stations consistently contributed to high catches of 0-group cod, particularly in Åkvika where high catches were observed only on the two eel grass stations (Fig. 5, Supplementary Fig. 5a). In Araneset and Lauvøysvaet, areas covered either with red algae or eel grass were where most 0-group cod were caught (Fig. 5, Supplementary Figs. 5b and d). The Dromnessundet spawning area

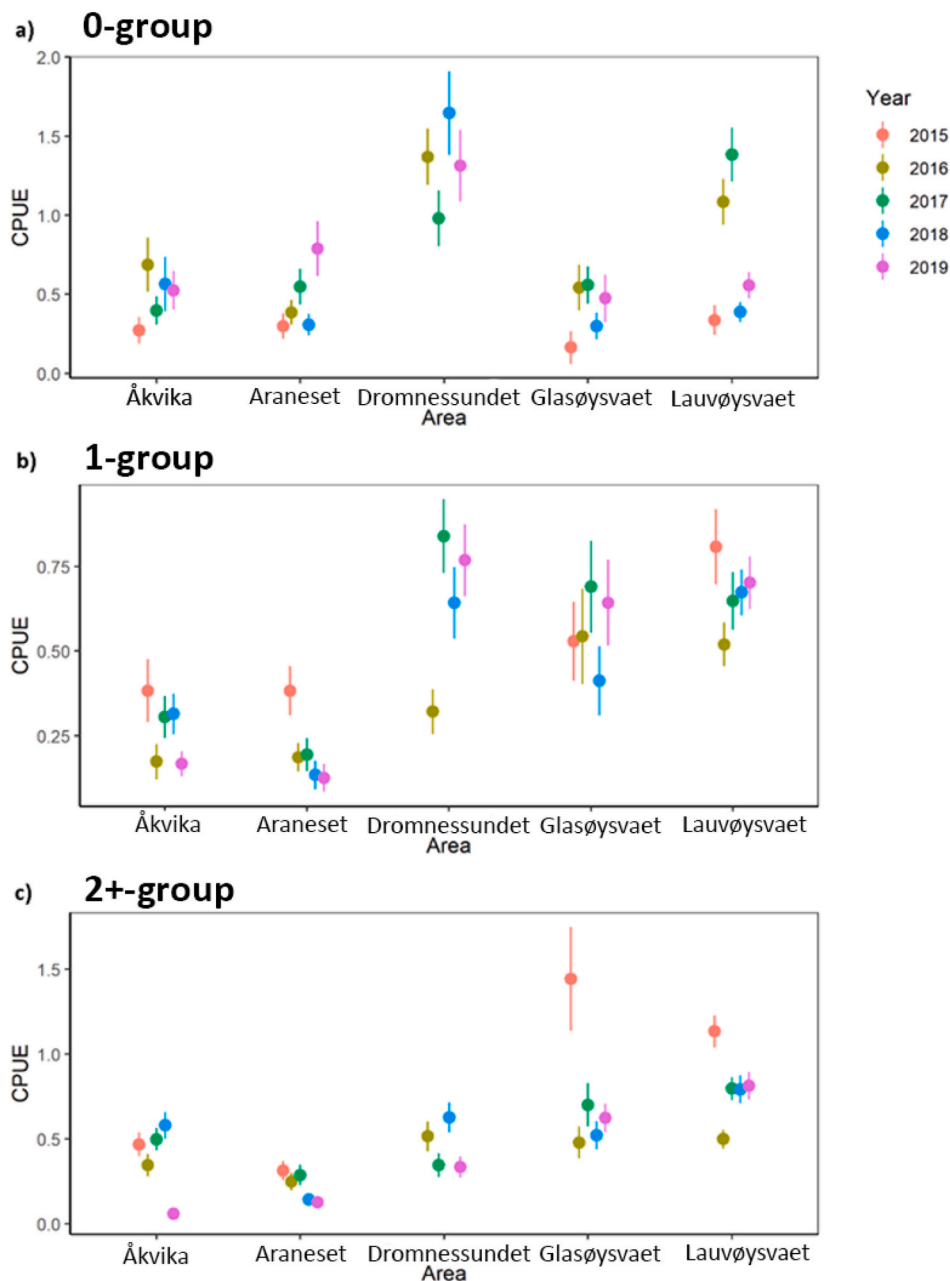


Fig. 3. a–c. Mean  $\pm$  standard error of CPUE of cod of a) 0 – group, b) 1 – group and c) 2+ - group for all stations in the different areas in all sampling years.

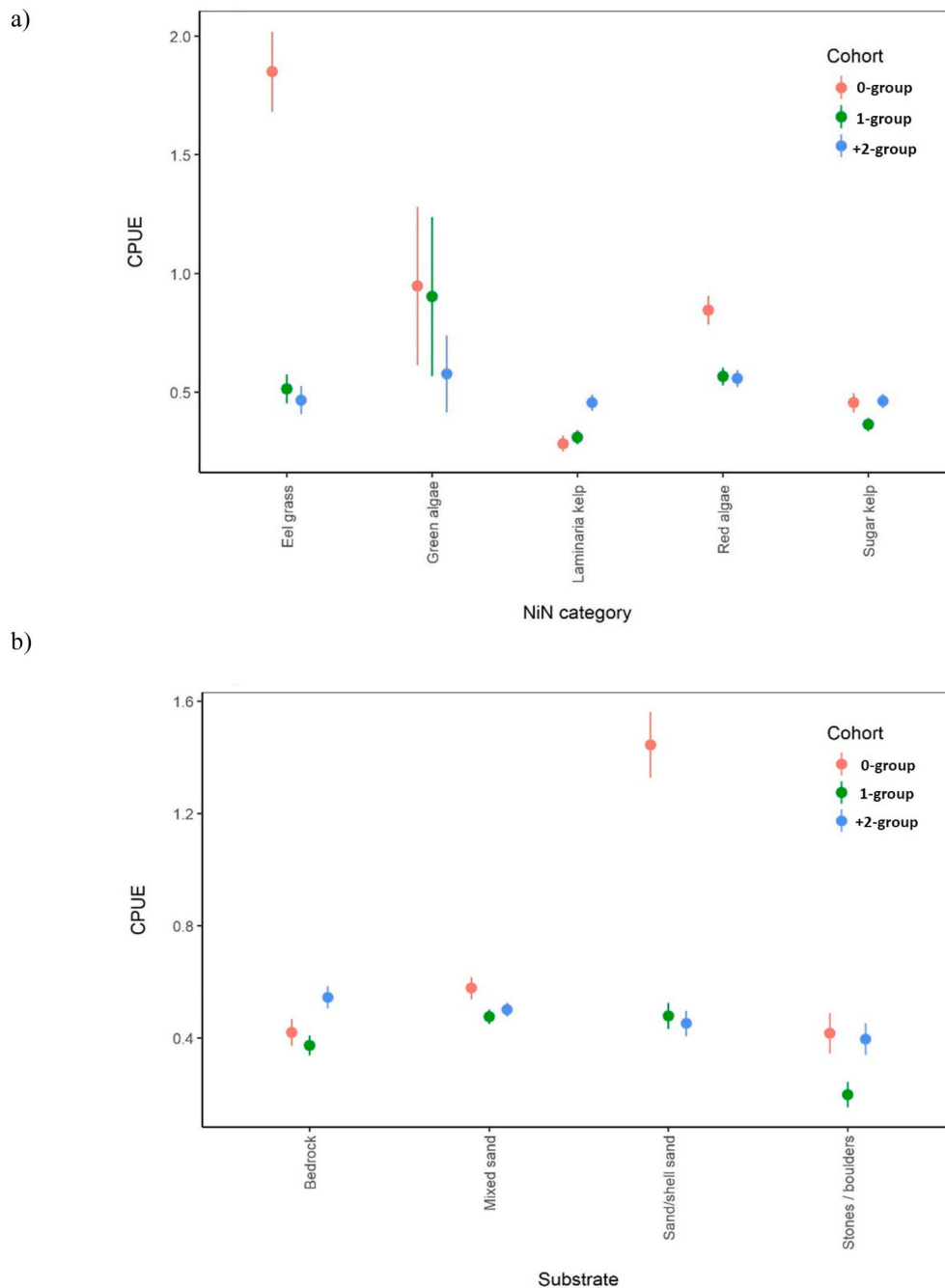
mainly consisted of red algae stations, with three of these contributing most to 0-group cod catches (Fig. 5, Supplementary Fig. 5c). In Glasøysvaet none of the areas had eel grass or red algae, and most 0-group cod in this area were caught on two sugar kelp stations (Fig. 5, Supplementary Fig. 5d).

### 3.5. Cod cohort substrate associations

The abundance of 0-group cod was significantly higher on sand and shell sand substrate than on bedrock stones and mixed sand substrate (Fig. 4b, Table 5). Except for 1-group cod catches on stones/boulders substrate, which were significantly lower than on any of the other substrates, substrate did not have any significant effect on the abundance of 1-group and 2+-group cod (Fig. 4b; Supplementary Tables 4c and d). Most sand and shell sand, and mixed sand substrates were covered either by eel grass or red algae.

### 3.6. Demersal fish community biotic habitat and substrate associations

In addition to cod, the gadoids saithe, pollack, corkwing, goldsinny and ballan wrasse represented the highest catches of other demersal fish species. Across all five years, the mean CPUE was 2.3 saithe, 1.2 pollack, and 1.9 wrasse (Supplementary Fig. 6a – c). The structure of the demersal fish community varied significantly between substrate (Adonis;  $R^2 = 0.03$ ,  $p = 0.001$ ) and biotic habitat types (Adonis;  $R^2 = 0.04$ ,  $p = 0.001$ ) across all spawning areas and years (Supplementary Table 5a). Post hoc tests revealed that the largest differences in demersal fish community composition were between those caught on green algae and eelgrass beds compared to both sugar and laminaria kelp biotic habitats. In addition, the demersal fish community caught in red algae and Laminaria kelp beds (Supplementary Table 5b). Saithe and pollack were common across all nature habitat types in catches in all five years (Fig. 6a, Supplementary Table 6a). Goldsinny and corkwing wrasse generally showed a preference for laminaria and sugar kelp and red



**Fig. 4.** Average cod catch per unit effort by length group (cohort) and different types (for all years combined) of a) primary substrate category, b) biological habitat type (NiN category). Lines indicate the range of standard error.

algae biotic habitats. Particularly a higher average abundance of goldsinny wrasse was observed in areas characterized by sugar kelp, such as Araneset, which largely contributed to the dissimilarity in community composition between sugar kelp and other primary habitat types (Laminaria, green algae, and eel grass). The corkwing wrasse showed some preference for laminaria, sugar kelp, and red algae habitats present particularly at Araneset and Åkvika spawning areas, however few wrasses were observed at Dromnessundet, a site dominated by red algae (Fig. 6a). The shorthorn sculpin and long spined bullhead clearly characterizes demersal fish habitats at eelgrass substrates (Fig. 6a, SIMPER results in Supplementary Table 6a).

SIMPER analysis examining the effect of substrate on demersal fish community composition showed that the greatest dissimilarity was driven by saithe which had a higher average abundance at bedrock sites

compared to all other substrate categories (Fig. 6b). Pollack, goldsinny wrasse, and corkwing wrasse largely contributed to the remaining dissimilarity in composition between substrate types. Highest average abundance of both pollack and goldsinny wrasse were found on stones and boulder substrates, while the corkwing wrasse showed preference for sand and shell sand substrates. Pollack and wrasse were abundant at all spawning areas, except at Dromnessundet where fewer wrasse were caught. Both species, however, generally made the greatest contribution to the community structure at Araneset and Åkvika, areas dominated by mixed sand substrates and stones and boulders (Fig. 6b, Supplementary Fig 3b). The shorthorn sculpin (*Myoxocephalus scorpius*) and longspined bulthead (*Taurulus bubalis*), both ambush predators, characterized demersal fish communities in positions dominated by sand and shell sand substrates (Fig. 6b, SIMPER results in Supplementary Table 6b).

**Table 4**

Post-hoc tests showing the results of the two-way comparisons based on the initial generalized linear mixed effect model of the 0-group cod association with different biotic habitat categories.

Contrast	Estimate	SE	df	z.ratio	p.value
Sugar kelp - Eel grass	-1.78	0.37	Inf	-4.78	<0.001
Sugar kelp - Red algae	-0.83	0.27	Inf	-3.11	0.02
Sugar kelp - Laminaria kelp	0.38	0.31	Inf	1.23	0.73
Sugar kelp - Green algae	-1.18	0.84	Inf	-1.40	0.63
Eel grass - Red algae	0.94	0.37	Inf	2.58	0.07
Eel grass - Laminaria kelp	2.16	0.40	Inf	5.39	<0.001
Eel grass - Green algae	0.60	0.88	Inf	0.68	0.96
Red algae - Laminaria kelp	1.21	0.30	Inf	3.98	<0.001
Red algae - Green algae	-0.35	0.84	Inf	-0.41	0.99
Laminaria kelp - Green algae	-1.56	0.86	Inf	-1.82	0.36

**4. Discussion**

**4.1. Habitat associations of juvenile coastal cod**

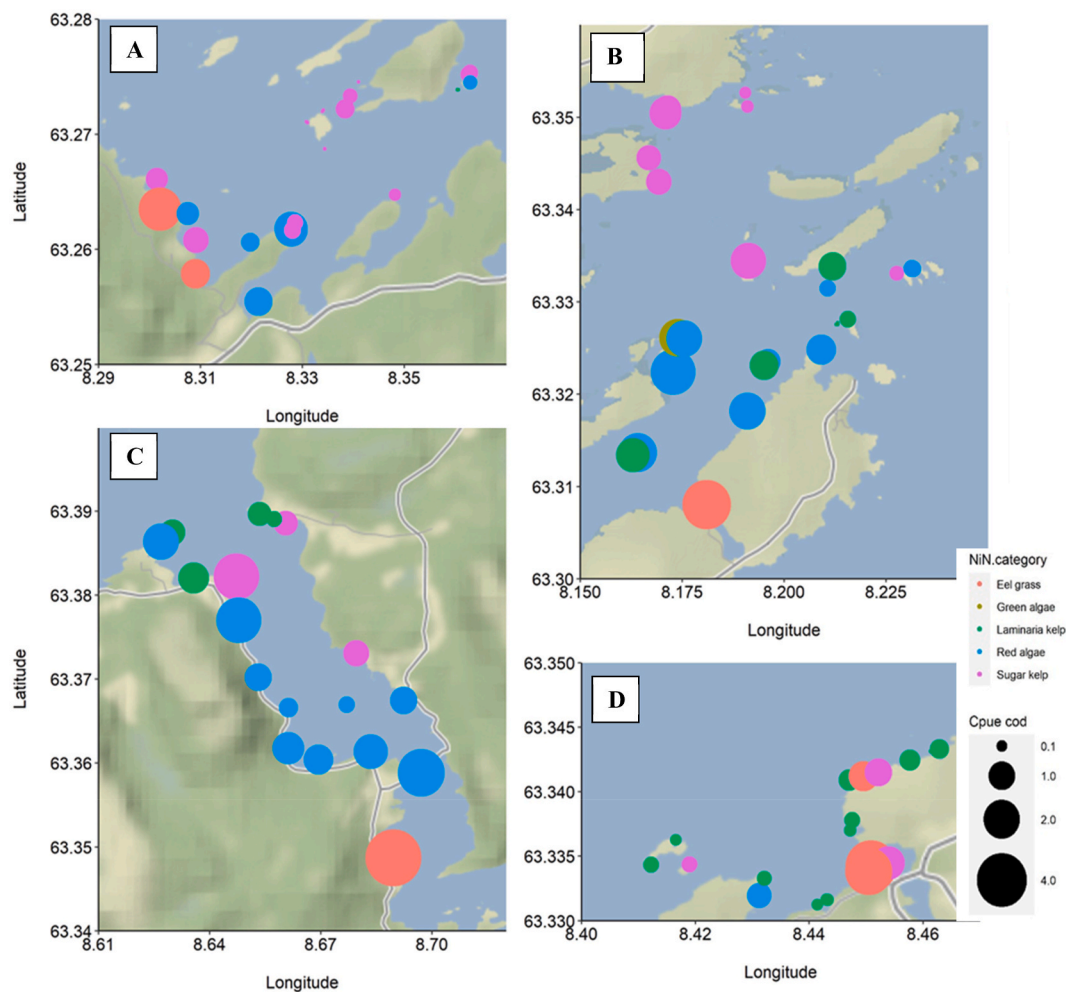
Findings from five years of extensive sublittoral fish surveys clearly identified that eelgrass and red algae biotic habitat types on sand and shell sand substrates provide particularly important habitats for newly settled 0-group juvenile cod less than 20 cm in length. Vegetative cover is known to be important in defining essential habitats for juvenile gadoids because of the shelter it provides from predators and currents

through increased habitat complexity and high primary productivity for feeding (Keats et al., 1987; Hamilton and Konar, 2007; Renkawitz et al., 2011; Lazzari, 2013). Young fish use unvegetated areas close to protective vegetation for foraging (Orth et al., 1984). Indeed, in coastal Skagerrak, south-east Norway, juvenile cod tend to be larger (i.e., grow faster) in vegetated compared to more barren habitats, and individuals inhabiting eelgrass habitats are generally larger than those found amongst kelp (Knutsen et al., 2018). Parts of the Norwegian coast have seen a long-term increase in eelgrass vegetation (Barceló et al., 2016). Even so, the same areas have seen a severe decline in the recruitment of cod and other cold-water gadoids (Barceló et al., 2016; Rogers et al.,

**Table 5**

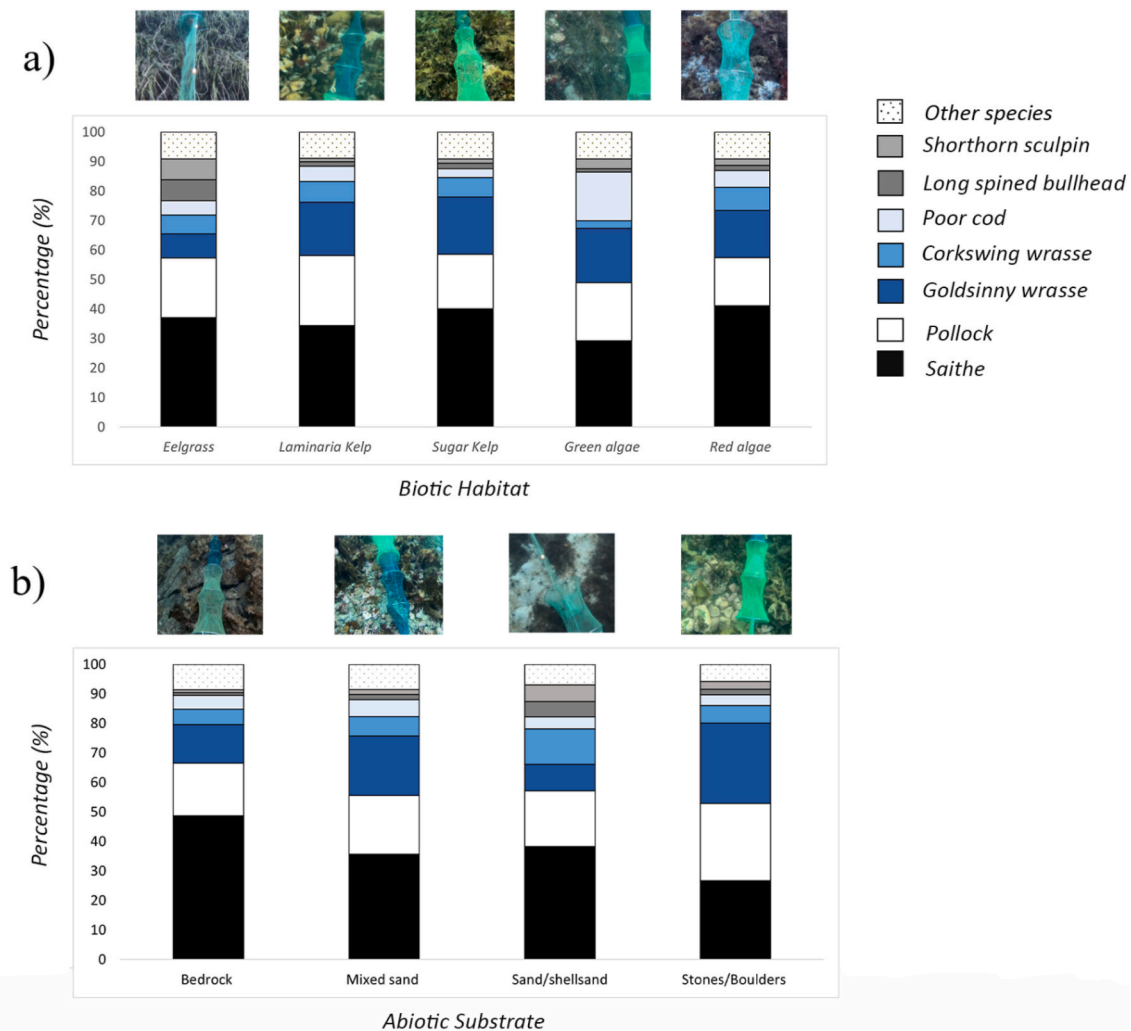
Post-hoc tests showing the results of the two-way comparisons based on the initial generalized linear mixed effect model of the 0-group cod association between the different substrates.

Contrast	estimate	SE	df	z. ratio	p.value
Bedrock - Mixed sand	-0.36	0.32	Inf	-1.14	0.66
Bedrock - (Sand/shell sand)	-1.58	0.39	Inf	-4.02	<0.001
Bedrock - (Stones/boulders)	-0.32	0.73	Inf	-0.44	0.97
Mixed sand - (Sand/shell sand)	-1.22	0.32	Inf	-3.77	<0.001
Mixed sand - (Stones/boulders)	0.04	0.68	Inf	0.06	1.00
(Sand/shell sand) - (Stones/boulders)	1.26	0.72	Inf	1.76	0.29



**Fig. 5.** Average standardised CPUE of 0-group cod caught at a) Araneset, b) Glasøysvaet and Lauvøysvaet, c) Dromnessundet, and d) Åkvika. Circle size indicates average number of cod caught and colours biotic habitat type. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)





**Fig. 6.** Percentage contribution of the main species to the community composition of demersal fish (other than cod) caught in fyke nets at different biotic habitat and abiotic substrates categories.

2017). Potential (and interacting) drivers of this negative trend are climate warming (Rogers et al., 2011; Barceló et al., 2016; Laurel et al., 2017), shifts in the plankton community (Beaugrand et al., 2003; Johannessen et al., 2012) and very high fishing pressure on mature fish (Fernández-Chacón et al., 2015). Recent rising summer sea surface temperatures in the coastal Skagerrak have been linked to deeper waters (~15–20 m) use by cod and low growth potential (Laurel et al., 2017; Freitas et al., 2021). The current study focuses on slightly deeper water (2–8 m) than previous beach seine surveys (on average 3.4 m deep) and therefore provides added knowledge of juvenile cod habitat use in warming waters.

The specific association of juvenile cod with eelgrass beds has previously been documented on both sides of the Atlantic (Tupper and Boutilier, 1995b; Warren et al., 2010; Freitas et al., 2016; Knutsen et al., 2018) and juvenile cod in coastal Newfoundland are known to be more abundant within brown algal beds (Keats et al., 1987; Cote et al., 2001). However, the association with red algae, found here consistently across five years, has previously gone unnoticed on the NW Atlantic. Cod are known for their extensive color variation likely to reflect individual habitat associations and feeding ecology, and a “red cod” color variant can be observed in nearshore habitats in southern Norway while cod on the Labrador coast in Canada holds a similar looking “golden cod” (Wroblewski et al., 2005). In line with our results, the availability of cover from eelgrass and coastal algae was found to be important for a juvenile cod laboratory study from the west coast of Sweden (Borg et al.,

1997). Vegetative cover was used by juvenile cod during daylight to shelter from predators, while adjacent sandy substrate provided nocturnal feeding grounds. In the present study, fyke nets were deployed during both night and day and thus allowed both nocturnal and diurnal habitat-use to be included in the analysis. It is therefore feasible that 0-group cod use lower relief red algae habitats on sandy seafloors during the night to forage, explaining why this association has previously gone undetected in daytime beach-netting studies (Michaelsen, 2012; Johannessen et al., 2012; Sørensen and Pedersen, 2021). A preference of age 0 cod to use sandy substrates at night after the use of more structurally complex habitats during the day was observed by Cote et al. (2001) in Bonavista Bay Newfoundland.

The habitat associations for 0-group cod were not observed for larger and older cod (over 1 year), which had no particular association with any one biotic habitat or substrate type. Cod older than one year (1-group and 2+-group) that measured 20 and 35 cm in length utilized a wider range of sublittoral habitats as nursery grounds around Smøla. The compact structure of eelgrass is thought to be a less optimal refuge for larger cod for which the habitat is likely to provide less coverage and reduce maneuverability (Borg et al., 1997). Larger fish are also less susceptible to predation, meaning larger cod size classes are likely to become less reliant on vegetative cover. Larger 2+-group cod in Porsanger and Ullsfjord, northern Norway were also found to be more loosely associated with macroalgae than younger groups. It was suggested that macroalgae was primarily used for feeding and less so for

predation protection (Michaelsen, 2012). Video, trammel net, and fyke net surveys in the shallow water (<30 m depth) of the Lofoten-Vesterålen region in North Norway also found that cod  $\geq 1$  year had no obvious bottom habitat preference, while 0-group cod were found in less exposed shallow water closer to the shoreline on flat seafloor bottoms with sand, gravel, or small cobbles, along with some vegetation (Sundby et al., 2013). Nevertheless, larger cod are known to still utilize vegetated areas such as eelgrass during night, probably for foraging, and as part of a diurnal vertical migration strategy (Freitas et al., 2016). In the current study, an occasional large cod was caught in positions dominated by eelgrass. The spreading of 2+-group cod into a range of sublittoral habitats will reduce the reliance of this group on eelgrass and red algae habitats favored by 0-group cod. This will have the likely effect of reducing cannibalism (Blom and Folkvord, 1997) from larger 2+-group cod on the smallest 0-group. Age 0 cod in the NW Atlantic measure between 10 and 12 cm total length (Gregory and Anderson, 1997), meaning that a 1-group cod in Norway is of comparable size to a 2+-group in Newfoundland or Nova Scotia. As habitat selection is most likely related to size rather than age, juvenile cod on the NW Atlantic cod could be considered as more likely to remain within eelgrass and red algae refugia longer than their Norwegian equivalents.

#### 4.2. Habitat associations of other gadoids and wrasse

Aside from cod, young saithe and pollack were common across all sublittoral vegetation biotic habitat types but saithe showed a preference for moderately exposed sites dominated by bedrock while the highest abundances of pollack were seen at rough stone and boulder substrates in more sheltered areas. After a pelagic larval stage, 0-group juvenile saithe settle in the shallow rocky intertidal and subtidal zones, where they will remain for two to four years foraging on crustaceans living within macroalgae (Nedreaas, 1986; Rangeley and Kramer, 1995a). The habitat use of pollack has received less research attention than saithe (Rangeley and Kramer, 1995a, b). A study from southern Norway showed that fjord-resident pollack was typically associated with steep walls and boulder habitats, rather than eelgrass and kelp (Freitas et al., 2021). The present study demonstrated that some separation exists between the habitat use of young saithe and pollack, with pollack favoring more sheltered areas and mixed substrates. Mature pollack with ripe gonads have been observed in Masfjorden, western Norway, indicating that the species spawns in Norwegian fjords similar to cod (Heino et al., 2012). Adults are known to feed on gobies, wrasse and crustaceans (Salvanes, 1995), potentially providing some explanation for an overlap in substrate and habitat preference with wrasse.

Habitat associations of wrasses varied among species, but the higher abundances were typically seen in kelp forests and red algae habitats on rough and sand and shell sand substrates. Goldsinny wrasse was associated with sublittoral kelp forests and complex seafloor substrates, while the corkwing wrasse was found more on sand and shell sand habitats and utilized a range of macroalgal habitat types. Previous studies on these species and their habitat association are limited, despite the Norwegian fishery for wrasse increasing rapidly over the past decade, with clear signs of reduced abundance and body size in some heavily fished populations (Blanco Gonzalez and de Boer, 2017; Halvorsen et al., 2017a, b). Along the complex Norwegian coast, these wrasse species form isolated populations and often use home territories within a limited range (Villegas-Ríos et al., 2021). It has therefore been recommended that a network of small marine protected areas (MPA) along the Norwegian coast (~600 m of coastline), would be effective in ensuring sufficient recruitment and protection from fisheries (Halvorsen et al., 2021; Villegas-Ríos et al., 2021). Information on species-specific habitat association will help create coastal MPA networks that protect the substrate and biotic habitats most important for commercially valuable wrasses. However, goldsinny and corkwing wrasse are generally known to use vegetative refuges on complex reef habitats, often in exposed locations (Sayer et al., 1993; Hunter and Sayer, 2009; Skiftesvik

et al., 2015). Here vegetation is used to avoid predation and to feed on small mesoherbivores found within coastal algal forests (Bourlat et al., 2021). No preference was seen for more exposed sites in goldsinny catches in the current study, but results do provide specific evidence of sugar kelp forests being largely utilized for feeding and shelter. The corkwing wrasse male uses filamentous algae to build a nest and unlike the goldsinny wrasse was found to prefer flat sand and shell sand substrates, where filamentous algal coverage was greatest. Such results indicate that an MPA network to protect goldsinny and corkwing wrasse would be best designed to include both complex rocky reef habitats colonized by sugar and laminaria kelp and red algae and lower relief shell sand substrates.

The shorthorn sculpin and long spined bullhead are demersal ambush predators that wait amongst vegetation to catch and feed upon juvenile gadoids and other small fish like gobies (King et al., 1983; Pedersen et al., 2020; Strand et al., 2020). 0-group cod in Newfoundland have been observed to alter their swimming behaviour in the presence of predatory *Myoxocephalus scorpius* and shelter within the upper layer of vegetation (Laurel and Brown, 2006). Catches of sculpin and bullhead in cod nursery areas close to Smøla showed the same preference for eelgrass habitats on sand and shell sand as 0-group cod. A higher abundance of the shorthorn sculpin was also observed in eelgrass habitats compared to those that were unvegetated in Newfoundland (Cote et al., 2013). The increased numbers of juvenile cod within eelgrass beds are therefore likely to have enhanced predation opportunities for sculpin and bullheads, making it a valuable habitat for these species.

#### 4.3. Coastal fisheries management

Understanding the specific relationships between juvenile fish and habitats and substrates “necessary to fish for spawning, breeding, feeding, and growth to maturity” is a key element of fisheries management to conserve and manage coastal gadoid fish stocks (Lazzari, 2013). The results presented here on the habitat associations of cod and other demersal fish with individual biotic habitat types and substrates within or in close vicinity of cod spawning areas are of high practical use to improve current recovery plans and protect other valuable coastal species. For example, the knowledge that red algae habitats upon sand and shell sand substrates are highly important to 0-group cod can be used to prioritize the protection of sublittoral red algae habitats alongside eelgrass to maximize the protection and recovery of coastal cod populations. In addition, new measures to develop coastal marine protected areas should include both sheltered kelp forest habitats on rocky substrates and sand and shell sand substrates to help sustain wrasse communities extracted for aquaculture delousing. Enhanced coastal mapping efforts will identify the distribution of sublittoral biotic habitat types, information that combined with knowledge of important juvenile cod habitats can be used to prioritize areas for protection. Such information can be utilized during decisions on shoreline development and the placement of the coastal industrial facilities which can emit organic and inorganic waste, such as salmon aquaculture facilities. Planning efforts can use available information on coastal fish habitat utilization to place infrastructure where waste and shoreline modification will have a minimal impact on habitats of particular importance for early juvenile coastal cod stages and other demersal fish species.

#### 4.4. Study limitations

Fyke nets are a passive gear that is dependent on movements of the fish to enter the trap. However, the activity and catchability of nearshore demersal fish species can depend on the prevailing physical conditions such as light levels, tides and storms (Villegas-Ríos et al., 2014; Freitas et al., 2021). To overcome such limitations, fishing with fyke nets was carried out over longer periods (1–3 weeks) including night and daylight conditions. Even so, passive gear have the added advantage of sampling a wider variety of habitats, including more rocky reef habitat, compared

to active capture methods such as beach seines. It was observed that traps could be held higher off the seabed by kelp beds on rocky reef than on lower relief habitats such as within eelgrass. This could introduce some effect on capture rates, however we consider that the impacts would be limited as juvenile cod will often move up into higher vegetation layers to feed (Laurel and Brown, 2006). This effect could be minor compared to the variation in catch rates introduced by differences in how young cod use the habitats (resting, feeding or transition). For example, swimming speeds of older juvenile cod were faster in open habitats compared to structurally complex habitats (Cote et al., 2004). Finally, length data was not collected for saithe, pollock and wrasse as the focus of field collections were cod. This meant that any ontogenetic shifts in the habitat use of other species were not resolved. It is known that saithe move away from shallow waters after 2–4 years and that pollock move to deeper water as they become older but still hunt in shallow waters (Nedreaas, 1986; Rangeley and Kramer, 1995a). Wrasse seasonally move to deeper water, but establish territories in shallow water related to breeding, meaning they do not move long distances (Villegas-Ríos et al., 2021). Therefore, even though this study does not show ontogenetic shifts it does provide results on the habitat association of saithe, pollock and wrasse while inhabiting shallow waters.

## 5. Conclusion

This study contributes to a broad and novel understanding of the specific associations of juvenile cod with sublittoral habitats and substrates, specifically eelgrass and red algae habitats, and sand and shell sand substrates. Such information is critical when deciding on habitats that are a priority for protection in coastal cod recovery and management programs. Our study also provides specific biotic and abiotic habitat association of other commercially valuable juvenile gadoids (saithe and pollack), and wrasses widely used in the salmonid aquaculture industry to be incorporated in coastal protection planning.

## Credit statement

Katherine Dunlop – writing - original draft preparation, data analysis, visualization; Arved Staby – writing – original draft preparation, data analysis, visualization; Terje van der Meeren – Conceptualization, field data collection, writing – reviewing and editing; Nigel Keeley – data analysis, visualization, writing – reviewing and editing; Esben Olsen – Conceptualization, writing – original draft preparation, Raymond Bannister – Conceptualization, writing – reviewing and editing; Jon Egil Skjæraasen – Conceptualization, data analysis, visualization, writing – original draft preparation.

## CRedit authorship contribution statement

**Katherine Dunlop:** Writing – review & editing, Writing – original draft, Visualization, Formal analysis, Data curation. **Arved Staby:** Writing – review & editing, Writing – original draft, Formal analysis, Data curation. **Terje van der Meeren:** Writing – review & editing, Resources, Methodology, Funding acquisition, Data curation, Conceptualization. **Nigel Keeley:** Writing – review & editing, Writing – original draft, Visualization, Formal analysis. **Esben M. Olsen:** Writing – review & editing, Writing – original draft, Validation, Methodology. **Raymond Bannister:** Writing – review & editing, Project administration, Methodology, Funding acquisition, Conceptualization. **Jon Egil Skjæraasen:** Writing – review & editing, Writing – original draft, Resources, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization.

## Data availability

Data will be made available on request.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecss.2022.108111>.

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