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Attraction of cod *Gadus morhua* from coastal spawning grounds to salmon farms

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ABSTRACT: Wild fish aggregate at aquaculture net-pens, but the underlying mechanisms are not fully understood. This study examined how salmon farms attract coastal Atlantic cod *Gadus morhua* from their inshore spawning grounds. Acoustic receivers were deployed at 5 known cod spawning grounds and 6 salmon *Salmo salar* farms located at varying distances from these grounds in a mid-Norway study site. Cod were caught at each spawning ground annually from 2017–2019, fitted with acoustic transmitters and released (n = 535). A total of 289 tagged cod (54%) were detected at the salmon farms, with more cod detected at farms closest to the focal spawning grounds and at operational farms. The latter result is likely linked to the availability of feeding opportunities at farm locations. Those cod that were detected by the receivers spent less time at farms farther from their release locations. For the farm-associated cod, 70% were detected for <1 wk at the farms. However, 48 cod spent >1 mo close to the farms, with 1 individual staying 720 d underneath the farm. A total of 135 cod visited 2 or more farms, with farms in proximity more connected in terms of inter-farm movement. Some of the cod utilizing these local spawning grounds likely have considerable dietary input from salmon feed.

KEY WORDS: Acoustic telemetry · Atlantic cod · *Salmo salar* · Spawning · Fish farms · Network

1. INTRODUCTION

There are more than 1150 locations currently licensed for salmonid farming along the Norwegian coast (https://www.fiskeridir.no/English/Aquaculture/Statistics/Atlantic-salmon-and-rainbow-trout). Farming of salmonids is mainly carried out in open net-pens, allowing the transfer of diseases, organic waste (feed pellets and feces) and chemicals to the surrounding water masses. The production of salmonid fishes, mainly Atlantic salmon *Salmo salar*, amounted to 1.4 million t in 2019, whilst the corresponding feed usage was 1.8 million t (Norwegian Directorate of Fisheries 2020). The amount of organic waste varies between sites, seasons, and production stage, but has been estimated to typically be around 3–5% of the total feed usage at each production site (Otterå et al. 2009, Svåsand et al. 2015).

Wild fish are known to aggregate around salmon farms (Dempster et al. 2009) and feed on uneaten pellet feed and feces (Carss 1990, Skog et al. 2003). This feeding opportunity is assumed to be one of the

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main reasons for the aggregation of wild fish at farms (Tuya et al. 2006, Dempster et al. 2011, Fernandez-Jover et al. 2011). In terms of biomass, the most common species around Norwegian farms are saithe *Pollachius virens*, Atlantic haddock *Melanogrammus aeglefinus*, Atlantic cod *Gadus morhua*, and mackerel *Scomber scombrus* (Dempster et al. 2010). Though there are both seasonal and regional variations in species composition and abundances, the number of fish gathering around farms may be considerable.

The physical farm structure, acting as a fish aggregating device (FAD) or artificial reef, as well as the provision of food are considered the main reasons wild animals are attracted to marine finfish cages (Callier et al. 2018). FADs are attractive to the fish since they provide shelter and supply habitats that aggregate prey species, which in turn may attract larger predatory fish (Serra Llinares et al. 2013), while feed waste and feces from the farms provide a direct trophic supplement to wild fish (Dempster et al. 2011, Sanchez-Jerez et al. 2011, Uglem et al. 2014). Other farm activities such as boating, noise from feed machines, or the use of continuous light to prevent maturation, may both attract and repel wild fish (Callier et al. 2018). Fish farms may therefore influence the distribution, behaviour, resident time, age and size of the community, and the diet of the wild fish. As such, farms may affect the fish community through altered life histories, gross chemical composition, and behaviour.

Acoustic tagging studies in a northern fjord system demonstrated that numerous saithe aggregated around multiple farms, and that a high frequency of inter-farm movements led to high connectivity between farms (Uglem et al. 2009). However, the spatial movement of the commercially valuable coastal Atlantic cod, also commonly observed in association with fish farms, has been less studied. In response, Skjæraasen et al. (2021) studied the possible impact of salmon farms on the spawning dynamics of cod on monitored spawning grounds. In the present study, we focused on the farms; determining the extent of attraction of Atlantic cod to the salmon farms from the local spawning grounds as well as quantifying cod movement between farms. Atlantic cod were captured at 5 known spawning grounds, fitted with acoustic telemetry tags and released at their capture ground in the years 2017–2019. Movements of these cod were subsequently monitored through a grid of receivers placed on the spawning grounds and at the 6 salmon farms closest to these clusters.

2. MATERIALS AND METHODS

2.1. Grid deployment and fish tagging

Details of telemetry receiver grid deployment, detection range testing, the capture of fish, the fish tagging procedure, and the transmitter specifications are given in (Skjæraasen et al. 2021) and therefore not reiterated in detail here. In brief, Innovasea VR2W receivers were deployed at 33 fixed stations in a semi-exposed coastal region in mid-Norway in November 2016. These receivers detected and stored acoustic signals emitted from acoustic transmitters, with an estimated detection efficiency of ~50% at 500 m from the transmitter (see Skjæraasen et al. 2021). Receivers were moored in catch clusters (CC) at 5 known cod *Gadus morhua* spawning grounds (Skjæraasen et al. 2021): Glasøysvaet (CC1), Lauvøysvaet (CC2), Araneset (CC3), Åkvika (CC4) and Dromnessundet (CC5). Single receivers were also placed on 6 salmon *Salmo salar* farms neighboring these spawning grounds (Fig. 1; Stns 28–33). Skjæraasen et al. (2021) examined the influence of salmon farms on the spatio-temporal dynamics of mature cod during the spawning period. Data from 2 additional receivers placed at 2 separate stations on different spawning grounds where no cod were caught and tagged are not considered in this study. Here, we focused on the fish detected at the salmon farms (Fig. 1) to determine (1) what influences their temporal and spatial variation, (2) what characterizes cod detected at the farms and (3) how strong the connectivity is between farms, in terms of inter-farm cod movement.

Cod were caught annually from 2017–2019 at each of the 5 spawning grounds (Fig. 1) during late January to mid-February. Fishing was primarily done with 2-chamber baited pots at depths <25 m to minimize barotrauma and physical damage to the fish. In 2018, additional handline fishing was needed to catch sufficient cod for tagging. Post-capture fish were transported to the site of tagging (MOWI Vikan; 63.3804° N, 8.2011° E) and placed in 5 marked net-pens corresponding to each of the CCs. In mid-February each year, fish were sedated, measured for length and weight and, if possible, sex and maturity stage was ascertained using ultrasound (Karlsen & Holm 1994) and biopsies (females only; 2018–2019). After these measurements, a Vemco V13 tag was surgically implanted into the abdominal cavity of the fish (n_{2017} = 194, n_{2018} = 175, n_{2019} = 189). These tags transmitted fish ID and depth (2017 and 2019) or alternated between transmitting fish ID and either depth or temperature (2018). In all years, the tags

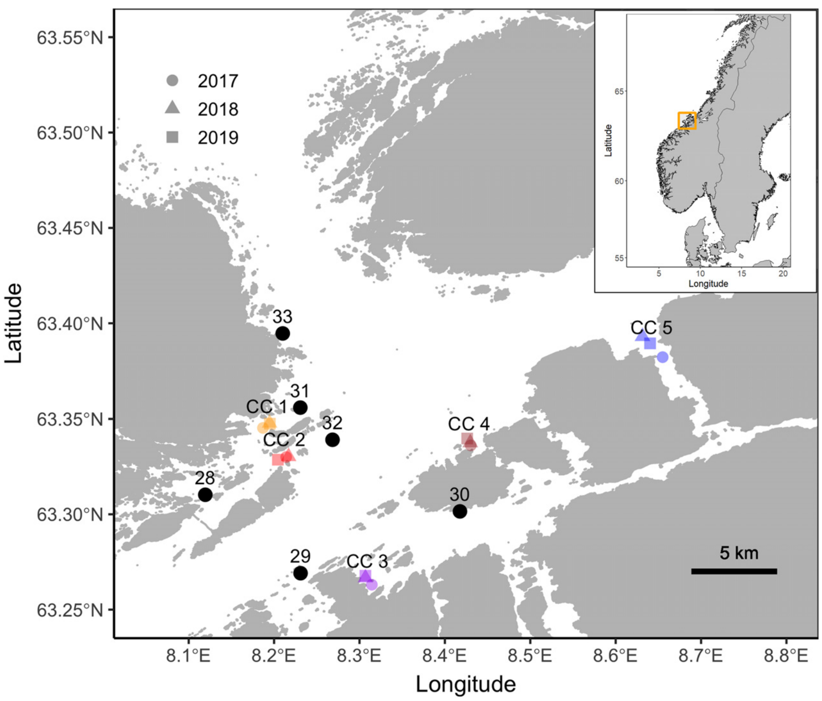

Fig. 1. Study area on the Norwegian coast (orange box in inset), positions of the salmon farms (black circles; numbers are station numbers given to the farms in the study) and yearly release positions of cod in the 5 respective catch clusters (CC): CC1: Glasøysvaet; CC2: Lauvøysvaet; CC3: Araneset; CC4: Åkvika; CC5: Dromnessundet

transmitted a signal on average every 250 s with a minimum and maximum off time of 200 and 300 s, respectively. The tags were programmed to turn off permanently after a period of 860 (2017), 920 (2018) or 807 (2019) d, close to the end of the expected battery life. In the present study, only fish ID and depth information were used for the analyses of the finalized data set (see Section 2.2). After measurements and tagging, fish recovered overnight in the net-pens before being released in their respective CCs (Fig. 1). No food was offered during this short recovery period, and very little mortality (<0.5%) occurred. In total, 558 cod were acoustically tagged and released during the study.

2.2. Data analyses

All graphing was conducted using the R package 'ggplot2' v.3.3.5 (Wickham 2016), and mapping of the data was done by 'qqmap' v.3.0.0 (Kahle & Wickham 2013). Data organization used the 'tidyverse' v.1.3.1 packages (Wickham et al. 2019), while data analyses were conducted using the base library of R v.4.0.4 (R Core Team 2021), in addition to a variety of other packages when necessary (listed in the descriptions of the specific statistical analyses). Model selection involved the following steps: an initial model was first employed, followed by use of the dredge command in the 'MuMIn' library (Bartoń 2020) in R to arrive at the most parsimonious model with the lowest Akaike's information criterion for small sample sizes (AICc) score. All variables included in the best model, or in a model with an AICc score within 2 units of the best model, were retained for the final model used for inference, given that those models have similar empirical support (Hurvich & Tsai 1989).

2.2.1. Initial data handling and filtering

Data was downloaded (VUE Software v.2.7.0; Innovasea) from the loggers biannually, typically in late May and late October. To correct for receiver clock drift, a linear correction based on the satellite clock time stamp at receiver initiation and download was applied. The time-corrected data set was used for all further data handling in R. The present study encompassed the period from 13 February 2017 (first release of fish) to 30 October 2020 (final data download). Unfortunately, receivers at Stns 28, 32 and 33 were lost after the data downloading session in June 2019, restricting the time span available for some analyses (see Section 2.2.2).

Prior to statistical analyses, the time-corrected data was filtered to (1) remove fish that were detected but did not exhibit vertical movement for >1 d and thus were assumed to be dead, (2) avoid multiple counts of the same signal transmission if detected at different receivers, and (3) exclude dubious/erroneous detections, defined as a single daily detection of a given fish ID within the grid. For (1), if the fish never displayed any vertical movement, all data was removed, whereas if the fish initially displayed vertical movement, only the period after vertical movement ceased was removed. For (2), we only included the first detection if any data from the same fish was detected within 200 s with the same sensor value at different stations. This filtering process reduced the total number of detections from 15 424 517 to 9 594 669 valid detections from 535 fish in the final data set. Of the 558 tagged and released cod, 23 are missing from the finalized data set: 15 were never detected, and 8 were deemed not to have survived the tagging and release process because they never displayed vertical movement.

2.2.2. Determinants of the number of cod detected daily at a farm and fish depth

We first explored what factors affect the daily number of tagged fish observed at a given farm. Examination of exploratory plots indicated an effect of distance from the farm to the release sites at the spawning grounds ('DISTmin'; closest Euclidean distance at last release to each farm) and pulses of detections roughly coinciding with the time of fish release ('DLR'; days since last release). These variables and their interaction were therefore incorporated into the model. We also examined if the number of fish detected was affected by whether the farm site had salmon in it ('SIF'; categorical variable) or not, i.e. whether the farm was operational. During the salmon production cycle (~18 mo in this region), the farmed salmon are offered pelleted food. After the salmon are harvested, there is an obligatory fallowing period lasting from 2–5 mo. During this period, there are no salmon in the facility and consequently no pelleted food released. Incorporating operational status into the model can thus inform as to whether the farm site, or some aspect of active salmon farming such as feeding opportunities, is affecting cod attraction patterns. The latter variable was allowed to interact with DLR in the initial model. Finally, we controlled for the number of fish released at the closet release site at the time of last release ('NRELmin') and the total number of fish at large still transmitting ('FAL'). The latter number incorporated the release date and the off time for transmitters in each tag year, the reported date for recaptures, and, for all cod assumed to have suffered mortality based on the lack of vertical movement, the day when they were removed from the data set. A negative binomial model was fitted to the data to account for zero inflation and overdispersion. The following initial model was then employed using the 'lme4' v.1.1-27.1 library (Bates et al. 2015):

$$\text{FISH} = \text{DISTmin} \times \text{DLR} + \text{NRELmin} + \text{SIF} \times \text{DLR} + \text{FAL} + \text{expday} \quad (1)$$

where FISH is the number of fish detected daily at each farm station, and 'expday' is the random effect of experimental day counted as days since 12 February 2017, i.e. the first release date of fish into the grid. Continuous variables were divided by their standard deviations to make their relative scales similar before running the model.

We also examined if fish depth was influenced by operational status of the farm, using the following model and the 'lmer' function of the 'lme4' library:

$$\text{DEPTH} = \text{SIF} \times \text{DAY\_NIGHT} + \text{LENGTH} + \text{Day of Year} + \text{Serial} + \text{Station} \quad (2)$$

where 'DEPTH' is the swimming depth (m) of the fish corrected for tidal variation (see below), SIF is the same categorical variable as in Eq. (1) and 'DAY_NIGHT' is a categorical explanatory variable with a value of 0 if the depth recording occurred during the day and 1 if it occurred at night. We used the 'suncalc' library of R (Thieurmel & Elmarhraoui 2019) to obtain the daily time for sunset and sunrise in our study. Day was defined as the time from sunrise to sunset and night as the time from sunset to sunrise. 'Day of Year', 'Serial' ('fish_ID') and 'Station' were included in the model as random effects. To negate tidal differences influencing our results, the difference between the current and average sea level was subtracted from the swimming depth to correct for tidal variation. Sea level data was downloaded from the Norwegian Mapping Authority, Hydrographic Service (https://www.kartverket.no/) for a central position within our study area (63.38265 N, 8.34387 E). Tidal data are provided for every 10 min; therefore, we used linear interpolation between each 10 min measurement point to obtain data with a resolution of 1 s so that the tidal data had the same resolution as the telemetry data.

2.2.3. Characteristics of cod visiting farms and the number of days spent at a farm

We examined which traits affected (1) fish visiting a farm or not and (2) the number of detection days for fish that did visit farms, using 2 separate tests. For (1), we employed a logistic regression where each fish was given a value of 1 if they had been present at a farm and 0 if not. This categorical variable was then included as a binomial response variable. The categorical variable CC, the continuous variable fish length (cm) and their interaction were included as logical predictors in the initial model. For (2), we used number of days at a farm as the response variable. The candidates for explanatory variables tested in the initial model were the Euclidian distance to the farm in question from the release point for the fish detected there, fish length (cm) and their interaction. Given that the same fish may be detected at several farms, fish_ID and farm station were included as additive random effects. To account for an excess of small values and overdispersion, we initially explored 2 different approaches: a Poisson distribution with a log-link function and a negative binomial distribution. The 2 alternatives were compared by investigating rootograms and comparing the AICc values and, based on this information, the negative binomial distribution was chosen. The continuous explanatory variables were again divided by their standard deviations to make their relative scales similar before applying the model. We explicitly also wanted to check if differences existed between CCs in the amount of time fish spent at salmon farms. An additional model was therefore employed incorporating CC as the single explanatory categorical variable of the number of farm days. These analyses (1 and 2) were performed on the subset of data covering the period February 2017–May 2019. Finally, we used a paired *t*-test to determine if the number of days individual cod were observed at a farm differed between the first and second year post-release. The input data to this test were limited to cod that had been observed at a farm and were not reported recaptured or inferred to have suffered mortality the first 2 yr after release (n = 231).

2.1.4. Farm detections — connectivity between farms

Connectivity between farms was analysed using a network approach, where each station was defined as a node and fish movements between stations were defined as edges (Jacoby et al. 2012). Specifically, we used the 'igraph' v.1.2.7 library in R (Csárdi & Nepusz 2006) to calculate the eigenvector value for each node (farm) in the farm network for each cod that had visited 2 or more farms, weighting the edges (i.e. connections between nodes) by the number of times the cod had used that edge. To produce one value for each farm, these values were then averaged across fish and subsequently standardized by dividing the averaged value for each farm by the maximum averaged value so that the farm with the highest eigenvector value would receive a score of 1. The eigenvector value is a measure of the centrality of a node and its importance in the network; it is a function of the number of edges connected to the node and the eigenvector values of the nodes to which it is connected (Jacoby et al. 2012). This analysis was performed on a subset of data only covering the period February 2017–May 2019 to focus on the period when the entire farmed grid was logging data.

3. RESULTS

Of the 535 fish included in the final data set, 530 could be sexed (Table 1), of which 484 were deemed

Table 1. Physical data for the acoustically tagged cod (n = 536). Mean (±SD) length (nearest cm), mean weight (nearest g) and numbers tagged in each year (Tyear) are provided for the different catch clusters (CC): CC1: Glasøysvaet; CC2: Lauvøysvaet; CC3: Araneset; CC4: Åkvika; and CC5: Dromnessundet. Fish are separated by sex (females, males, and unknown); empty cells: no available data

Tyear	CC	Female			Male			Unknown		
		Length	Weight	N	Length	Weight	N	Length	Weight	N
2017	1	63 (±16.3)	3267 (±2986)	20	63 (±7.5)	3116 (±1557)	18	49 (±0.4)	1142 (±32)	2
2017	2	76 (±15.7)	5779 (±3686)	23	62 (±8.2)	2647 (±1055)	23			
2017	3	69 (±11.6)	3601 (±2043)	22	60 (±7.3)	2242 (±863)	19			
2017	4	73 (±12.7)	4540 (±2404)	14	63 (±8.9)	2586 (±1075)	17			
2017	5	66 (±13.5)	3590 (±2564)	19	58 (±6.9)	2126 (±793)	15			
2018	1	76 (±11.6)	4827 (±2288)	9	67 (±7.5)	3338 (±1151)	22			
2018	2	69 (±13.5)	4001 (±2451)	13	64 (±17.0)	3228 (±3392)	21			
2018	3	67 (±10.1)	3303 (±1470)	12	59 (±9.6)	2334 (±1234)	13	52 (±3.2)	1455 (±315)	2
2018	4	67 (±10.1)	3564 (±1606)	18	64 (±11.6)	3175 (±2028)	27			
2018	5	65 (±12.6)	3318 (±1987)	16	67 (±12.4)	3658 (±2338)	10	46	890	1
2019	1	75 (±14.5)	5199 (±3222)	16	62 (±8.5)	2767 (±1205)	21			
2019	2	74 (±12.9)	4590 (±2655)	18	63 (±9.7)	2730 (±1367)	26			
2019	3	68 (±5.7)	3104 (±800)	14	60 (±6.7)	2853 (±1650)	9			
2019	4	75 (±11.6)	4764 (±2773)	24	64 (±9.9)	3063 (±2318)	24			
2019	5	80 (±12.7)	5838 (±3115)	14	66 (±8.2)	2967 (±1634)	13			

to be sexually mature based on the ultrasonographic and biopsy examinations. Typically, tagged cod *Gadus morhua* were between 50 and 80 cm long (80%), whilst the minimum and maximum size recorded was 42 and 117 cm, respectively (Fig. 2). Sizes were generally similar between CCs (Table 1), although CC2 fish were larger than CC3 fish ($p < 0.05$). Females were also larger than males ($p < 0.0001$) (Table 1).

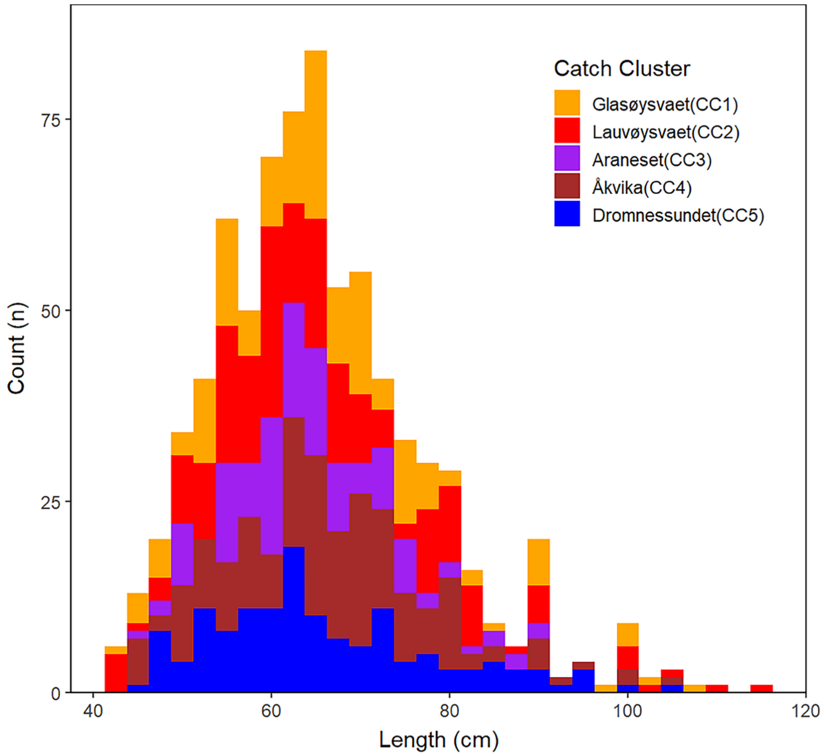

Fig. 2. Size of cod from the different catch clusters (CCs)

3.1. Determinants of the number of fish detected daily at the salmon farms and fish depth

More fish were detected at the salmon *Salmo salar* farms closer to release sites ($p < 0.001$; Table 2, Fig. 3), and the number detected increased with the number of cod released at the closest release site ($p < 0.001$; Table 2) but decreased with time since last release ($p < 0.001$; Table 2, Fig. 3). Importantly, we also found that more cod were present if salmon were in the farm ($p < 0.001$; Table 2, Fig. 3) than when the farm was empty, although this effect was less pronounced with increasing time since release ($p < 0.05$; Table 2).

When farms were not operational, cod were observed in somewhat shallower waters during the night than in the day ($p < 0.05$; Table 3). In contrast, when farms were operational, cod were observed in slightly shallower waters during the day than at night ($p < 0.05$; Table 3). Fish length was negatively associated with depth, with larger fish being observed in shallower waters ($p < 0.05$; Table 3).

3.2. Characteristics of cod at salmon farms

Cod from CC1, CC2 and CC3 were more likely to be detected at a farm than those from CC5. Cod from CC1 were also more likely to be detected at a farm than CC4 cod (Tukey post hoc test, all $p < 0.01$; Table 4, Fig. 4). The mean and maximum Euclidean distance cod moved from their release point to the farm where they were detected were 4.9 and 24.6 km, respectively. Fish length was also included in the final model, as it tended to have a positive effect on the likelihood of fish being detected at a farm, albeit not significantly so ($p = 0.095$). Fish were likely to spend more days at farms closer to their original CC ($p < 0.0001$; Table 5). However, this effect was less pronounced with size (Fig. 4,

Table 2. Negative binomial model on independent variables influencing the daily number of cod detected at different salmon farms. DISTmin: closest Euclidean distance at last release to farm; DLR: days since last release; SIF: farm operational status; FAL: fish at liberty still transmitting. The treatment contrast of R was used with the intercept representing the value for farms when non-operational. Square brackets indicate a categorical variable tested against the reference variable. Only fixed effects are shown. Significant p-values are in **bold** ($p < 0.05$)

Predictors	Fish			
	Log-mean	SE	Statistic	p
(Intercept)	−2.60	0.17	−15.38	**<0.001**
DISTmin	−0.64	0.02	−29.98	**<0.001**
DLR	−0.52	0.05	−11.18	**<0.001**
SIF [1]	1.10	0.06	19.48	**<0.001**
NRELmin	0.42	0.02	25.13	**<0.001**
FAL	0.48	0.02	27.14	**<0.001**
DISTmin × DLR	0.16	0.01	11.28	**<0.001**
DLR × SIF [1]	−0.09	0.04	−2.05	**0.040**
Observations	6578			
Marginal R^2 / conditional R^2	0.432 / 0.492			

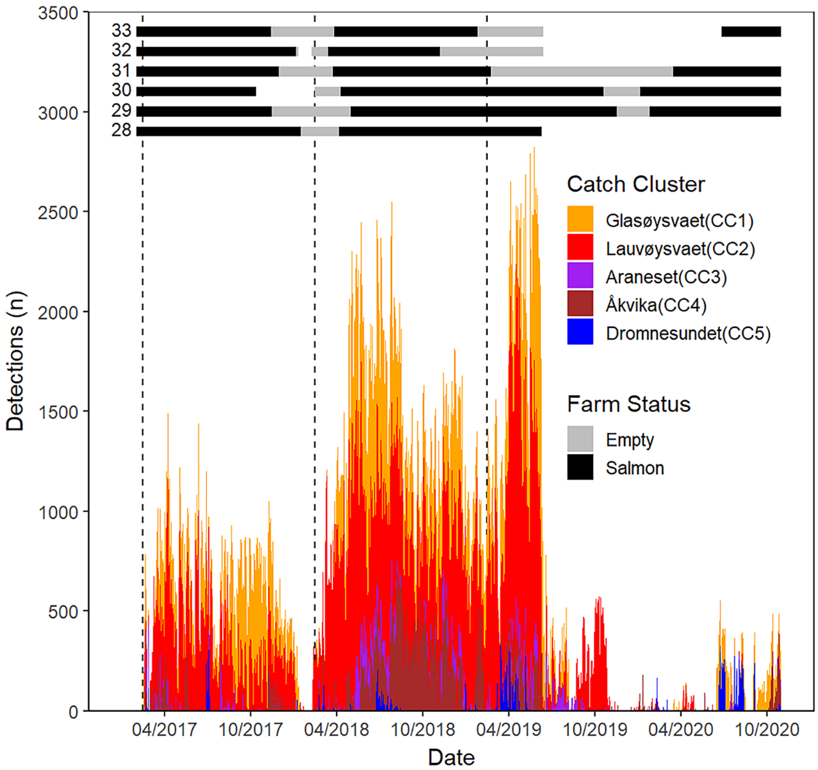

Fig. 3. Number of daily detections of cod across all salmon farms during the study. Colours represent catch clusters. Vertical dotted lines: yearly release dates of fish

Table 5) and only explained 5% of the variation. Fish from CC1 and CC2 spent more days at the farms than fish observed at farms originating from the other areas (Fig. 5, Tables 6 & 7). Most cod detected at farms (n = 179) were detected for ≤5 d (Fig. 5, Table 6). However, 48 cod were detected for more than 30 d, and 21 of these cod were detected for more than 100 d, with a maximum of 720 d (Fig. 5, Table 7).

The bulk of the farm detections arose from fish caught and released at CC1 and CC2 spawning grounds (Figs. 3 & 5), although numerous detections, especially from 2018 onwards, also arose from fish from the CC4 spawning ground (Fig. 3). Stns 29 and 30 were predominantly visited by fish from CC3, CC4 and CC5, whilst the other farms were visited primarily by fish from CC1 and CC2 and to a lesser extent from CC4 (Fig. 6). Overall, fish were likely to spend fewer days at a farm the second year after tagging and release compared to the first year at liberty (paired 2-way *t*-test, t = 5.13, p < 0.0001), although 27 of the 231 fish showed the reverse pattern.

3.3. Connectivity of salmon farms

A total of 289 tagged cod (54.0%) were detected at salmon farms. The most common occurrence (n =160) was that fish were only detected at one farm, although numerous cod were detected at 2 or 3 different farms (n = 110), and 5 fish were detected at 5 different farms (Fig. 7). Comparing the farms, 128 different fish were detected at farm Stn 31 (Fig. 6, Table 8),

Table 3. Results of linear mixed effect on the influence of salmon farm operational status (SIF), day or night (DAY_NIGHT) and fish length (LENGTH, cm) on cod depth. The treatment contrast of R was used with the intercept representing the value for a non-operational farm during the day. Square brackets indicate a categorical variable tested against the reference variable. Significant p-values are in **bold** (p < 0.05). Only fixed effects are shown

Predictors	Depth (m)			
	Estimates	SE	Statistic	p
(Intercept)	51.20	7.05	7.26	**<0.001**
DAY_NIGHT [1]	−1.31	0.05	−24.37	**<0.001**
SIF [1]	−0.19	0.05	−3.53	**<0.001**
LENGTH	−0.29	0.09	−3.39	**0.001**
DAY_NIGHT [1] × SIF [1]	1.76	0.06	29.72	**<0.001**
Observations	730842			
Marginal R^2 / Conditional R^2	0.031 / 0.812			

Table 4. Binomial model for the likelihood of cod being detected at a salmon farm depending on the categorical variable (catch cluster, CC) and fish length. The treatment contrast of R was used with the intercept representing the value for Glasøysvaet (CC1). Square brackets indicate a categorical variable tested against the reference variable. Letters show the results of Tukey's post hoc tests, with different letters indicating significant differences (p < 0.05). Significant p-values are in **bold**

Predictors	BIN			
	Log-odds	SE	Statistic	p
(Intercept)	0.07	0.53	0.14	0.892
CC2 [Lauvøysvaet][ab]	−0.39	0.28	−1.38	0.169
CC3 [Araneset][b]	−0.67	0.30	−2.25	**0.025**
CC4 [Åkvika][c]	−0.98	0.28	−3.52	**<0.001**
CC5 [Dromnessundet][c]	−1.69	0.31	−5.39	**<0.001**
Length	0.00	0.00	1.63	0.103
Observations	536			
R^2 Tjur	0.072			

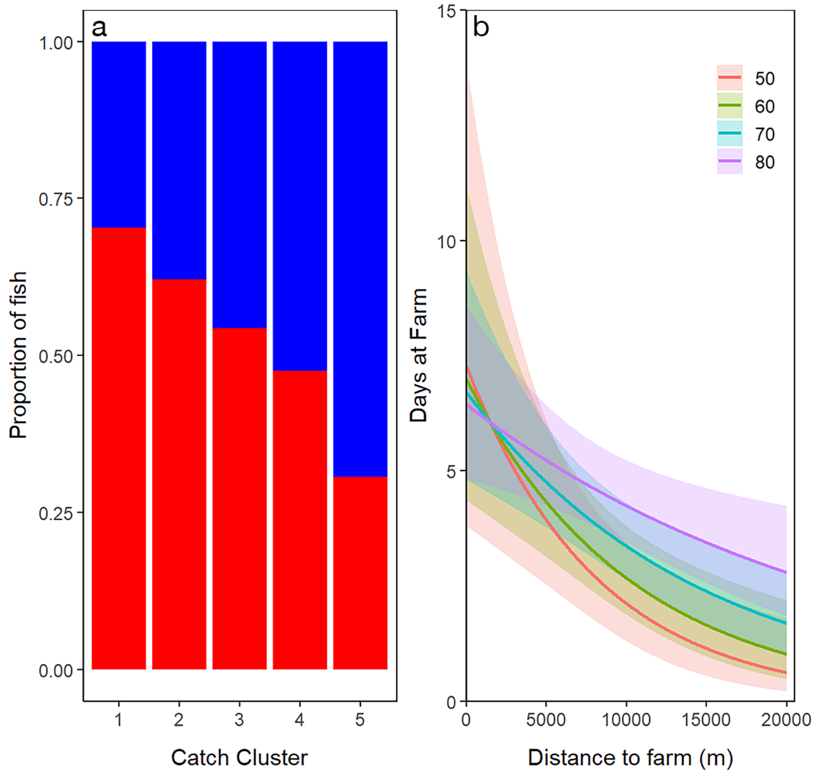

Fig. 4. (a) Proportion of cod from each catch cluster that were recorded at a salmon farm on at least 1 d (red: proportion observed at a farm; blue: proportion not observed at farm) and (b) model results (solid lines show the model results with shaded areas representing the modeled uncertainty of the fixed effects) showing the modeled number of days fish would be observed at a farm as a function of distance from release point to the farm. Given that there was an interaction between predicted days at a farm and fish length, model results are shown for 4 example fish of 50, 60, 70 and 80 cm (most common lengths of our study fish)

whereas only 23 fish were detected at farm Stn 28 (Fig. 6, Table 5). The centrality analysis of the farm network gave Stn 31 the highest eigenvector value, i.e. it was the one most connected to other farms through cod movement, followed by Stns 33 and 32, whereas Stn 28 had the lowest eigenvector value (Fig. 8, Table 8).

4. DISCUSSION

This study provides empirical support for the expectation that salmon *Salmo salar* farming activity attracts wild fish from local spawning grounds. A total of 558 Atlantic cod *Gadus morhua* equipped with acoustic transmitters were released at 5 different spawning grounds. More than 50% of the tagged cod were subsequently detected at salmon farms 0.5–10 km from their focal spawning grounds. Cod visits to salmon farms increased when farms were operational compared to periods when farms had empty net-pens. Further, more cod were detected if the farm was close to one of the focal spawning grounds and, if detected, were also likely to stay longer at a farm if it was closer to their release area. Most cod were only detected at one farm, but a substantial proportion visited 2 or more farms. We discuss the relevance of our results for achieving a mechanistic understanding of fish attraction to aquaculture net-pens as well as the potential ecological consequences of salmon farming in open ecosystems.

4.1. Determinants of the number of cod at a salmon farm

Fish presence underneath aquaculture installations has been well documented across regions and farmed species (Bagdonas et al. 2012, Özgül & Angel 2013, Callier et al. 2018, Akyol et al. 2019, Santhanakumar et al. 2021, Talijančić et al. 2021). The present study offers new insights, as tagged fish were not caught underneath the farms but instead at an important life-history hot spot (i.e. spawning grounds) at varying distances from the monitored farms. Our approach sheds light on the linkages of cod observed underneath farms to nearby areas and factors influencing the daily numbers of cod observed underneath farms. However, regarding the latter, the present results

Table 5. Negative binomial model on the number of days cod spent at a salmon farm as a function of Euclidean distance from release point to farm and fish length. Only fixed effects are shown. Significant p-values are shown in **bold**

Predictors	Farm days			
	Log-mean	SE	Statistic	p
(Intercept)	2.19	0.84	2.63	**0.009**
Distance	−1.50	0.55	−2.74	**0.006**
Length	−0.06	0.15	−0.39	0.694
Distance × length	0.22	0.10	2.30	**0.022**
Observations	473			
Marginal R^2 / Conditional R^2	0.058 / 0.684			

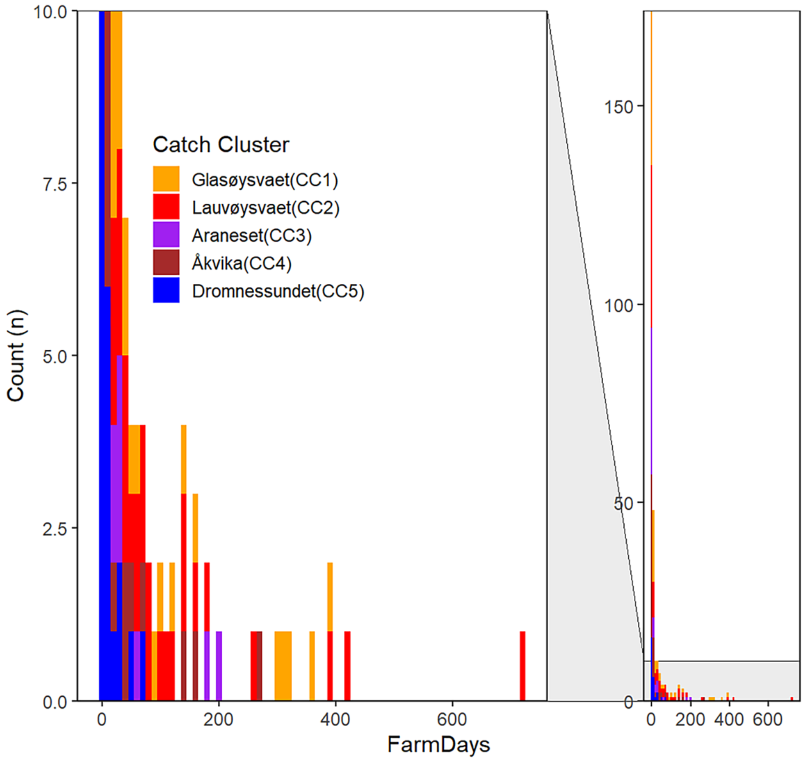

Fig. 5. Number of days cod spent at a salmon farm; bin width: 10 d. Fill colours represent catch clusters (CC). Left panel: results of bins with ≤10 counts

grounds associated with the spawning period (Skjæraasen et al. 2011). In the present context, tagged cod moving away from the spawning grounds might pass farm stations, with some (but not most) then spending varying amounts of time in the vicinity of the farms. This is a parsimonious explanation for why the number of cod detected is negatively associated with days since release. More cod were also detected at farms closer to release points. This result should not be viewed as indicative of the actual number of cod underneath the studied salmon farms. Rather, the most biologically meaningful interpretation is that cod using feeding or spawning areas close to salmon farms are more likely to visit farms than cod utilizing such areas situated further away from any farming activity.

Feeding is assumed to be the primary aggregation mechanism for wild fish at farms (Tuya et al. 2006, Dempster et al. 2011, Fernandez-Jover et al. 2011). Our results support this assumption, with significantly more tagged cod being present when the farm was operational (i.e. when pelleted feed was available) (Table 3, Fig. 3). If the farming site itself was the attraction, we would not expect the farm's operational status to have a large influence on the number of cod detected. However, farms may be acting as FADs when operational (e.g. Callier et al. 2018), and the removal of structures during fallowing causes the cessation of the FAD effect. Nevertheless, feeding attraction is also strongly supported by a parallel study that measured fatty acid trophic markers (FATMs) in cod livers from a different set of fish caught at the same spawning grounds

must be interpreted and understood in terms of the study design. Even though Norwegian coastal cod generally show strong site fidelity (Bergstad et al. 2008, Barth et al. 2017) and somewhat limited movement in contrast to the highly migratory Northeast Arctic cod (Bergstad et al. 1987), there is still considerable movement of cod to and from the spawning

Table 6. Negative binomial model on the number of days cod spent at a salmon farm as a function of the categorical variable catch cluster (CC). The treatment contrast of R was used with the intercept representing the value for CC1 (Glasøysvaet). Square brackets indicate a categorical variable tested against the reference variable. Letters show the results of Tukey's post hoc tests, with different letters indicating significant differences ($p < 0.05$). Significant p-values ($p < 0.05$) are in **bold**

Predictors	Farm days			
	Log-Mean	SE	Statistic	p
(Intercept)[a]	3.63	0.18	20.50	**<0.001**
CC2 [Lauvøysvaet][a]	0.24	0.25	0.96	0.336
CC3 [Araneset][b]	−1.01	0.28	−3.56	**<0.001**
CC4 [Åkvika][b]	−0.85	0.27	−3.14	**0.002**
CC5 [Dromnessundet][b]	−1.29	0.35	−3.68	**<0.001**
Observations	289			
R^2 Nagelkerke	0.162			

Table 7. Proportion of cod from different catch clusters (CCs) that were detected at a salmon farm for 1 day (PD), at least 7 d (1 wk; PW) and at least 30 d (1 mo; PM)

Catch cluster	No. tagged	PD	PW	PM
Glasøysvaet (CC1)	108	0.70	0.31	0.13
Lauvøysvaet (CC2)	124	0.62	0.28	0.19
Araneset (CC3)	92	0.54	0.14	0.04
Åkvika (CC4)	124	0.48	0.13	0.06
Dromnessundet (CC5)	88	0.31	0.09	0.05

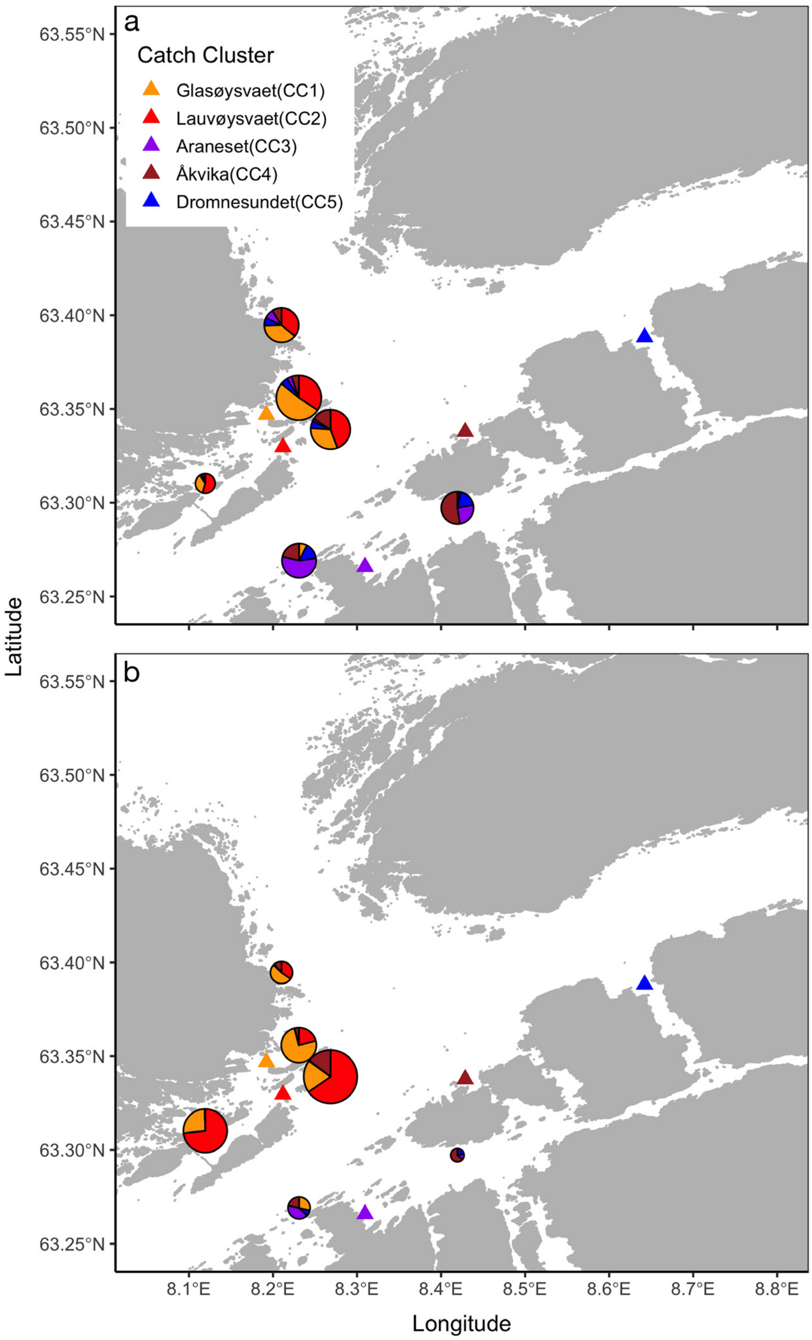

Fig. 6. Origins of cod detected at a salmon farm based (a) the number of fish detected or (b) the number of detections. Sizes of pie charts are scaled to the numbers at the different stations. Triangles: averaged release point positions for each catch cluster (CC) in 2017–2019

around Smøla (i.e. CC1 and CC2) in 2018 (n = 330) and 2019 (n = 487) (S. Meier et al. unpubl. data). Analysis of FATMs is a well-established method for studying trophic interactions (Dalsgaard et al. 2003). Due to the high terrestrial lipid composition in salmon feed such as oleic acid (18:1n-9), linoleic acid (18:2 [n-6]) and α-linolenic acid, (18:3 [n-3]), FATM analysis is an effective tool for detecting whether fish have eaten salmon feed or a natural marine diet (e.g. Fernandez-Jover et al. 2011, Skilbrei et al. 2015). The FATM analysis showed that a substantial proportion of cod (17% in 2018 and 23% in 2019) caught at CC1 and CC2 were likely feeding on waste pellets from the farms.

Interestingly, cod were observed in somewhat shallower waters during the day than at night when farms were operational and the reverse was true when farms were not operational, although the estimated depth differences were small. If we assume that this observation is at least partly explained by pellet-feeding when the farms are operational, cod appear to move in slightly shallower waters during the day to feed on pellets in the water column around the net-pens when they are available. A negative association between cod size and swimming depth has also been reported previously for coastal cod, depending on time of day, season and water temperature (Olsen et al. 2012, Freitas et al. 2015, Barth et al. 2019).

4.2. Characteristics of cod detected at salmon farms

The present study provides insights into the characteristics of the cod detected at salmon farms; there were differences between spawning grounds not only in the likelihood of cod tagged at the specific grounds being detected at salmon farms, but also how long cod stayed around the operational farms when they were detected. Fish were more likely to stay longer at a given farm if it was closer to their capture spawning ground, elucidating a likely mechanism for the latter result. Whilst most cod detected at a farm remained there for <1 wk, some cod spent months or even years at the salmon farms. The finding that individual cod generally spent fewer days at farms during the second year after tagging and release compared to the first year aligns with the

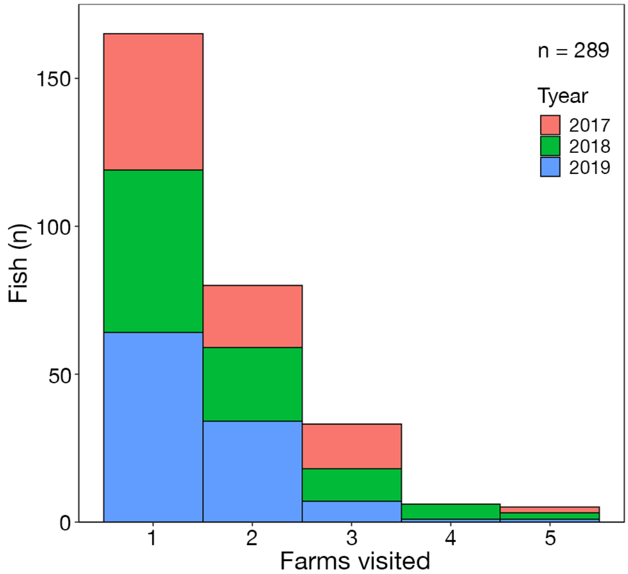

Fig. 7. Number of salmon farms visited by individual cods (n = 289 cod detected at all farms). Tyear: tagging year

basic finding that the number of fish detected at a farm decreased with time since tagging and release.

Using a subset of the present data, Skjæraasen et al. (2021) focused on the spatial ecology of mature cod during the putative spawning period from February to April and found that salmon farms did not appear to disrupt the spawning dynamics of the cod using these grounds. Here, we considered data from all tagged cod during the entire year, with a specific focus on the salmon farms. This clearly shows that some cod are attracted to these farms and will spend considerable amounts of time there. Hence, salmon farming likely impacts the overall spatial and temporal dynamics of some cod utilizing nearby spawning grounds, which is in line with findings from other studies (Giannoulaki et al. 2005, Machias et al. 2005, Uglem et al. 2014). Further, cod spending months at the salmon farming sites undoubtedly receive considerable dietary supplement from pelleted, formulated feed. Feeding on such pellets has a large effect on the energy status and biochemical composition of cod (S. Meier et al. unpubl. data), as pellet-eating cod typically develop extremely large and lipid-rich livers compared to cod eating a natural marine diet. The fatty acid composition of the cod livers, gonads and muscles are strongly modified by the high levels of plant lipids in the formulated feed. Aquaculture studies indicate that cod can tolerate a diet based on plant proteins and oils without negative impacts on growth and health (Hansen & Hemre 2013). However, even though it is still unclear how feed sources of non-marine origin affect wild fish reproduction, there are strong reasons to suggest that the highly modified lipid composition can have negative consequences on cod egg/sperm quality and larval survival (Gonzalez-Silvera et al. 2020). In theory, salmon farming could therefore impact cod reproductive success on nearby spawning grounds even if it does not affect their spatial and temporal distribution during the spawning period. Such an effect is also likely to be related to distance from spawning ground to the nearest aquaculture facility. For example, based on spawning-ground-specific presence at the salmon farms, we would expect more cod from the Glasøysvaet and Lauvøysvaet grounds than the Araneset, Åkvika and Dromnessundet spawning grounds to show any such dietary effects (Table 6). Larger cod were also marginally more likely to be detected at a farm site (Table 3), which is probably related to the generally larger dispersal capacity of big fish (Roff 1988).

It is worth noting that cod detected at farms farther away from their capture spawning grounds remained there for a shorter time. This finding suggests that cod are more likely to spend time at farms situated close to their spawning grounds, as shown here, and possibly also at farms close to important feeding areas. However, over time, the presence of salmon farms might still alter the overall utilization of different grounds; for example, some cod may start using spawning or feeding grounds in the vicinity of aquaculture farms instead of their natal grounds. Indeed, salmon farming may have caused life-history

Table 8. Summary statistics for the farms (station numbers). Longtitude and latitude gives the geographical location of the farms in decimal degrees. Capacity: maximum standing biomass; depth: bottom depth underneath the farms. Number of fish detected and number of detections across the study are also shown. EigenVal: the eigenvalue centrality of the different stations/farms in the network analysis (i.e. how central the farm is in the network). The latter was calculated using data from 13 February 2017–31 May 2019 only, whereas number of fish and detections are totals from 13 February 2017–30 October 2020. RecDays: number of days data was recorded at each station

Station	Longitude	Latitude	Capacity	Depth (m)	Fish	Det	EigenVal	RecDays
28	8.1194	63.3102	780	25	23	246733	0.091	847
29	8.4194	63.2972	7800	50–60	84	86221	0.267	1354
30	8.4177	63.3015	4680	100–120	77	50317	0.231	1231
31	8.2307	63.3559	5460	60–70	128	184091	1.000	1354
32	8.2684	63.3391	3120	40–55	89	363647	0.629	816
33	8.2101	63.3947	7020	60–70	67	60971	0.653	976

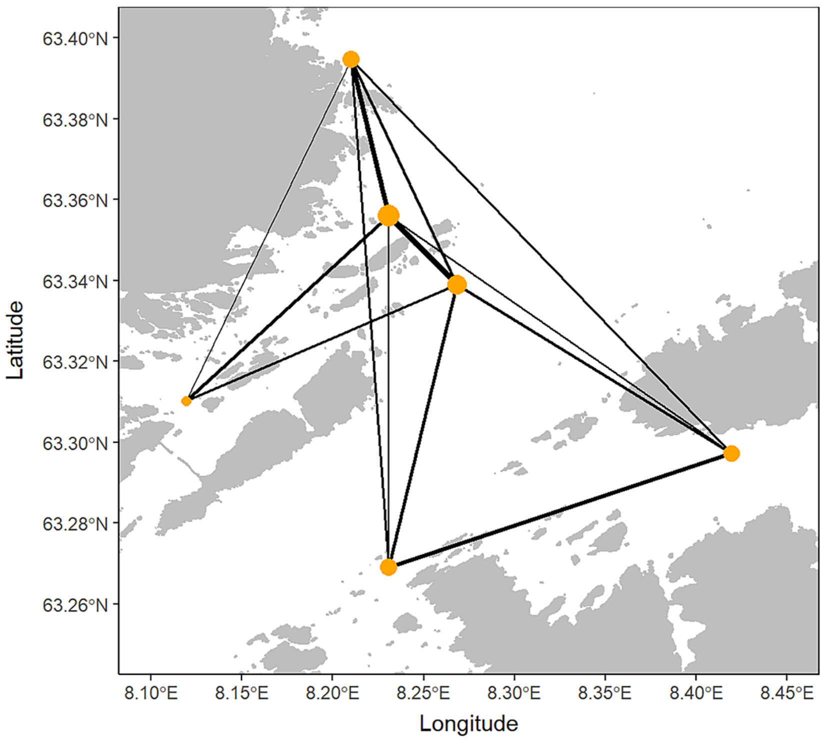

Fig. 8. Salmon farm network. Node size is scaled to number of cod detected; line widths connecting different farms are scaled to the log of the number of fish that used that edge

shifts for saithe, resulting in populations now spending their entire life cycle within fjords (Otterå & Skilbrei 2014). Other gadoids species known to be attracted to fish farms in Norway are Atlantic haddock *Melanogrammus aeglefinus*, pollack *Pollachius pollachius*, and poor cod *Trisopterus minutus* (Dempster et al. 2010, Uglem et al. 2014). These fishes are all regarded as late winter/spring spawners, and their life histories, although poorly understood, appear to resemble that of saithe and cod (Heino et al. 2012). A meta-analysis indicated that farm-associated fish tend to be larger and heavier, with similar or higher body condition metrics (Barrett et al. 2019), as seen for cod. However, neither the proportion of fish affected nor if there are any spatial patterns in such effects have been examined for any of these gadoids.

4.3. Connectivity between salmon farms

More than 100 tagged cod were detected at more than one salmon farm. Such high connectivity between salmon farms was also reported by Uglem et al. (2009) investigating saithe movement. Individual movement between farms shows not only their repeated attraction but also the potential for wild fish to act as vectors for disease transfer to other conspecifics and possibly between different farming operations (Arechavala-Lopez et al. 2013, Uglem et al. 2014). For the latter to occur, fish attracted to salmon farms must share diseases with farmed salmonids. A range of viruses, diseases and parasites may be shared by salmonids, saithe, and other gadoids, including the salmonid alphavirus (Graham et al. 2006), the infectious pancreatic necrosis virus (Wallace et al. 2008), the ectoparasitic copepod *Caligus elongatus* (Øines et al. 2006), the *Vibrio anguillarum* bacteria (Håstein & Smith 1977), and approximately 20 other pathogens (Bricknell et al. 2006). Recently, horizontal disease transfer was shown experimentally from blennies to rainbow trout (Quintanilla et al. 2021). However, it remains unclear whether salmon can infect gadoids resident in the near vicinity of sea-cages and vice versa, and this question merits further investigations.

4.4. Conclusions

Our study identified the extent of wild cod attraction from local spawning grounds to open net-pen salmon farms in coastal marine habitats. Importantly, we have shown that cod are more likely to visit farms close to their spawning grounds and to visit farms when they are operational. Whilst most cod spent less than 1 wk at the farms overall, many spent months or even years in the vicinity of the farms. Thus, it appears likely that some cod have considerable dietary input from salmon feed, potentially impacting their reproductive success. More than 100 cod also visited 2 or more farms, with farms in proximity being more connected in terms of inter-farm movement.

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