


Macrophytes as habitat for fish

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As different macrophyte habitats house different distributions of invertebrates, we questioned if differences in the composition of fish in these habitats also could be identified. Additionally, we addressed the question if the fish communities could be affected a few years after sugar kelp beds had shifted to degraded turf habitats. Gill-nets of different mesh sizes were used to catch fish in the then four dominating subtidal macrophyte habitats; the kelp species *Laminaria hyperborea* and *Saccharina latissima*, the turf algae, and the seagrass *Zostera marina*. Each habitat was sampled in South Norway, day and night, and at two following months. Altogether, 31 species of fish and five species of larger crustaceans were caught. Both individuals and species numbers were dominated by wrasses and codfish. The wrasses were most active at daytime, while most codfish entered the habitats at night. Wrasses were mainly occurring in the seaweed habitats, while codfish dominated the seagrass samples. The kelps had highest numbers of individuals, while seagrasses showed highest species diversity. The turf habitats did not result in dramatic negative effects on the fish fauna. Fish can take advantage of other adjacent habitats, a benefit that could be reduced by expanding shifts from kelps to turfs.

Keywords: coastal fish, cod, kelps, macrophyte habitats, seagrass, turf, wrasses.

Introduction

In a changing world, where the coastal marine habitats have been affected by climate change, eutrophication, water darkening, and overfishing, habitat alterations may be followed by changes in associated species. There has been a global decline of the macrophyte habitats kelp forests (Krumhansl *et al.*, 2016) and seagrass beds (Waycott *et al.*, 2009), resulting in regime shifts from perennial seaweeds and seagrasses to ephemeral and more seasonal algal covers, mainly turf or filamentous algae (Baden *et al.*, 2012; Moy and Christie, 2012; Filbee-Dexter and Wernberg, 2018; O'Brian and Scheibling, 2018). This structural degradation in macrophyte composition has negatively altered the species composition and abundance of invertebrate fauna (Christie *et al.*, 2009), and is likely to also have consequences further up the food chain. In comparing shallow, subtidal seaweeds, and seagrass beds within an area, Fredriksen *et al.* (2005) found distinct differences in invertebrate fauna composition, while invertebrate abundances were very similar. By comparing 13 different macrophyte habitats, Christie *et al.* (2009) found differences in both fauna composition and fauna abundance between these different macrophyte habitats (seagrass, brown, green, and red seaweeds). The highest abundances and diversities were found in kelps and seagrasses, and less in turf (different species of filamentous algae). Also, animals seemed to have different preferences for habitat structure and vertical level within the habitat (Christie *et al.*, 2007) and this seemed to affect the fish distribution and feeding preferences (Norderhaug *et al.*, 2005). It could, therefore, be questioned if the different habitats generally house different species of fish, then would changes in macrophyte composition lead to alterations in the fish fauna.

The major macrophyte habitats in southern parts of the North Sea and Skagerrak areas were beds of two species

of kelps (*Laminaria hyperborea* and *Saccharina latissima*), and the seagrass *Zostera marina*. After the year 2002, some of the *Saccharina* beds have been replaced by a composition of turf/filamentous algae (Andersen *et al.*, 2011; Moy and Christie, 2012; Christie *et al.*, 2019). While dominating faunal species showed distinct preferences for one or the other of these four habitats, the faunal groups dominating these habitats were the same, e.g. amphipods, isopods, other small crustaceans, gastropods, bivalves, polychaetes, and echinoderms (Christie *et al.*, 2009). Thus, fish fauna was offered more or less the same type of food in these habitats, and as the most common fish species in these coastal habitats are generalists (Fjøsne and Gjøsaeter, 1996; Norderhaug *et al.*, 2005; Bourlat *et al.*, 2021), their prey organisms should be occurring in all habitats. However, when flipping from kelp forest to turf algae, the density and variety of prey organisms were reduced (Christie *et al.*, 2009; Moy and Christie, 2012), and the three-dimensional structure of the habitat was changed. Similarly, a change from seagrass to a denser mat of filamentous green algae may be negative for small fish, as finding shelter and food may become more difficult (Pihl *et al.*, 1995, 2006).

There are few comparisons of data on fish species associated with different macroalgal species and seagrasses from Scandinavian waters, with the exception of a comprehensive study by Pihl and Wennhage (2002), particularly distinguishing between shallow hard and soft bottom habitats in Western Sweden. As most fish are highly mobile, a more similar composition of fish than of less mobile species could be expected among different habitats in an area. However, Pihl and Wennhage (2002) found clear differences in fish communities between hard and soft bottoms. Norderhaug *et al.* (2005) found more than 20 species of fish in a kelp (*L. hyperborea*) forest, where wrasses (Labridae) and codfish (Gadidae)

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dominated. There, most species were living and feeding inside the kelp forest. The exception was the abundant saithe and a few species that were more pelagic in behaviour, feeding on top of the kelp canopy. Similarly, rich fish fauna was found in the same area later (Kne, 2008). By fishing in seagrasses (Gjøsæter and Paulsen, 2004; Steen *et al.*, 2006; Christie *et al.*, 2014) and seaweed habitats (Norderhaug *et al.*, 2005; Skiftesvik *et al.*, 2015) the families Labridae (wrasses) and Gadidae (codfish) seemed to be the most abundant, while a number of other species were typical but more moderate in density, and similar to Pihl and Wennhage (2002), indicating differences in composition between habitats. Many studies use methods where the numerous small gobiids (Gobiidae) escape the fishing gear (own observations, Steen *et al.*, 2006), and many studies could, therefore, not report the same high diversity found by Pihl and Wennhage (2002) who used both fyke-nets and gill-nets of different mesh sizes, and diving transects.

When fishing in seagrass beds, beach seine is a useful gear (Gjøsæter and Paulsen, 2004; Barcelo *et al.*, 2016), but this is not possible in kelp forests, particularly in *L. hyperborea* beds where a beach seine will get stuck or only catch from the canopy layer of these rigid kelps. For comparison between different macrophyte habitats, gill-nets of different mesh sizes could be a better method (Pihl and Wennhage, 2002). Also, fyke-nets and smaller pots have been used, mainly for wrasses (Gjøsæter, 2002; Skiftesvik *et al.*, 2015), but with the risk of not collecting all species. However, Synnes (2020) achieved high diversity of coastal fish mainly by use of fyke-nets, but with a very large effort over consecutive years.

In South Norway there has, during the years 2000–2002, been a severe shift from earlier sugar kelp beds (*S. latissima*) to turf/filamentous algae reducing the *Saccharina* forests by more than 50% (Bekkby and Moy, 2011; Moy and Christie, 2012). In addition to the persistent and voluminous kelps *L. hyperborea* and *S. latissima* and the seagrass *Z. marina*, this area has a new macrophyte habitat consisting of turf algae that has become more widespread since the observations in 2002, replacing mainly earlier observed *Saccharina* sites (Moy and Christie, 2012). As this led to alterations in macrofauna composition and habitat structure (Christie *et al.*, 2009; Moy and Christie, 2012), the main goal of the present work was to study the distribution of fish among the four most common macrophyte habitats in general, and in particular to evaluate how the observed change in macrophyte habitats may impact fish communities. The study took place at different locations in Skagerrak, South Norway, in 2007. Since then, there has been further dramatic changes in the coastal zone in Skagerrak (Frigstad *et al.*, 2013; Baden *et al.*, 2012), affecting habitats and probably fish fauna by both bottom up and top down processes. A severe reduction in coastal cod (Weijerman *et al.*, 2005; Baden *et al.*, 2012; Östman *et al.*, 2016; Synnes, 2020) has led to an increase of smaller prey fish as gobiids and labrids. On the other hand, a recent extensive fishery of labrids for cleaner fish in fish farms (Halvorsen *et al.*, 2017; Bourlat *et al.*, 2021) may also alter fish community composition. In these areas, the coastal fish community has become more attractive as both codfish and wrasses now are of commercial interest. Our results from 2007 should, thus be of importance for understanding future changes in composition of fish in the wake of changes in anthropogenic, environmental, and biological factors. Effects of changes in fish fauna on shallow benthic ecosystems have been studied to a limited extent earlier, but

are getting increasing focus (Heck and Valentine, 2007; Baden *et al.*, 2012; Christie *et al.*, 2020).

Methods

The study took place in two areas of the Norwegian Skagerrak coast, Grimstad and Homborsund, about 15 km apart (see map, Figure 1). In each area, four sites were chosen, representing one *L. hyperborea* forest (called *Laminaria*), one *S. latissima* forest (*Saccharina*), one turf algae bed (Turf, a composition of several ephemeral and bushy seaweeds, see Moy and Christie, 2012), and one *Z. marina* bed (*Zostera*). All beds were clearly separated, each with a sufficient areal extent for creating a continuous habitat for repeated fishing. The *Laminaria* sites were situated on wave-exposed outer archipelago, more or less continuously dominated by *Laminaria* forest. The *Saccharina* sites were selected on moderately wave-exposed coastline dominated by *Saccharina*, with a forest size of 15–50 hectare. The *Zostera* meadows were 2.5 hectare and 1.5 hectare respectively, and both with strong and dense eelgrass shoots. The turf sites were on moderately exposed sites where *Saccharina* forest had been lost (Bekkby and Moy, 2011). The same fishing method was used in all four habitats in both areas, during the day (12 h) and night (12 h), in September (25–27) and October (8–10). Altogether, eight fishery samples were collected from each habitat.

Fishing was conducted with a combination of trammel net (30 m long, 1.8 m deep, smallest, and inner mesh size 52 mm) and a multi-mesh gill-net that were 30 m long and 1.5 m deep. The multi-mesh nets were divided in 2.5 m panels with mesh sizes 43.0, 19.5, 6.5, 10.0, 55.0, 8.0, 12.5, 24.0, 15.5, 5.0, 35.0, and 29.0 mm. This net design is mostly used in fresh water and often referred to as a NORDIC gill-net (Appelberg *et al.*, 1995). Also, fyke-nets (double eel traps connected with a net) were used by the September fishing in all habitats, but since the gill-nets caught a high number of fish and the fyke-nets caught almost nothing (7% of the crabs, and 1.8% of the fish), the fyke-nets were not used after the September fishing, and the catches are not presented further. The gears were placed horizontally at the bottom at a depth of 4–5 m in all habitats.

The fish were immediately released from the nets and killed. Species identification and total length and weight measurements were done when coming back to the lab within a short period of time. All fish representing different nets and mesh sizes were lumped and called one sample catch.

The data were plotted and analysed using the R software (R Core Team, 2020). Graphics were for the most part produced using the *ggplot2* and *patchwork* packages (Wickham, 2016; Lin Pedersen, 2020). The number of species and the species diversity (as measured by the Shannon index) were calculated and analysed using ANOVAs (which was deemed appropriate based on plot diagnostics). The variation in species composition was then further explored using both detrended correspondence analysis (DCA) and non-metric multidimensional scaling (NMDS) using the *decorana* and *metaMDS* functions available in the *vegan* package (Oksanen *et al.*, 2019). Comparing these two fundamentally different ordination techniques, paves the ground for solid evaluation of whether the ordination results can be trusted. Comparisons were made using the *protest*-function also available in the *vegan* package, which repeatedly performs a symmetric Procrustes analyses (in this case 999 times), to estimate the significance of the

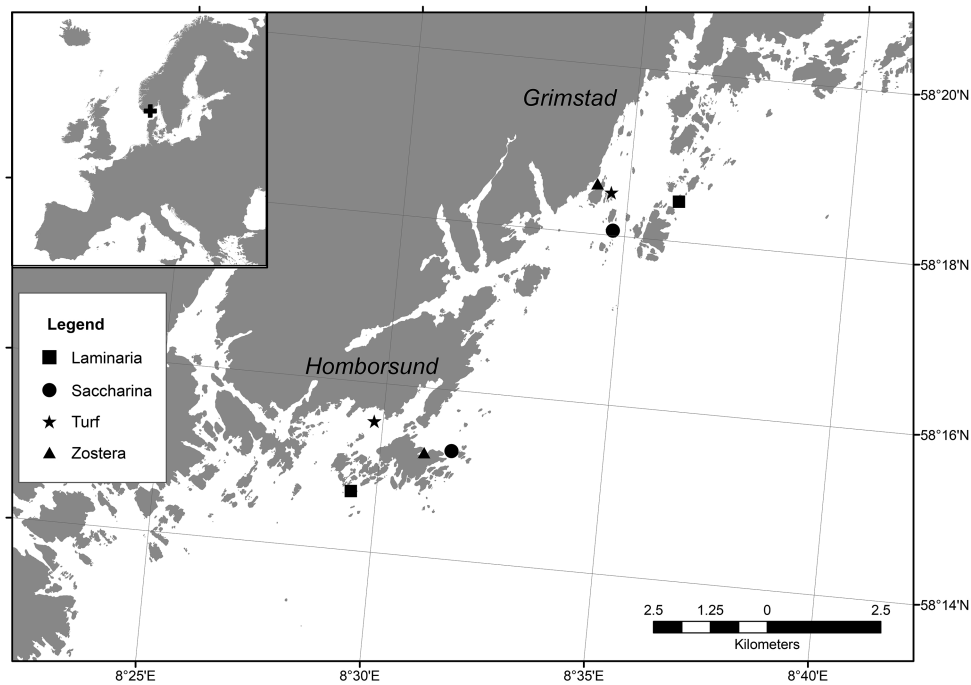


Figure 1. Map of the sampling sites in Skagerrak, South Norway.

similarities between the results from the two different ordination methods. A permutational multivariate analysis of variance (*adonis*-function in the R-package *vegan*) was performed on the results from the ordination (the site scores) in order to partition the variation in site scores among: (1) sampling area, (2) habitat type, and (3) day/night.

Results

Altogether, 1601 fish and 77 larger crustaceans were caught in the study, representing 31 species of fish and five species of crustaceans. The most common fish families were Labridae (wrasses, five species) and Gadidae (codfish, seven species; Table 1). The goldsinny wrasse (*Ctenolabrus rupestris*) was the most abundant species overall. Crustaceans were mainly the crabs *Cancer pagurus* and *Carcinus maenas*.

Among the habitats, 700 individuals were caught in *Laminaria*, 353 individuals were caught in *Saccharina*, 340 individuals were caught in Turf, and 285 individuals were caught in the *Zostera* beds (Table 1). Table 1 also shows the total number of each species caught in each of the four habitats, and the groupings of species in the following groups: codfish, wrasses, demersal fish (other than codfish and wrasses), pelagic fish, and crustaceans. A total of 14 species were classified as demersal fish in addition to the demersal species of codfish and wrasses.

Species numbers and species diversity (measured by the Shannon index) were significantly higher in night than in day samples (tested by ANOVA, $\alpha = 0.025$, $p < 0.001$). Both varied with habitat type, though significantly only in the case of diversity ($\alpha = 0.025$, $p = 0.02$; Figure 2). The highest species numbers and diversity of catches were found in eelgrass beds. Sample location did not explain any significant part of the variation when tested (Table 2). The site scores from the DCA, i.e. the positions of the different samples, were further investigated using PERMANOVA. The result showed

that the observed patterns in species composition related to both day/night and habitat type were clear and significant, while the species composition was generally similar between sampling areas (Table 2).

There were significant patterns in the distribution of fish species among day and night catches and among the four different habitats (see Table 2). The wrasses were generally most abundant in the three macroalgal habitats, while codfish were most abundant in the seagrass meadows (Table 1 and Figure 3). Codfish amounted to only 9% of the total catch in the *Laminaria* beds, while the number was as high as 51% in the *Zostera* meadows. The results indicate that codfish, to a lesser extent, utilize the turf during daytime but may intensively hunt in turf areas as well as in the other vegetation types during night. The saithe (hunting over long distances) and the more stationary corkwing wrasse were most numerous in the Turf beds (Table 1). Figure 3 shows the overall diurnal pattern of catches. The catches reflect that wrasses were generally most active during daytime, and codfish during night. The codfish seemed to enter the macrophytes (less in *Laminaria* than other habitats) at night. Whiting was only caught in *Zostera* during daytime but were evenly caught in both Turf and *Zostera* during night. The common poor cod was only caught by night and mostly at *Saccharina* sites. Pelagic fishes like mackerel and sea trout were (almost) only caught in Turf and *Zostera* meadows (daytime). The demersal fish species seemed to be most active at night (Figure 4). The overall distribution of all fish species in day as compared to night catches, and comparisons among the four different habitat types are illustrated in more detailed in the online Supplementary Appendix Figures A1, A2, and A3.

The 56 cod (*Gadus morhua*) in the samples, ranged between 14 and 60 cm in length (Figure 5). The measured weight ranged between 28 and 2408 g, the largest being the heaviest fish caught in the present study. There was a peak in cod of size class 30–40 cm, with weights ranging between 300 and 500 g.

Table 1. Species name of fish and crustaceans caught in the study. Total number of fish from each species, and number of each species in the different habitats is given. The species are also given a code name for the DCA plot. NB: the earlier *Labrus bimaculatus* and *Labrus mixus* are sex variants of *L. mixus* (and red or blue coloured).

Latin name	Code	English name	<i>Laminaria</i>	<i>Saccharina</i>	Turf	<i>Zostera</i>	Total day/night
Codfish							
<i>Gadus morhua</i>	GAMO	Atlantic cod	11	7	21	17	3/53
<i>Pollachius virens</i>	POVI	Saithe	21	41	49	38	9/140
<i>Pollachius pollachius</i>	POPO	Pollack	27	22	23	40	40/72
<i>Merlangius merlangus</i>	MEME	Whiting/Merling	2		10	43	33/22
<i>Trisopterus minutus</i>	TRMI	Poor cod	2	31	12	10	0/55
<i>Merluccius merluccius</i>	MERL	Merluccid hake	2		1	1	0/4
<i>Raniceps raninus</i>	RARA	Tadpole fish		1			0/1
Wrasses							
<i>Labrus bergylta</i>	LABE	Ballan wrasse	102	40	27	7	128/48
<i>Ctenolabrus rupestris</i>	CTRU	Goldsinny wrasse	404	107	59	28	360/238
<i>Symphodus melops</i>	SYME	Corkwing wrasse	73	46	95	28	218/24
<i>Centrolabrus exoletus</i>	CEEX	Rock cook	27	11	2		40/0
<i>Labrus mixtus</i>	LABB	Cuckoo wrasse	6	9	11		0/26
Demersal fish							
<i>Myoxocephalus scorpius</i>	MYSC	Shorthorn sculpin				3	0/3
<i>Taurulus bubalis</i>	TABU	Longspined bullhead	8	5	1	6	4/16
<i>Trachinus draco</i>	TRDR	Greater weever				1	0/1
<i>Eutrigla gurnardus</i>	EUGU	Grey gurnad			1		0/1
<i>Callionymus lyra</i>	CALY	Common dragonet		1	2		1/2
<i>Cyclopterus lumpus</i>	CYLU	Lumpfish/lumpsucker	1		1	4	5/1
<i>Pholis gunnellus</i>	PHGU	Rock gunnel/Butterfish	1			1	1/1
<i>Syngnathus sp</i>	SYNG	Pipefish	1	2	1		1/3
<i>Gobius niger</i>	GONI	Black goby			4		0/4
<i>Gobisculus flavescens</i>	GOFL	Two spotted goby		1	1		2/0
<i>Pleronectes platessa</i>	PLPL	European plaice			1	9	3/7
<i>Microstomus kitt</i>	MIKI	Lemon sole		1			0/1
<i>Scophthalmus rhombus</i>	SCRH	Brill				2	1/1
<i>Anguilla anguilla</i>	ANAN	European eel				1	0/1
Pelagic fish							
<i>Scomber scombrus</i>	SCSC	Mackerel	1	1	6	3	10/1
<i>Trachurus trachurus</i>	TRTR	Atlantic horse mackerel			5	4	0/9
<i>Ammodytes tobianus</i>	AMTO	Lesser sand eel				1	0/1
<i>Salmo trutta</i>	SATR	Sea trout			2	4	6/0
Larger Crustaceans							
<i>Carcinus maenas</i>	CAMA	Green shore crab			2	10	0/12
<i>Cancer pagurus</i>	CAPA	Edible crab	10	27	3	22	1/61
<i>Galathea intermedia</i>	GAST	Squat lobster	1				0/1
<i>Pagurus sp</i>	PAGU	Hermit crab				1	0/1
<i>Macropodia rostrata</i>	MARO	Spider crab				1	0/1
		TOTAL	700	353	340	285	1 678

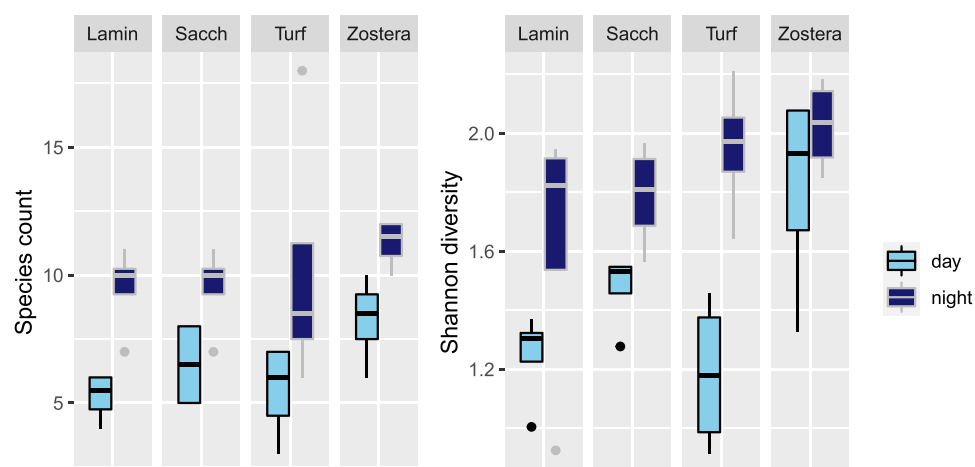
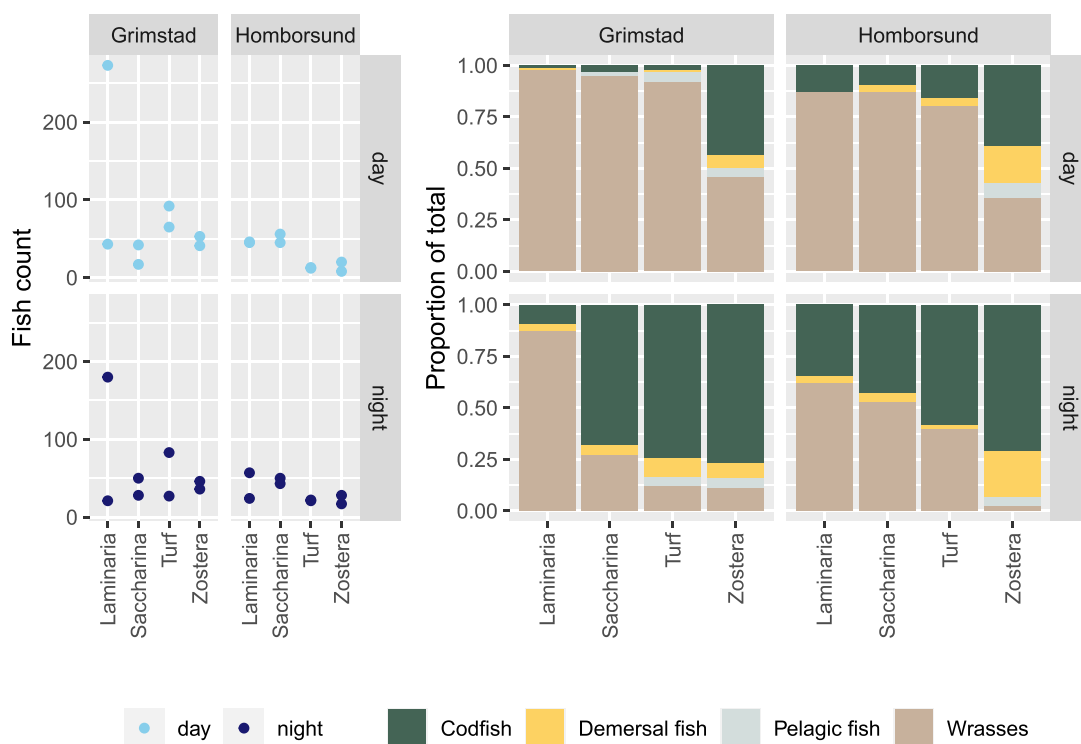


Figure 2. Species numbers (fish and crustaceans) and Shannon diversity index plotted for each habitat in day and night samples.

Table 2. Permutational Multivariate Analysis of Variance (PERMANOVA) of the site scores from the DCA-ordinations.

Variable	Df	Sums of Sqs	Mean Sqs	F. model	R ²	Pr (> F)	
Day/night	1	16.977	16.9770	32.581	0.43 364	0.001	***
Habitat type	3	8.348	2.7827	5.340	0.21 323	0.001	***
Sampling area	1	0.277	0.2771	0.532	0.00 708	0.641	
Residuals	26	13.548	0.5211	0.346			
Total	31	39.150	1.0000				

**Figure 3.** The total fish count in each sample (left, some September and October samples are overlying), and the distribution of four groups of fish in proportions of total (right) with September and October samples pooled.

The correlation between the DCA and the NMDS ordination diagrams was significant ($\alpha = 0.05$, $p < 0.001$) with a coefficient of 0.82. The DCA plot (Figure 6), shows a clear diurnal pattern in fish fauna composition, but also patterns related to habitat type.

The site scores (dots in Figure 6) position the samples in relation to each other according to similarities in species composition. Samples that are plotted close to each other are more similar than samples with more distance between them. The day and night samples were clearly separated along both main ordination axes, which means that there is a prominent diurnal pattern in the species composition that is consistent across all four habitats. Within the day and the night samples, species composition seemed generally similar within habitat type irrespective of sampling area (Grimstad or Homborsund).

The species scores (plotted as text in the background of Figure 6) indicate where the estimated optima of the given species lie, in other words, where the abundance is expected to be the highest. This means that the species placed close to the night samples in the DCA-diagram (within the ellipse) are species likely to have higher numbers at night, and lower

at day. Day samples were separated from night samples by generally higher abundances of wrasses like ballan wrasse (LBE), corkwing wrasse (SYME), and rock cook (CEEX), while night samples had generally higher abundances of cod (GAMO), saithe (POVI), longspined bullhead (TABU), edible crab (CAPA), and pollack (POPO). This diurnal pattern across habitats is displayed on a group level in Figure 3.

Discussion

This study shows a high number of fish species associated with the different macrophyte habitats. The total number of species was higher than other studies from Norwegian kelp forests (Norderhaug *et al.*, 2005; Kne, 2008), but less than what Pihl and Wennhage (2002) found in their comprehensive study in Sweden. Essential for results on diversity is the efficiency of the gear used, the variety of habitats, and the fishing effort. In comparison to Pihl and Wennhage (2002), this study did not catch the smallest species among the gobids (except for the abundant two spotted goby) and sticklebacks. Such tiny nekton may be caught by use of beach seine (Gjøsæter and Paulsen, 2004), a gear useful in seagrass beds while not in the

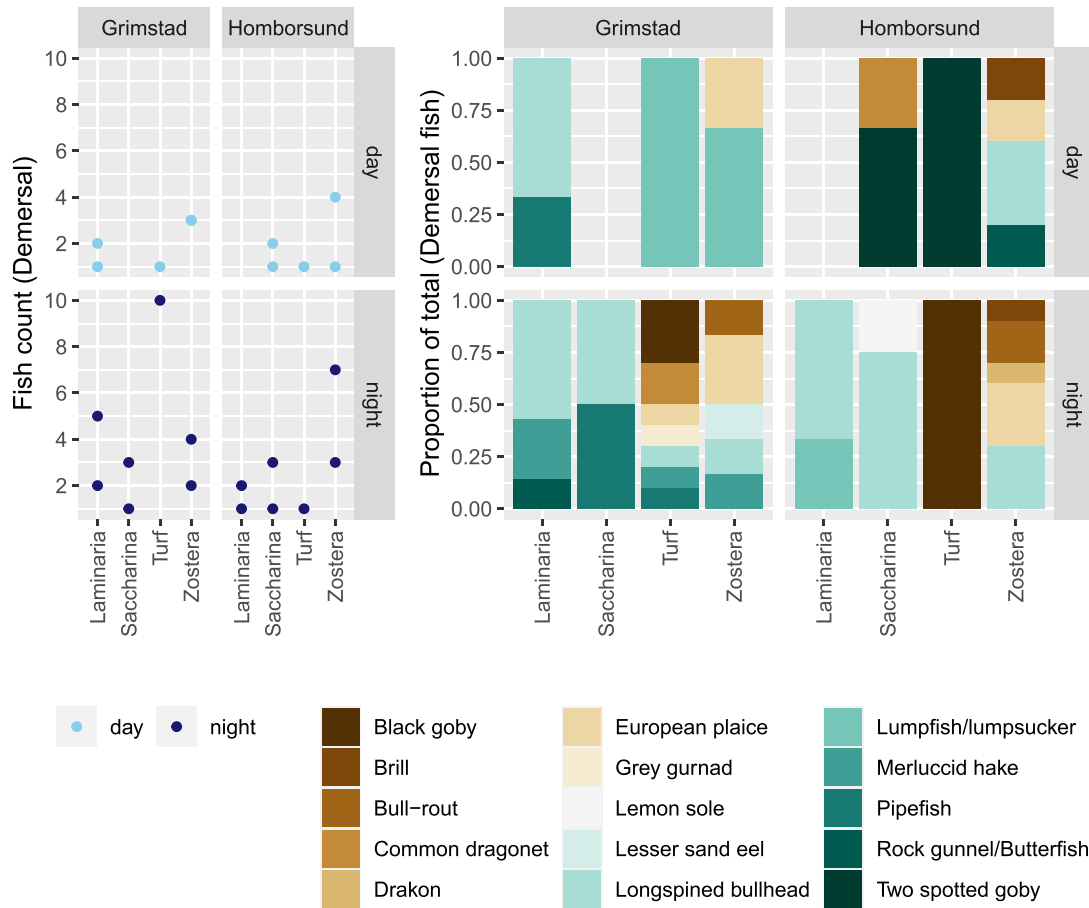


Figure 4. The total fish count categorized as “Demersal fish” (see Table 1) in each sample (left), and the distribution of the species in proportions of total (right) with September and October samples pooled.

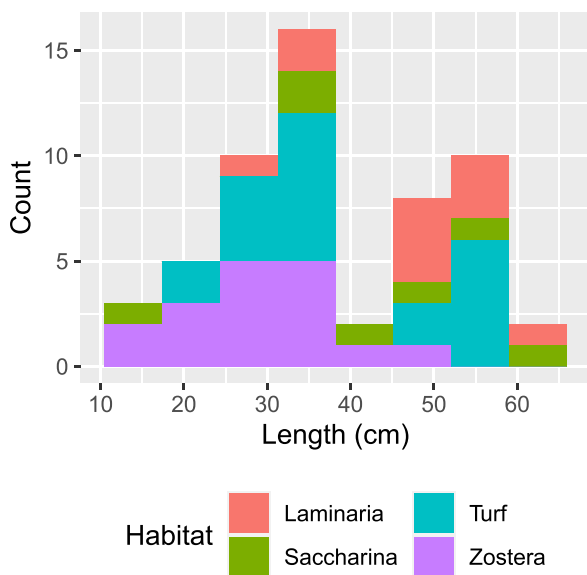


Figure 5. Length distribution of cod pooled over sampling areas and September and October catches.

seaweed habitats. It was difficult to decide on gear that could compare these four habitats better than the different gill-nets placed down into the macrophyte habitats. The catches of stationary demersal species together with pelagic ones indicate

representative fishing across the habitats and across the vertical levels within each habitat. Further, visual or camera observations that may observe smaller individuals or reveal eventual artefacts (Peterson and Black, 1994) may not be relevant for comparison of day and night, and the now supplementing eDNA methods was not “available” at that time. Most of the fish species and individuals in the samples were demersal and have been found to feed on prey organisms typical for macrophyte beds (Fjøsne and Gjørseter, 1996, 1997; Norderhaug *et al.*, 2005; Bourlat *et al.*, 2021), while only a few were more pelagic and highly mobile (as saithe and mackerel). The pattern of fish distribution was similar among the two areas and among the 2 months investigated. Differences in patterns were found as a combination between differences in diurnal activity and habitat preferences among the species. In order to get a representative picture of the distribution of coastal fish species and fish numbers in any given area, different habitats should be sampled at both day and night and with the appropriate gear.

While the kelps/seaweeds were preferred by the wrasses, the seagrass beds housed relatively more codfish and other demersal fish. In particular, the daytime samples showed differences between soft bottom (seagrass) and the three reef habitats. Wrasses are found to be most common among seaweeds at rocky reefs (Gjørseter, 2002; Skiftesvik *et al.*, 2015). In this study, wrasses were most abundant in the *Laminaria* kelp forest, but also common in the *Saccharina* beds and at the Turf habitat. The large numbers of wrasses in the



Figure 6. The results from the DCA-ordination of the species composition (fish and crustaceans) in each sample. Colouring corresponds to habitat type, while the size of the dot reflects the number of different species found in the sample. The estimated species optima (see Table 1 for codes) are plotted as text in the background.

Laminaria samples at daytime contribute to the difference between this habitat and the others. The corkwing wrasse was found to prefer the Turf beds and were observed to defend their nests made by filamentous algae (own observations by diving, see also Bourlat *et al.*, 2021). Wrasse were mainly active at day, while codfish were mainly found in seagrass at daytime, and more frequent in all habitats at night. While the green crab seemed to be attracted to seagrass beds, the edible crab was more evenly distributed among the habitats, except for in Turf where crab catches were low. The distribution catches of crabs could be affected by attraction to fish prey fastened in the gill-nets (crab foraging attacks on the fastened fish can spoil exact weight measurements).

The macroalgal beds, and particularly the *Laminaria* forest, had the highest numbers of fish, mainly due to the high number of small wrasses in these habitats. Also, *Laminaria* forms the largest and most upright of the macrophyte species, the one with most suitable shelter (three-dimensional and forest-like), and also with most prey organisms in a variety among vertical levels between the bottom and the canopy (Norderhaug *et al.*, 2005; Christie *et al.*, 2007). These

three-dimensional characteristics are less pronounced for the *Saccharina* and Turf habitats, as reflected by the number of fish catches in the present study. In a comparison of 13 different macrophyte systems as habitat for fauna, *Laminaria* was the one with highest numbers of fauna (Christie *et al.*, 2009), but high macrofauna diversity and density has also been found in seagrasses and other seaweeds (Fredriksen *et al.*, 2005; Christie *et al.*, 2014), and lower numbers in smaller seaweeds belonging to the group “turf” (Christie *et al.*, 2009). However, with number of invertebrate species between 50 and 100 per sample of macrophyte, densities between 20000 and 150000 individuals per m² (Christie *et al.*, 2009), with high secondary production and short-generation periods giving high turnover rates (Christie and Kraufvelin, 2004; Norderhaug and Christie, 2011), all these factors indicate food items to be plenty in all four habitats. A possible difference could be the more three-dimensional feeding possibilities for fish underneath the *Laminaria* canopy (see Norderhaug *et al.*, 2005; Christie *et al.*, 2007), particularly where epiphytic algae form rich microhabitats on the kelp stipes (Christie *et al.*, 2003).

The fish community similarities between the *Saccharina* and Turf beds may indicate that the shift from *Saccharina* to Turf (see Bekkby and Moy, 2011; Moy and Christie, 2012) had not severely impacted the fish fauna found in 2007. However, habitat structure (obviously) and prey species composition (Christie *et al.*, 2009) varies between the four habitats, and the present study has shown clear differences in the associated fish communities as well. Our study indicates that the different species of fish may use the habitats differently during day and night. The importance of the different habitat types seems also to vary among the different life stages in the life cycle of some fish species. The overall diversity of the coastal systems does, therefore, most certainly depend on the availability of a range of different vegetation types. In 2007, the fish caught in the Turf habitat could benefit from structurally more voluminous habitat types in the surroundings (see Figure 1). If the negative trend with increasing Turf and/or filamentous algae cover replacing kelps continues, negative impacts on the fish fauna may become very pronounced over time. While the differences in potentially prey species associated with the different macrophytes were mainly at species level belonging mainly to the same higher level of taxa within crustaceans, gastropods, bivalves, and polychaetes, the reduced abundance in Turf (Christie *et al.*, 2009) may be reflected in fish abundance. Dramatic and rapid alterations in near shore ecosystem functions and services may, therefore, emerge as more and more of the perennial macrophyte vegetation becomes pressured (Pihl *et al.*, 2006), leaving mostly seasonally fluctuating habitats if perennials are overgrown by impenetrable filamentous algae mats in summer (Pihl *et al.*, 1995, 1999). By an extensive deterioration of benthic macrophyte habitats due to climate change, water darkening, eutrophication, overfishing, and other stressors, further similar studies combined with more detailed studies of spatial distribution of the habitats may uncover poorer fish assemblages in the expanding turfing habitats than what was found in this study.

For a comparison of fish between such three-dimensional habitats, the choice of gear is essential. In seagrass beds, the beach seine has been used with success during long-term studies in the same region (Gjøsæter and Paulsen, 2004; Steen *et al.*, 2006; Espeland and Knutsen 2019; Barceló *et al.*, 2016), and labrids have been sampled in pots or fyke-nets (Gjøsæter, 2002; Skiftesvik *et al.*, 2015). The results from the present study indicate a variety of gill-net's mesh sizes to be the most suitable for comparisons of catches. The average CPUE (catch per unit effort) was 52.2 for fish in this study, compared to 8.5 by Synnes (2020) using fyke-nets. Synnes (2020) recorded 34 species of coastal fish in 930 fyke-net hauls over a 3-year period. Although a limited effort, the present study indicates efficient methods for collecting coastal fish in different near-shore habitats for comparisons, that is essential in a timeline of changing habitat structures.

The present study performed in 2007 may be an important baseline for investigating potential drivers in changes in abundances of economically and ecologically valuable fish species such as cod and wrasses. Although cod (*G. morhua*), already in 2007, were described as a fish species with decreasing abundance, the reduction of this species has continued during the last decades, as the coastal ecosystems in Skagerrak have undergone dramatic changes (Weijerman *et al.*, 2005; Östman *et al.*, 2016; Synnes, 2020). The cod is now severely threatened in the area (Synnes, 2020) and particular older

year classes of Atlantic cod are rare, in contrast to indications given by the size distribution presented in the present study. As a response to the drastic reduction in abundance of the important top predator coastal cod, *G. morhua* (Cardinale and Svedäng, 2004; Baden *et al.*, 2012), several mesopredators have increased considerably in abundance (mesopredator release *sensu* Prugh *et al.*, 2009). Smaller fish and crustacean predators (mesopredators) have been reported to increase in rocky shore ecosystems forcing new top down effects on the benthic invertebrate fauna (see Christie *et al.*, 2020) and contribute to changes in trophic cascade interactions (e.g. Eriksson *et al.*, 2009, 2011). In contrast to the increase in mesopredators, some among these (the wrasses) have been heavily caught in traps at some sites for transfer to fish farms for cleaning ectoparasites, leading to local variations in fish assemblages (Halvorsen *et al.*, 2017). Overfishing and the consequential predator release, as well as intense local harvesting of more stationary mesopredator species (like wrasses) is expected to have substantial impacts on near-shore ecosystems. Thus, the present study may be repeated, in order to get an indication of how fish fauna have been affected by a wide range of different pressures (i.e. climate change, eutrophication, and overfishing) over the recent decades.

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Data availability statement

The data underlying this article will be shared on reasonable request to the corresponding author.

Supplementary data

Supplementary material is available at the ICESJMS online version of the manuscript.

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