Predation mortality from ambush and cruising predators on newly-settled 0-group gadoids

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ABSTRACT

We investigated predation from an ambush predator (shorthorn sculpin) and two cruising predators (Atlantic cod and saithe) on bottom-settled 0-group cod and saithe juveniles in a fjord in northern Norway. Stomach contents of potential fish predators caught by gill net in shallow waters (depth of 3–10 m) during September in 2013–2015 were analysed. The frequency of occurrence (FO) of 0-group gadoid prey was highest for shorthorn sculpin (FO = 10%) and cod (FO = 9%), while it was lower for saithe (FO = 0.8%). Each predatory fish species had different alternative prey to 0-group gadoids: shrimps for cod; sandeels for saithe; and Brachura/Anomura for shorthorn sculpin. Amongst the fish predators, shorthorn sculpin had the highest catch rates in gill nets. The mean number of 0-group cod and saithe in shorthorn sculpin stomachs increased with increasing abundance of prey as measured by beach seine hauls.

Predation mortality from shorthorn sculpin was estimated based on abundance of shorthorn sculpins, number of 0-group cod and saithe juveniles in predator stomachs, prey recognition times and abundance of 0-group cod and saithe. The average predation mortality rate from shorthorn sculpin on 0-group gadoid juveniles varied from 0.40 to 1.14 month^{-1} between years and the pooled estimate from 2013 to 2015 was 0.70 month^{-1} (95%CI: 0.30, 1.73). This is comparable to mortality rates from other studies on newly-settled 0-group Atlantic cod, other gadoid species and plaice. Based on gill-net catches and stomach data from this study and literature values for gill-net catching area, calculated predation mortalities from the cruising cod and saithe were less than 47% of the sculpin predation mortality rates. This show that predation mortality from the ambush sculpin predator was much higher than from the cruising Atlantic cod and saithe.

1. Introduction

Two groups of Atlantic cod (*Gadus morhua*), Coastal cod and Northeast Arctic cod are present along the coast of Norway (Jakobsen, 1987). In contrast to the Northeast Arctic cod, all stages of Coastal cod are present along the coast year-round. The Coastal cod stocks north of 62° N decreased in the mid-1990s due to reduced recruitment, and attempts to rebuild the stocks have so far proved unsuccessful. The two cod groups differ markedly in their early life history (Loken et al., 1994; Fevolden et al., 2012). While Northeast Arctic cod juveniles settle at the bottom in deep water (200–300 m) in late autumn of their first year of life, Coastal cod juveniles settle near the shore in late summer (Loken et al., 1994; Fevolden et al., 2012). Small pelagic saithe juveniles drift into the same settlement areas as those used by Coastal cod (Olsen et al., 2010). Saithe spend their first 1–4 years in inshore and coastal waters (Olsen et al., 2010).

Reduced survival in the early life stages has been regarded as the main reason for lack of Coastal cod recovery (ICES, 2018), but the understanding of the mechanisms underlying recruitment variability in both Coastal cod and northeast Arctic saithe is sparse. Predation causes a fast decline in marine fish egg and larvae abundance (Bailey and Houde, 1989), but there is increasing evidence that determination of year-class strength might also be shifted towards the juvenile stages (Sissenweine, 1984; Lough, 2010; Laurel et al., 2017). High mortality rates characterize the transition from the pelagic habitat to life on the bottom and post-settlement mortality may contribute both to recruitment variability and to density-dependent regulation of recruitment (Beverton and Iles, 1992; Bailey, 1994; Temming et al., 2007). Small bottom-settled juvenile fish are exposed to a suite of predators including both cruising and resident ambush fish predators, invertebrate

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predators, birds and mammals (Bailey, 1994; Hixon and Carr, 1997; Larsen and Pedersen, 2002).

The shorthorn sculpin (*Myoxocephalus scorpius*, Cottidae family) is a common ambush predator in shallow waters and occurs both in the northern part of the Atlantic and in the Arctic ocean (Luksenburg and Pedersen, 2002; Laurel and Brown, 2006; Gray et al., 2017). Along the Norwegian coast, the shorthorn sculpin is a resident species distributed mainly in shallow coastal areas (Luksenburg and Pedersen, 2002), and spatially it overlaps with newly-settled juvenile Coastal cod and saithe (Lie, 1961; Larsen and Pedersen, 2002; Fevolden et al., 2012). The shorthorn sculpin has a sit-and-wait predation strategy (Laurel and Brown, 2006), and in northern marine shallow-water habitats, cottid predation on settled 0-group gadoids is common (Tupper and Boutilier, 1995; Larsen and Pedersen, 2002). Larger cod and saithe are also common in the coastal zone and are defined as cruising predators on small fish. Saithe are a potential predator on 0-group gadoids and cannibalism from cod is generally common in cod stocks (Pedersen and Pope, 2003; Aas, 2007). Predation mortality on early stages of fish may depend on the abundance of alternative prey (Hallfredsson and Pedersen, 2009), but it is unknown which groups may be alternative prey for the various predators on settled 0-group gadoids.

Cruising predators who may aggregate and target post-settled juvenile fish may play a different role than resident ambush predators in shaping recruitment patterns, and the two suites of predators might also reinforce each other's efficiencies as well as cause a density-dependent juvenile mortality pattern when they operate in concert (Hixon and Carr, 1997; Auster et al., 2009). Despite the rapid digestion rates for fish larvae and small juveniles, quantification of predation mortality based on predator stomach analysis and predator abundance have given valuable information regarding predator importance (Temming et al., 2007; Hallfredsson and Pedersen, 2009).

The study took place in Porsangerfjord, northern Norway (Fig. 1), and the main objective was to compare predation mortality from the ambush predator shorthorn sculpin and the two cruising predators Atlantic cod and saithe. The specific objectives were to: (i) identify the diet and predatory role of cruising and ambush predators on 0-group settled cod and saithe; ii) identify alternative prey other than 0-group cod and saithe; and (iii) quantify and compare predation mortality rates from shorthorn sculpin, Atlantic cod and saithe on 0-group cod and saithe. The main approach in this study was to sample predators by gill nets and analyse their stomach contents, estimate sculpin abundance from a mark-recapture experiment and sculpin digestion rates from an experimental set up. Uncertainty in mortality rates was assessed by Monte Carlo simulation (Efron and Tibshirani, 1993), based on re-sampling from distributions of input values.

2. Materials and methods

2.1. Gill net sampling and stomach analysis

The study area in Porsangerfjord has slightly sloping bottom with mixed sand, gravel, stone, and rock bottom partially covered with the kelp species *Saccharina latissima* and *Alaria esculenta,* and lower abundances of other seaweed species (Fig. 1). To catch potential predatory fish, test fishing was conducted with multi-mesh gill nets that were 30 m long and 1.5 m deep and were set at the bottom. Each net was divided into 2.5 m panels with mesh sizes of 43.0, 19.5, 6.25, 10.0, 55.0, 8.0, 12.5, 24.0, 15.5, 5.0, 35.0 and 29.0 mm. This net design is often referred to as a NORDIC gill net (Appelberg et al., 1995). Fishing took place between 3 and 26 September. Six locations were fished three times at approximately weekly intervals (± two days to allow for poor weather) (Fig. 1). At each location and week, the nets were set at slightly different positions (200–1100 m apart). Thus, 18 sets were sampled each year. The nets were deployed perpendicular to the shoreline at depths of 3 to 10 m and were set between 9 and 11 a.m. one

day and hauled during the same time period the next day. Nets were emptied at the laboratory in Holmfjord situated at B3 in Fig. 1 and fish were dissected, weighed and measured. Time from capture to stomach dissection was less than 6 h.

Fish caught by gill nets were weighed ($+/-$ 0.1 g precision) and total lengths (cm) were measured for all fish except for fish caught in 2013 where lengths were measured only for predators. The stomachs of all fish except the smallest specimens (< 10 cm in length) were opened and inspected. Individual fish were defined as predators if they had identifiable remains of fish in their stomachs. All stomachs were used in the calculations of frequency of occurrence of prey. Prey was assigned to a species only when a clear visual identification could be made (SM2).

All fish were opened with a scalpel and the stomach contents were visually inspected. Net-caught cod and saithe smaller than 15 cm (0-group) were opened to investigate if their stomachs contained fish but were not investigated for other prey. Cod and saithe prey could sometimes be identified to species level when they were in a low state of digestion, but more digested preys were very difficult to identify to species and they were grouped as 0-group cod/saithe. Otoliths in cod and saithe less than 10 cm long are very similar and were not used to identify species. No cod/saithe in the stomachs were longer than 15 cm, and they were thus designated "0-group". Arctic lyre crabs, red king crabs and hermit crabs (Brachyura and Anomura) were grouped as "crab".

Other prey items identified in predator stomachs were categorized as "snail/mussel", "amphipod−/isopod", "krill", "shrimp", "fish", "sandeel", "undefined". Empty stomachs were categorized as "empty". "Sandeel" was treated as a separate category because it was very common in saithe stomachs, and 0-group cod/saithe were pooled with other fish prey species – identified as well as unidentified ones – when presented in the figures. While stomachs were only investigated for fish prey in 2013, a more comprehensive analysis that allocated prey to the categories described above was conducted in 2014 and 2015.

Frequency of occurrence (FO) was calculated on pooled samples as the number of occurrences of a prey category divided by the number of stomachs inspected (including empty stomachs) for each predator species, multiplied by 100. Statistical analyses (Chi-square test with continuity correction) were performed in R (R Development Core Team 2013).

2.2. Overview of major steps in estimation of predation mortality rate

The estimation of predation mortality rate on cod and saithe 0-group juveniles from sculpins was carried out in three main steps (s1-s3) using four major data sets (A-D) (Fig. 2, Table 1). The abundances of 0-group prey and sculpin predators were calculated per m shoreline within the 0–15 m depth range, as both the 0-group juveniles and sculpins are mainly distributed close to the shore down to a depth of about 15 m. The main calculation steps were: (s1) estimation of the abundance (ind. m^{-2}) of sculpins from numbers caught per gill net ($CPUE_s$) and estimated gill net catching area (q, m^2) from mark-recapture experiments; (s2) estimating the number of 0-group juveniles consumed by sculpins per unit time from mean stomach content (MSC) from gill net-caught sculpins and average digestion time (A_{50}) from experiments; and (s3) estimating the predation mortality rate from number consumed per unit time and abundance of 0-group cod and saithe from beach seine hauls.

2.3. Estimating sculpin abundance from gill-net catches and effective catching area (s1)

To calculate population densities of sculpins from CPUE data from the predator-prey gill net sampling in 2013–2015, the effective sampling area q (catchability coefficient) of the gill nets was estimated by a
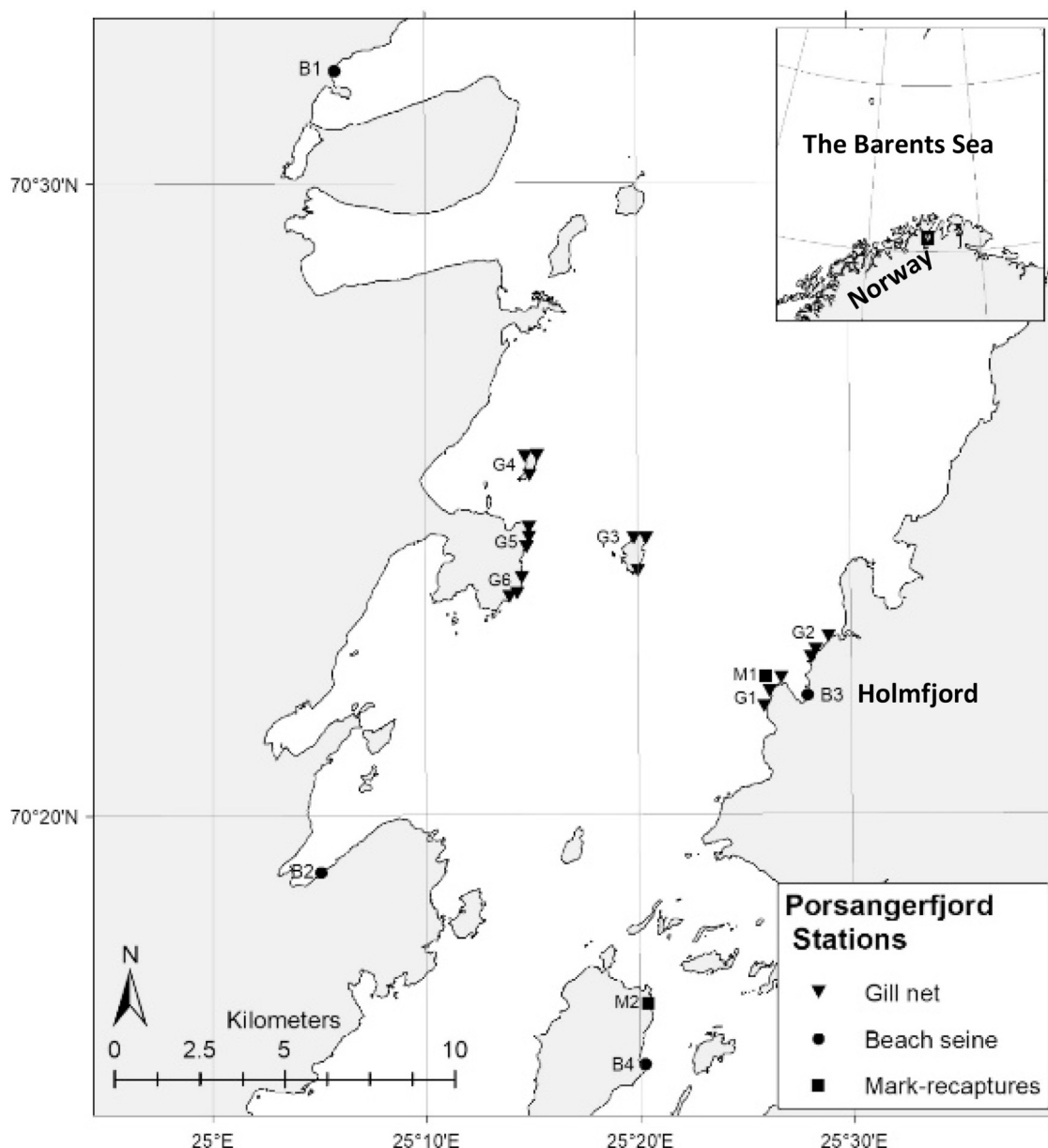
Fig. 1. Gill net sampling locations (G1-G6), the beach seine haul locations (B1-B4) and the locations for mark-recapture experiments (M1 and M2) in Porsangerfjorden during August–September 2013–2015. Gill nets were deployed three times within each location each year and distance between sampling sites (▼) varied from approximately 250–1100 m.

mark-recapture experiment. Shorthorn sculpins have low movement rates and typically move within home ranges of less than 10,000 m^2 (Ivanova et al., 2018).

2.3.1. Mark-recapture experiment (data set B)

To estimate the gill-net catching area (q), a mark-recapture experiment was carried out in two locations – Holmfjord (M1) and Reinøy (M2) – over the period 15–23 August 2016 (Fig. 1). Sculpins were caught by gill nets, length-measured and marked with individually numbered Hallprint T-bar tags and released back into the same location from which they were caught. A total of 338 individuals were caught and 169 individuals were marked. A total of 26 sculpins were recaptured in the two areas during the four days of scientific fishing following the first day of fishing and tagging (Table SM1). The POPAN formulation of the Jolly-Seber mark-recapture method was applied (Schwarz and Arnason, 1996), and the number of individuals was estimated using the program MARK (White and Burnham, 1999). This

method estimates abundances (N_{sar}) in the mark-recapture areas at the start of sampling. The sizes of each of the mark-recapture areas (Ar, m^2) were estimated as the area with a depth of 0 to 15 m from digital maps. The densities (N_{sm}, ind. m^{-2}) in the mark-recapture areas were calculated:
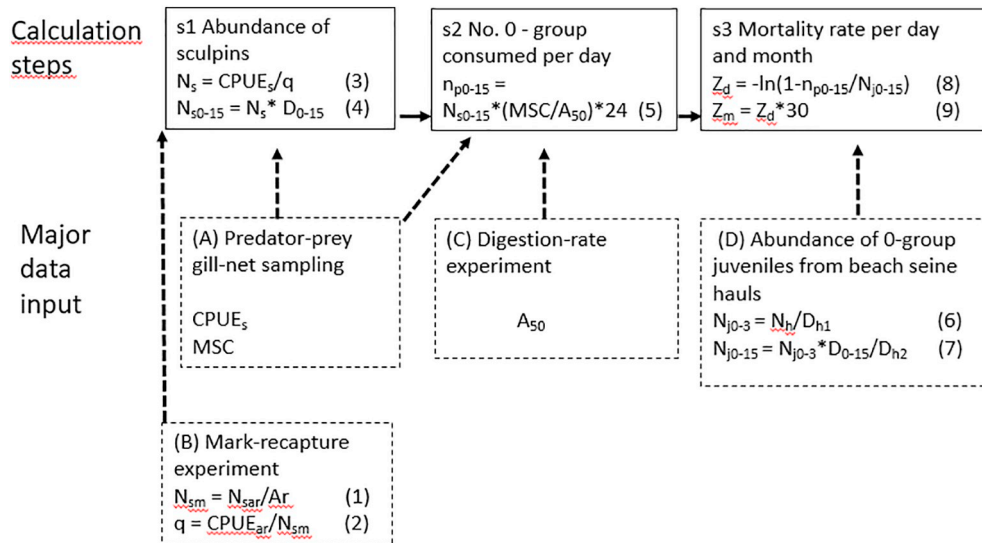
$$N_{sm} = N_{sar}/Ar \tag{1}$$

The catch per gill net per day (type NORDIC) for the first sampling day (16 August 2016) of the mark-recapture experiment, when three nets were set in each area, was used as the $CPUE_{ar}$ estimate since later in the week we also used other types of gill net. The effective catching area per gill net per day (q, m^2 gill net^{-1} day^{-1}) was then calculated as.

$$q = CPUE_{ar}/N_{sm} \tag{2}$$

2.3.2. Estimating sculpin density from gill-net CPUE (data set A)

The average density of sculpins in the 0 to 15 m depth range (N_s,

on 20 November and lasting for 96 h. 0-group saithe caught by beach seine in September were killed and kept frozen at −18 °C. One thawed 0-group saithe was presented to each individually-kept sculpin. The sculpins were fed pieces of herring fillet prior to experiment startup and were starved for 7 and 17 days prior to the start of the first and second experiments respectively. In the first experiment, sculpins took up to 12 h to ingest the juvenile offered, and on several occasions the juveniles had to be moved carefully around with a thin stick to simulate prey movement and stimulate attack. Only 12 sculpins accepted the prey and were used in the experiment.

In Experiment 2, 15 sculpins ingested the juveniles immediately on presentation and were used in the experiment. Average temperature was 5.4 °C (SD = 0.12) during the first experiment and 3.0 (SD = 0.09) °C during the second experiment. The sculpins held at 5.4 °C were sampled at 12, 24, 48 and 72 h, while the sculpins held at 3 °C were sampled at 24, 48, 72 and 96 h. Sculpins used in the digestion experiments ranged in length and weight from 17 to 28 cm and 77 to 480 g and saithe prey had lengths from 4.9 to 13.6 cm and weights from 8.5 to 11.5 g.

In Experiment 2, photos of prey after stomach dissection were used to determine whether the prey could be recognized as a 0-group cod or saithe when analysing stomach data from the field. The average time for 50% probability of prey recognition (A_{50}, hours) was estimated by logistical regression in R (glm procedure with logit link function). The prey recognition states (1 for recognizable prey and 0 for unrecognizable prey) from Experiment 2 were used as dependent variables and time since feeding was the independent variable. Before calculating prey consumption from the field data the estimate for A_{50} was adjusted to the ambient temperature conditions measured in Porsangerfjord at the time of field sampling by using a temperature coefficient of 0.078° C^{-1} estimated for whiting (Q_{10} = 2.18) (Andersen, 1999). Temperature values from the field were interpolated as the average temperature in the 2–15 m depth range measured by vertical CTD profiles from two hydrographical stations in Porsangerfjorden before and after the gill net sampling (Mankettikkara, unpublished obs.).

2.4.2. Estimation of number consumed per unit time from field data

The number of saithe and cod 0-group juveniles predated by shorthorn sculpin per day and shoreline distance (n_{p0-15}, $day^{-1}*m^{-1}$) was calculated (according to (Olson and Boggs, 1986) as:

$$n_{p0-15} = N_{s0-15} * (MSC/A_{50}) * 24 \tag{5}$$

where MSC is the mean number of 0-group cod and saithe per sculpin stomach from the predator-prey gill net sampling and A_{50} is the time (h) for 50% probability of prey recognition estimated from the digestion rate experiments. To convert the units in Eq. (5) from per hour to per day, it was multiplied by 24 $h*day^{-1}$.

2.5. Estimating the predation mortality rate (s3)

The predation mortality rate was estimated from number consumed per unit time (s2) and abundance of 0-group cod and saithe from beach seine hauls (Data Set D) (Fig. 2).

2.5.1. Abundance of 0-group cod and saithe from beach seine hauls (data set D)

A total of four locations were sampled with duplicate hauls each year during the period 2013–2015 (Fig. 1). In all of the years, the hauls were taken during the period 20–24 August. Locations with large rocks and steep areas covered by bedrock with kelp beds with a slope > 25% were avoided since it was not possible to operate the beach seine there. Areas with a very shallow slope (< 10%) with homogenous sand or mud bottom substrates were also avoided since it was impossible to launch the beach seine from an inflatable boat there.

The beach seine was 39 m long and 2.8 m high at the middle. The mesh sizes were 10 mm in the outer 15 m panels, 5 mm in the inner

central part and 7 mm in the cod-end. At the ends, the seine was 1.0 m high. Two 25 m-long ropes were connected to each end of the seine. The seine was launched from an inflatable boat and set in a semicircle with the middle part of the seine at a depth of about 3 m. Maximum depths ranged from approximately 1.5 to 4 m between locations. About 20 m of the ropes were set and each haul enclosed an area of about 450 m^2. The first rope of the seine for the second haul at each location started at the point where the last rope of the seine for the first haul ended. Beach seine hauls were not taken in the hour of maximum tide. At each location, duplicate hauls were taken, and each haul lasted for about 40 mins on average. There was no significant difference in 0-group number caught between the first and second haul (Sign test, *p* = .77).

The start position of each haul was recorded using GPS, and the time of starting the haul was noted. From each haul, animals were identified to species level and counted, and total length measurements (mm) were taken for all fishes. The distance D_{h1} (m) along the shore covered by one haul was on average 15 m, and the number of 0-group fish per m shoreline within the 0–3 m depth range (N_{j0-3}) was calculated as:

$$N_{j0-3} = N_h/D_{h1} \tag{6}$$

where N_h is the number of 0-group cod and saithe per haul. The distance from shore covered by each haul (D_{h2}) was on average 25 m. Video recordings from Porsangerfjorden show that 0-group juveniles are distributed and have similar density from the shoreline and down to a depth of approximately 15 m (Michaelsen, 2012). Assuming equal density of 0-group fish in the depth range 0–15 m as in the depth range 0–3 m covered by the beach seine, the density of 0-group cod and saithe per m shoreline in the depth range 0–15 m was:

$$N_{j0-15} = N_{j0-3} * D_{0-15}/D_{h2} \tag{7}$$

2.5.2. Estimation of mortality rate and sensitivity analysis

The total instantaneous predation mortality rate from shorthorn sculpin predation on 0-group cod and saithe on a daily (Z_d, day^{-1}) and monthly (Z_m, $month^{-1}$) basis was calculated as:

$$Z_d = -\ln(1 - n_{p0-15}/N_{j0-15}) \tag{8}$$

$$Z_m = Z_d * 30 \tag{9}$$

The monthly mortality (M, %) was calculated as:

$$M = 100 * (1 - \exp(-Z_m)) \tag{10}$$

To study how a change in the input variables N_h, q, $CPUE_s$, MSC and A_{50} affected the output value of Z_m, a sensitivity analysis was performed for each year. Baseline values of the input variables were set as the point estimates calculated from the samples of N_h, $CPUE_s$, MSC and from the mark-recapture (q) and digestion rate model (A_{50}). Then the baseline values of the input variables were changed one at a time by +20 and − 20% and the effects on Z_m were calculated using Eqs. (2)–(9).

2.5.3. Assessment of predation mortality rate from cod and saithe

Cod and saithe have much higher movement rates and move over large areas than shorthorn sculpin (Espeland et al., 2007; Ivanova et al., 2018). Thus, it was not possible to estimate the effective catching area of the gill-nets (q) for cod and saithe using the same mark-recapture method as for shorthorn-sculpin. We searched literature for plausible values for effective catching areas for similar species as cod and saithe as well as for literature data on digestion rates of cod and saithe. The values for q and A_{50} and values for CPUE in gill-nets and mean stomach content for cod and saithe from this study were used to calculate likely values for predation mortality from cod and saithe using the framework outlined in Fig. 2.

Table 2
Overview of variables and the resampling procedure in the Monte Carlo simulation procedure.

Variable	Monte Carlo resampling
N_{sar}	random resampling from lognormal distribution for 95% confidence intervals
$CPUE_{ar}$	resampling $CPUE_{ar}$ from three gill net sets per mark-recapture area
q	resampling q for two mark-recapture areas, calculate average
$CPUE_s$	resampling $CPUE_s$ from six locations within week and calculate average for three weeks of sampling
MSC	resampling MSC from the same six locations as for $CPUE_s$within each week and calculate average for three weeks of sampling
A_{50}	resampling from temperature-adjusted lognormal distribution of time for 50% probability of recognition
N_h	Resampling N_h from two hauls within each location and resampling average from the four locations within year

2.6. Monte Carlo procedure for assessing uncertainty

Uncertainty in predation mortality from shorthorn sculpin on 0-group cod and saithe was assessed using a Monte Carlo simulation procedure (MC). In the MC, uncertainty in the output value (Z_m, predation mortality rate) was estimated by bootstrapping 1000 samples resampled from data and distributions for input variables following the description in Table 2. Values for N_{sar} and A_{50} were output from statistical estimation models and were the only variables where a lognormal distribution were used. For all other variables, the empirical distributions from the bootstrapping procedure were used (Table 2). Sculpin gill net data and stomach data were firstly bootstrapped from six locations within week and an average for the three weeks were calculated. Beach seine hauls were firstly bootstrapped from the duplicate hauls within location and then from the four locations.

Output variables were calculated according to the procedure outlined in Fig. 2. Confidence intervals (95%) for output estimates were calculated as the lower 2.5% and upper 97.5% percentiles of the 1000 bootstrap samples (Haddon, 2001). The MC was run separately for each year.

An empirical *P*-value test was applied to test if the average number of juvenile cod and saithe per sculpin stomach (MSC, y-variable) increased significantly with increasing number of saithe and cod juveniles per beach seine haul (N_h, x-variable) for the period 2013–2015. In this test, each bootstrap sample consisted of one bootstrap sample with average MSC and N_h values for each year. A total of 1000 bootstrap samples were used. The slope (b in linear regression equation; MSC = a + b*N_h) for each bootstrap sample of MSC and N_h for the years 2013, 2014 and 2015 was calculated and it was also calculated if the 97.5% and 2.5% percentiles of the frequency distribution of the slope included zero (no significance) or not (significance). Empirical *P*-values were also used to test if average CPUEs, MSC and N_h from the Monte Carlo simulations were equal for all years. The P-value was calculated as: P = (r + 1)/(n + 1) where r is the number of replicates the value from a year is larger than or equal to the value from another year and n is the number ($n = 1000$) of Monte Carlo simulations (bootstrap replicates) (North et al., 2003).

3. Results

3.1. Gill net samples and diet compositions

Shorthorn sculpin ($n = 444$), saithe ($n = 385$) and cod ($n = 98$) were the most abundant fish species caught during the 54 net deployments in the years 2013, 2014 and 2015. In addition, smaller numbers of Norway redfish (*Sebastes viviparous*) ($n = 8$), European flounder (*Platichthys flesus*) ($n = 11$), rock gunnel (*Pholis gunnellus*) ($n = 5$), Atlantic halibut (*Hippoglossus hippoglossus*) ($n = 2$), haddock (*Melanogrammus aeglefinus*) (n = 1), plaice (*Pleuronectes platessa*) (n = 1) and sandeel (*Ammodytes* sp.) (n = 1) were caught. Some invertebrates were also caught: whelk *(Buccinum undatum)* ($n = 230$), sea urchins (*Strongylocentrotus droebachiensis)* ($n = 199$), Arctic lyre crab *(Hyas coarctatus)* ($n = 109$), red king crab *(Paralithodes camtschaticus)* ($n = 48$), and hermit crab (*Paguridae*) (n = 10).

Shorthorn sculpin, cod and saithe were the only species with fish prey in their stomachs. Saithe and cod 0-group occurred in the stomachs of gill net-caught shorthorn sculpin (FO = 10%), cod (FO = 9%) and saithe (FO = 0.8%). The smallest shorthorn sculpin predating on 0-group cod and saithe was 15.0 cm long, while the corresponding sizes for cod and saithe were 24.5 and 25.1 cm respectively (Fig. 3).

The gill net-sampled sculpins were mainly in the range 10–30 cm with an average length of 20.1 cm (SD = 4.5) (Fig. 3). Sculpins shorter than 25.1 cm ($n = 390$) had much higher FO for 0-group cod and saithe (12%) than sculpins longer than 25.1 cm ($n = 54$), which had no occurrence of 0-group gadoids in their stomachs ($\chi^2 = 5.98$, df = 1, $p = .015$). In the longer shorthorn sculpins, Brachyura/Anomura had a
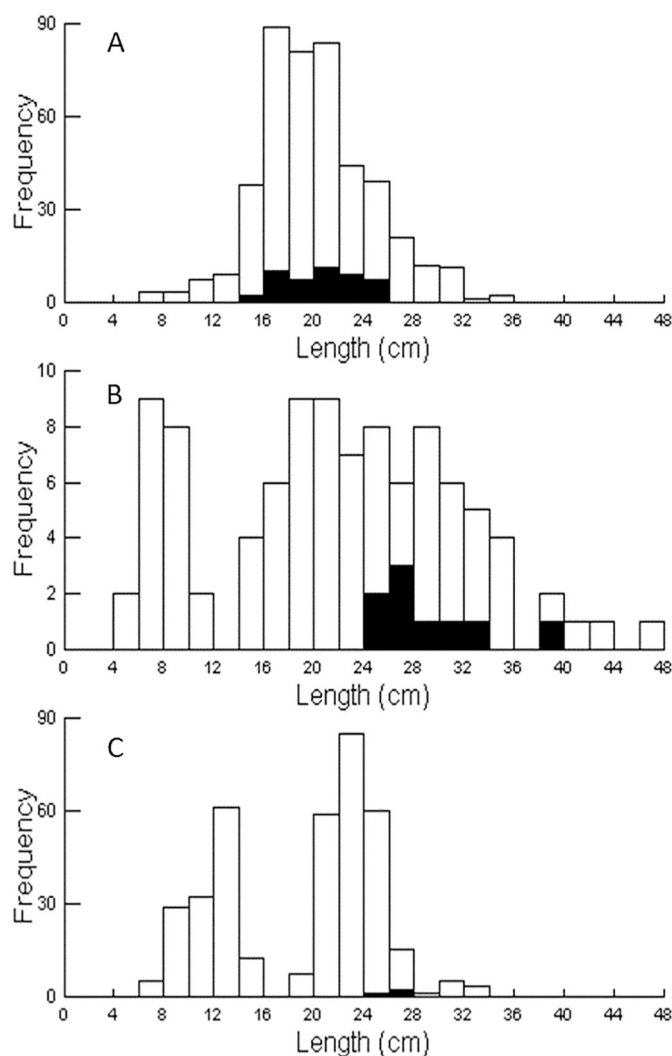
Fig. 3. Length-frequency distributions of predators on 0-group cod and saithe. A) shorthorn sculpin, B) cod and C) saithe. Predators with 0-group cod or saithe in their stomachs have black bars and those without have white bars.

Table 3

Empirical *P*-values for two-sided tests for equality of average values from Monte Carlo simulation for pairs of years for the following variables: CPUEs, average catch of sculpins per gill net per day; MSC, mean number of 0-group per sculpin stomach; N_h, average number of 0-group cod and saithe per beach seine haul, and Z_m, predation mortality rate from shorthorn sculpins. P-values that are below $\alpha = 0.025$ are underlined. The year with the highest value in the pairwise tests is shown in brackets.

Variable	2013 vs. 2014	2013 vs. 2015	2014 vs. 2015
$CPUE_s$	0.25	0.032 (2013)	0.010 (2014)
MSC	0.008 (2013)	0.69	0.006 (2015)
N_h	0.002 (2013)	0.54	0.026 (2015)
Z_m	0.44	0.64	0.25

higher occurrence (FO = 42%) than in sculpins shorter than 25.1 cm (FO = 19%) ($\chi^2 = 8.05$, df = 1, $p = .005$). Rock gunnel had a similar FO, of 6 and 8% respectively, in the long and short groups of sculpins ($\chi^2 = 0.02$, df = 1, $p = .88$). The sculpins cannibalized were small (< 4.2 cm in length) and the FO of cannibalism was on average 1.1%.

The average number of 0-group cod and saithe per sculpin stomach was higher in 2013 and 2015 than in 2014 (Table 3). 0-group cod and saithe occurred in only 6% of the sculpin stomachs in 2014, while the corresponding number in 2015 was 14%. For cod, shrimp had a higher FO (37 vs. 8%) in 2015 than in 2014 (Fig. 4), but the difference was not significant ($\chi^2 = 1.81$, df = 1, $p = .18$). Correspondingly, for saithe, sandeel had a higher FO (37 vs. 29%) in 2015 than in 2014 (Fig. 4) but this was not significant either ($\chi^2 = 0.72$, df = 1, $p = .40$). Saithe stomachs typically contained 5–12 sandeels and their stomachs were distended (SM2). In contrast, cod stomachs with sandeel usually contained only one, and appeared almost empty. Sandeels from saithe
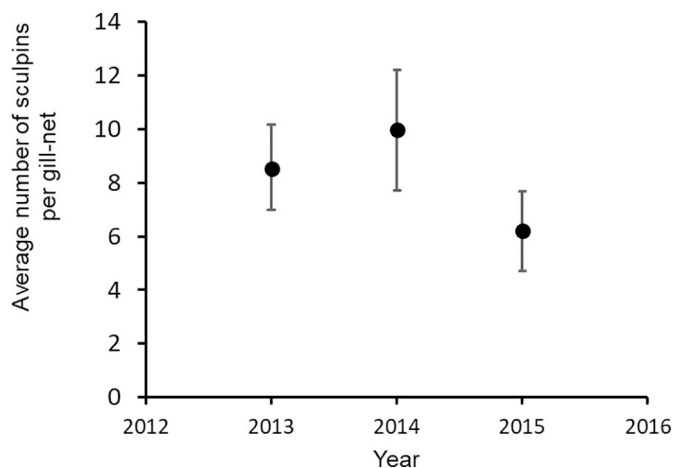
Fig. 5. Average number of sculpins per gill net from 6 locations sampled 3 times each year. Error bars show bootstrapped 95% confidence intervals.

stomachs had individual weights of about 0.8 g, and although sandeels were an important item in the diet of saithe, they had a low FO in cod and sculpin stomachs (Fig. 4). Anomura/Brachyura ("crabs") had an FO of 20 and 26% in sculpins in 2014 and 2015. The proportion of empty stomachs in sculpins was significantly higher (42 vs. 28%) in 2014 than in 2015 ($\chi^2 = 5.68$, df = 1, $p = .017$).

The average catch of sculpins per gill net per day was similar in 2013 and 2014, but was significantly lower in 2015 than in 2013 and 2014 (Fig. 5, Table 3). Only one of 54 gill-nets did not catch shorthorn sculpin (Table SM3, SM4 & SM5).
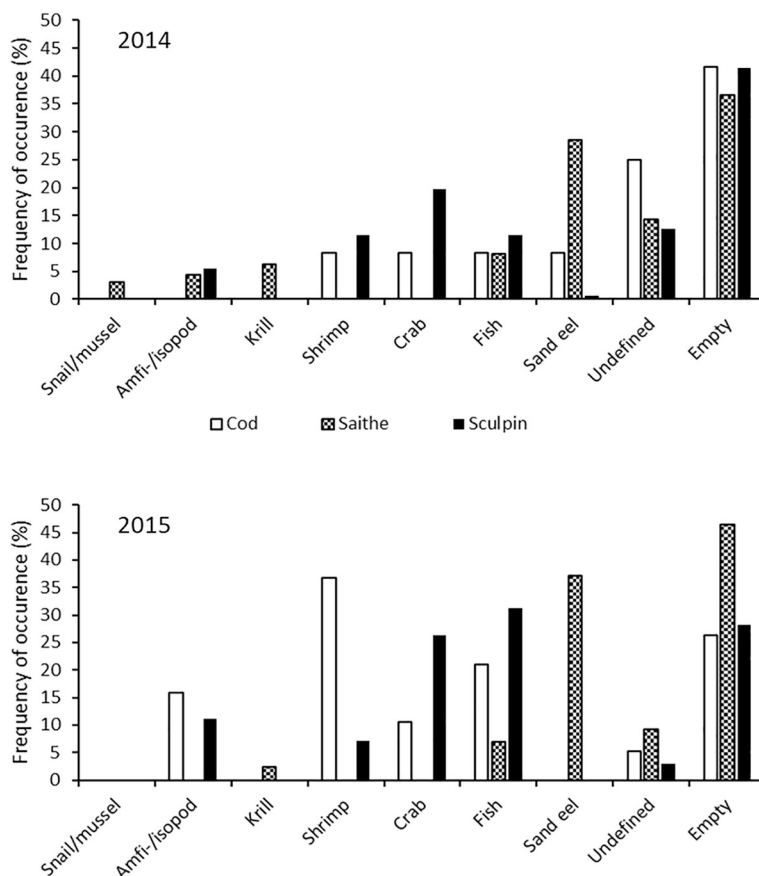
Fig. 4. Frequency of occurrence of various prey categories in Atlantic cod, saithe and shorthorn sculpin in 2014 and 2015. 0-group cod and saithe are included in the "fish" category, while sandeel is shown separately because it was such an important prey item in saithe.

Table 4

Overview of estimates of population size (N_{sar}) of shorthorn sculpin within the mark-recapture areas in 2016, area, density (N_{sm}), average catch per gill net night the first sampling day ($CPUE_{ar}$) and effective catching area (q, m^2) of the NORDIC gill nets. 95% confidence intervals for N_{sar} are given in brackets.

Mark-recapture area	N_{sar} (95% CI)	Area (m^2)	N_{sm} (ind. m^{-2})	$CPUE_{ar}$ (SD)	q (m^2)
M1 (Holmfjord	972 (564, 1677)	32,616	0.0298	6.67 (6.66)	224
M2 (Reinøy)	472 (254, 876)	9113	0.0518	8.67 (1.53)	167

3.2. Catching area from mark-recapture experiments (data set B)

The population estimates for shorthorn sculpins within the mark-recapture areas in M1 (Holmfjord) and area M2 (Reinøy) were 972 and 472 individuals respectively (Table 4). The effective catching area (q) of the Nordic gill nets was estimated from the mark-recapture experiment in 2016 as 224 and 167 m^2 for M1 and M2 respectively, and the pooled average value for q was 196 m^2 (95% CI; 115, 328).

3.3. Digestion rate and prey recognition experiments

Digestion rates of shorthorn sculpin fed 0-group saithe were very similar in the two experiments conducted at temperatures of 3 and 5.4 °C (Fig. 6).

At 24 h after ingestion all preys were recognizable as 0-group gadoids. At 48 h, three of four prey were recognizable. At 72 h one of four and at 96 h no prey were recognizable (Table SM6). The time for 50% probability of prey recognition (A_{50}) in digestion rate Experiment 2 was estimated at 48.6 h (95% CI: 29.5, 75.1 h). The temperatures measured in the field were 8.8, 9.3 and 9.0 °C in 2013, 2014 and 2015, respectively. Adjusted for differences in temperature between the experiments (average of 4.2 °C in Experiment 1 and 2) and field sampling using the assumed Q_{10} of 2.18, the values for A_{50} became 34.0 h (95%CI: 20.6, 52.5), 32.7 h (95%CI: 19.8, 50.5) and 33.4 h (95%CI: 20.6, 52.5) for 2013, 2014 and 2015 respectively.

3.4. Abundance of cod and saithe juveniles, functional response and predation mortality

The average number of 0-group cod and saithe per beach seine haul was similar in 2013 and 2015 but was significantly lower in 2014 than in 2013 and 2015 (Fig. 7, Table 3, SM7 & SM8). A total of 15 sculpins were caught by a total of 24 beach seine hauls (Table SM8). All sculpins
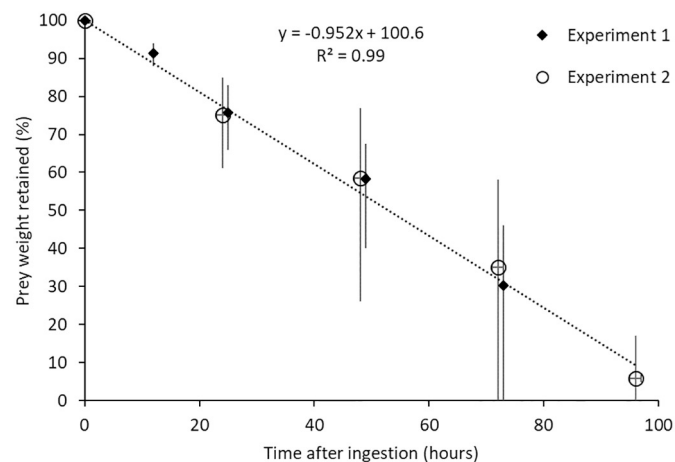

Fig. 6. Shorthorn sculpin digestion rate. Proportion of 0-group saithe prey weight (grams left in % of the initial weight of prey) retained at 5.4 °C (Experiment 1, black diamonds) and 3.0 °C (Experiment 2, white circles). Regression lines are superimposed on each other. Data points for Experiment 2 at 24, 48, and 64 h are displaced one hour to the right to show error bars. At 3 °C the last sampling was after 96 h, and at 5.4 °C the first sampling was after 12 h. Other sampling times were identical. Error bars show range of data.
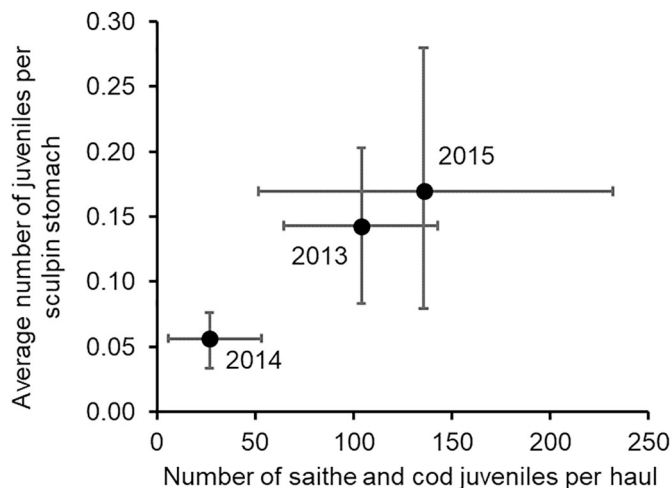

Fig. 7. Average number of 0-group cod and saithe juveniles per sculpin stomach plotted against average number of 0-group saithe and cod juveniles per beach seine haul in Porsangerfjorden for the years 2013, 2014 and 2015. Error bars show bootstrapped 95% confidence intervals.

caught by beach seine were less than 13 cm long.

The average number of juvenile cod and saithe per sculpin stomach (MSC, y-variable) increased significantly (slope > 0, bootstrap test, p = .016) with increasing number of saithe and cod juveniles per haul (N_h, x-variable) (Fig. 7).

The estimated average predation mortality rates of 0-group cod and saithe (Z_m) from shorthorn sculpins was 0.54, 1.14 and 0.40 $month^{-1}$ in 2013, 2104 and 2015, respectively. Z_m did not differ significantly between years (Table 3), and the pooled estimate was 0.70 $month^{-1}$ (95%CI: 0.30, 1.73) (Fig. 8). This corresponds to a monthly mortality of 50% $month^{-1}$ (95%CI: 26%, 82%). For all years, the output Z_m from the Monte Carlo simulations had relatively high absolute correlation (r_s) values ranging from 0.31 to 0.67 to the abundance of 0-group juveniles estimated from beach seine hauls (N_h), catching area of gill nets (q), average number of 0-group fish per sculpin stomach (MSC) and prey recognition times (A_{50}) (Table 5). Z_m were less correlated (r_s < 0.24) with sculpin gill net CPUE ($CPUE_s$) (Table 5).

The sensitivity analysis on effects of changes in input variables on Z_m resulted in very similar patterns all three years (Table SM9). A 20% increase in q, A_{50} and N_h resulted in a 17% decrease in Z_m from sculpins on 0-group cod and saithe. A 20% decrease in the same input variables resulted in a 25% increase in Z_m. A 20% increase in $CPUE_s$ and MSC gave 20% increase in Z_m and a 20% decrease in the same variables gave a 20% decrease in Z_m. Cancellation of the temperature adjustment of time for 50% prey recognition (A_{50}) resulted in a 30–33% decrease in Z_m (Table SM9).

Calculation of possible predation mortality rates from cod and saithe on 0-group cod and saithe were done for plausible values of effective catching area for the gill-nets (q) ranging from 141 to 605 m^2 (Table SM10). This resulted in ranges of monthly mortality values from cod and saithe predation for the years 2013–2015 corresponding to 4–36% and 0–17% of the mortality from shorthorn sculpin predation, respectively (Table SM10). The lowest assumed q of 141 m^2 resulted in the largest predation mortalities from cod and saithe, but the sum of
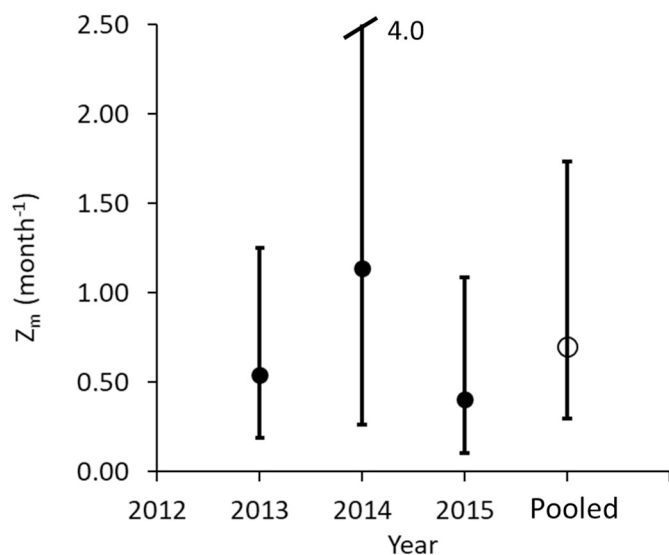
Fig. 8. Average predation mortality rate (month^{-1}) for cod and saithe juveniles due to predation from shorthorn sculpins for the years 2013, 2014 and 2015. Error bars show 95% confidence intervals estimated by Monte Carlo simulation. White circle shows pooled estimate for 2013, 2014 and 2015. Note that the maximum of the error bar in 2014 is 4.0 month^{-1}.

Table 5

Correlation (Spearman rank correlation, r_s) between predation mortality rate (Z_m, month^{-1}) from shorthorn sculpin on 0-group cod and saithe and input values (q, CPUE$_s$, MSC, A$_{50}$, N$_h$,) resulting from 1000 bootstrap replicates of the Monte Carlo simulation; q, gill net effective catching area (m^2); CPUE$_s$, catch of sculpins per gill net per day; MSC, mean number of 0-group per sculpin stomach; A$_{50}$, average time for 50% probability of prey recognition; N$_h$, average number of 0-group cod and saithe per beach seine haul for four stations.

Year	q	CPUE$_s$	MSC	A$_{50}$	N$_h$
2013	−0.58	0.18	0.44	−0.49	−0.45
2014	−0.46	0.22	0.31	−0.37	−0.67
2015	−0.41	0.24	0.48	−0.34	−0.58

predation mortality from cod and saithe each year always amounted to less than 47% of the mortality from sculpin predation.

4. Discussion

4.1. Main findings

The high occurrence of 0-group cod and saithe in the stomachs of shorthorn sculpin, and the high number of shorthorn sculpins caught per gill net relative to saithe and cod, suggest that predation from shorthorn sculpins may be very important. Each predatory fish species had different alternative prey to 0-group gadoids: shrimps for cod; sandeels for saithe; and Brachura/Anomura for shorthorn sculpin. The between-year patterns in mean number of 0-group fish per sculpin stomach and number of 0-group fish per beach seine haul were similar. The abundance of 0-group gadoids was lowest and the predation mortality rate was highest in 2014, suggesting an inverse pattern between 0-group gadoids abundance and predation mortality rates from sculpins.

4.2. Comparison of predator diets and alternative prey

In this study, the frequencies of occurrence of 0-group cod and saithe per predator stomach were similar in shorthorn sculpin and cod, and they were relatively high (FO approximately 6–14%) compared to the occurrence of small cod juveniles (FO < 2%) in the stomachs of

northeast Arctic cod in the Barents Sea (Bogstad et al., 1994) and in Norwegian Coastal cod (FO approximately 2.5%) (Pedersen and Pope, 2003). Capelin is an important prey source for cod in the Barents Sea and Yaragina et al. (2009) showed that the FO of cod prey in the stomachs of large cod from the Barents Sea may reach approximately 12% in periods with low capelin abundance. This suggests that in this study, the per capita consumption of bottom-settled 0-group cod and saithe by shorthorn sculpin was relatively high and comparable to periods of high cannibalism in northeast Arctic cod. Thus, recovery of Norwegian Coastal cod may be slowed by low abundance of alternative prey and high predation mortality on newly settled 0-group cod relative to other nurseries.

The frequent occurrence of Anomura/Brachyura in the diet of the largest shorthorn sculpins suggests that they are alternative prey for shorthorn sculpin. The Arctic lyre crab *(Hyas coarctatus)* is native (Nilsen et al., 2006) and the red king crab *(Paralithodes camtschaticus)* is introduced (Jørgensen and Primicerio, 2007) to the fjord systems in northern Norway. The Anomura/Brachyura prey group comprises several species and age-groups and is likely to be a stable prey source. For predatory cod, shrimps, amphipods and isopods were alternative prey to 0-group gadoid juveniles. For saithe, sandeels were an important alternative prey with a high FO. In the Tanafjord estuary in northern Norway, sandeels were very abundant and seemed to saturate a number of predators including piscivorous birds, saithe, cod and other fish species (Svenning et al., 2005). Our study suggests that sandeels had a less dominant role as alternative prey for cod and saithe in Porsangerfjorden. The pelagic feeding habits and high schooling tendency of predatory saithe suggest that they may aggregate on abundant prey and may have a larger predatory potential on pelagic 0-group juveniles before and during settlement than after settlement. In support of this, a relatively high FO (approximately 20%) of gadoid juvenile prey was found in stomachs of 20–40 cm long saithe in June and August in northern Norway (Aas, 2007). That the main predators had different alternative prey mean that it is likely that at least some predator populations will be able to sustain a relative high abundance if 0-group gadoid prey are not abundant.

4.3. Uncertainty in predation mortality estimation

The mortality modelling relied on the assumptions that sculpins and 0-group cod and saithe were evenly distributed across the 0–15 m depth range. In support of this, underwater video recordings from Porsangerfjorden indicated that the density of 0-group gadoids was similar at depths ranging from 0 to 15 m (Michaelsen, 2012). The low number of shorthorn sculpins caught by beach seine was most likely due to the low density of shorthorn sculpins during daytime in the 0–3 m depth range covered by beach-seine. Shorthorn sculpins are known to have pronounced diel movements from deeper to very shallow water at night (Gibson et al., 1998; Methven et al., 2001; Pihl and Wennhage, 2002), and this could explain the low catch rates of sculpins in beach seine hauls during the day.

The fact that shorthorn sculpins were the most frequent predator caught by gill nets and that they had a relatively high frequency and average number of 0-group cod and saithe in their stomachs, indicates that they may be the most important fish predator on settled 0-group cod and saithe. It was not possible to estimate the effective catching area for cod and saithe using mark-recapture methods. However, calculations with plausible literature based values for catching area for cod and saithe resulted in predation mortality from cod and saithe that were less than 47% of the predation mortality from shorthorn sculpin supporting that predation from sculpins was more important than from cod and saithe. In a tethering study with 0-group Atlantic cod as prey in Canadian waters, the ratio of predatory cod/shorthorn sculpin predators captured on tether lines was ca. 4 while the ratio of abundance from beach seine hauls of Atlantic cod/shorthorn sculpin predators in the same study was ca. 3 (Linehan et al., 2001). Thus, both the tethering

study and our study suggest that the per capita predator efficiency of cod and shorthorn sculpin on 0-group gadoids may be similar, but the abundance of shorthorn sculpin abundance relative to predatory cod in Porsangerfjorden is very high.

The linear gastric evacuation observed in our study was similar to results from earlier experiments with shorthorn sculpin (Bagge, 1977), but a square root model is more common (Temming and Herrmann, 2003). Bagge (1977) observed that at 14–15 °C and 8–10.4 °C, the times taken for 50% of a meal to be retained were approximately 50 and 88 h respectively. This is relatively long compared to the time of 50 h for 50% of prey retained in our experiment at 3.4 and 5 °C. The assumed Q_{10} of 2.18 used to adjust prey recognition times to field conditions was based on an experiment with whiting, but there is some uncertainty if digestion rate of shorthorn sculpin has the same temperature response as whiting. The effect of the temperature adjustment on Z_m is quite large as cancellation of the temperature adjustment gave ca 30–33% lower predation mortalities. The use of frozen prey in the digestion experiment may have biased the A50 towards a lower value since frozen prey are digested faster than fresh prey (Jackson et al., 1987).

The estimated predation mortality due to sculpin predation depended on several input variables with associated uncertainties. The sensitivity analysis revealed that a $+/-$ 20% change in each input variable had an effect of similar magnitude on Z_m. The fact that 0-group abundance (N_h), gill net catching area (q), mean number of 0-group per sculpin stomach (MSC) and prey recognition time (A_{50}) had similar, relatively high correlations with the output predation mortality rate in the Monte Carlo simulation suggests that uncertainties in these input variables contributed most to the uncertainty in the predation mortality rate. That sculpin catch per gillnet ($CPUE_s$) had lower correlation with Z_m and contributed less to the uncertainty than the other variables is due to the lower variability in $CPUE_s$. Despite the uncertainties and the relatively large confidence intervals of the predation mortality rate estimates, the estimates were informative and comparable to mortality estimates for other species during the post-settlement period (Table 6).

4.4. Functional response and predation synergies

Predation mortality rate from shorthorn sculpin did not differ significantly between years, but the number of 0-group fish per sculpin stomach appeared to increase linearly with increasing abundance of 0-group prey resembling a type I functional response (linear relationship) or the lower parts (low prey abundance) of type II and III responses (curved relationships) (Holling, 1959). This suggests that shorthorn sculpins were not saturated by 0-group gadoid prey. Given the observed FO of 6–14% for 0-group cod and saithe in shorthorn sculpin stomachs and the relatively high frequency of empty stomachs and relatively slow digestion rate, it is likely that the density of 0-group prey was too low to saturate the sculpins.

Laboratory experiments suggest that the presence of both predatory cod and shorthorn sculpin may contribute to synergistic and increased predation on gadoid juveniles compared to when a single type of predator is present (Strand et al., 2020). Synergistic predation by cruising transient midwater predatory fish and reef-resident predators resulted in density-dependent mortality amongst juvenile fish in a coral reef in

the post-settlement period (Hixon and Carr, 1997). Mortality in the absence of either of the two predator types was density-independent. The predatory synergism was explained by a lack of prey refuges for the juveniles when both types of predators were present. A density-dependent pattern in mortality has also previously been suggested for juvenile cod (Sundby et al., 1989; Myers and Cadigan, 1993). Since mortality in the juvenile stage may be an important determining factor for year class strength (Sissenweine, 1984; Laurel et al., 2017), identifying the sources and magnitudes of those mortalities could be important for the management of stocks such as the Norwegian Coastal cod.

4.5. Comparison of predation mortality from ambush and cruising predators

That the assessed predation mortality rates from Atlantic cod and saithe on 0-group were less than 47% the predation mortality from shorthorn sculpin is likely a result of the low abundance of predatory cod and the low per capita predation from saithe compared to the high abundance and high per capita predation of shorthorn sculpin in Porsangerfjorden. In support of this, the cannibalism mortality amongst 0-group cod during autumn in a dense Coastal cod population in a fjord in northern Norway (Pedersen and Pope, 2003) was estimated at approximately 0.18 month^{-1} (Table 6). This is much lower than the average predation mortality rate from shorthorn sculpin on 0-group cod and saithe (0.70 month^{-1}) from shorthorn sculpin during 2013–2015 in our study which is close to the lower part of the range (ca. 0.9 to 2.5 month^{-1}) for estimates of total mortality for newly-settled Atlantic cod (Table 6). The sculpin predation mortality rate in our study is within the range of approximately 0.2–1.6 month^{-1} for mortality estimates for other species of newly-settled juveniles of Pacific cod (*Gadus macrocephalus*) and Walleye pollock (*Gadus calcogrammus*) (Laurel et al., 2016), and also for plaice (*Pleuronectes platessa*) (Table 6).

The between-year variability in abundance of 0-group cod and saithe and the predation mortality from sculpins in Porsangerfjord was inversely related with lower abundance in 2014 than in 2013 and 2015 and higher but not significantly higher predation mortality from sculpins in 2014 (Z_m = 1.14 month^{-1}) than in 2013 and 2015 (Z_m = 0.54 and 0.40 month^{-1}, respectively). This suggest that between-year variability in 0-group abundance was established already in late August at the time of beach seine sampling and that the high post-settlement sculpin predation mortality documented in this study sustained and possibly increased between-year differences in abundance. The high mortality rates after settlement in 0-group Atlantic cod seem to be common and comparable to values for other boreal gadoids (Table 6). However, higher predation mortality was observed from whiting (*Merlangius merlangius*) wiping out a large aggregation of settled cod juveniles in five days in the North Sea (Temming et al., 2007). In line with this, very high predation mortality rates of more than 50% day^{-1} have been observed in tropical coral reef fish juveniles during the first two days after settlement (Almany and Webster, 2006).

We conclude that the ambush predator shorthorn sculpin was an important predator on 0-group cod and saithe in Porsangerfjorden. This study also suggest that predation on newly settled juveniles may limit Coastal Cod recovery.

Table 6
Overview of estimated instantaneous mortality rates (Z) of fish juveniles in the period following bottom settlement. 95% confidence intervals are shown in brackets.

Area and prey species	Z (month^{-1})	Comments	Reference
Porsangerfjorden, Atlantic cod and saithe 2013–2015	0.70 (0.30, 1.73)	Mortality due to cottid predation, pooled value 2013–2015	This study
Atlantic. Cod, Sørfjord, Northern Norway	0.18	Cannibalism mortality from September to end of December	Pedersen and Pope (2003)
Atlantic cod, Georges Bank	0.90–2.50	Total mortality rate, from mortality of 3–8% day^{-1}	Lough (2010)
Pacific cod, *Gadus macrocephalus,* Gulf of Alaska	0.17–1.61	Total mortality rate	Laurel et al. (2016)
Walleye Pollock, *Gadus calcogrammus*, Gulf of Alaska	0.80–1.54	Total mortality rate	Laurel et al. (2016)
Plaice, Europe	0.60	Average for many studies	Beverton and Iles (1992)
Plaice, Sweden	1.19	For 1991 and 1992	Modin and Pihl (1994)

Declaration of Competing Interest

The manuscript has not been published and is not under consideration for publication elsewhere. We have no conflicts of interest to disclose.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jembe.2020.151396.

References

Aas, C., 2007. The predation impact of juvenile saithe (*Pollachius virens* L.) on juvenile coastal cod (*Gadus morhua* L.) and other juvenile fishes. In: Master Thesis, Norwegian College of Fisheries Science. University of Tromsø, Tromsø.

Almany, G.R., Webster, M.S., 2006. The predation gauntlet: early post-settlement mortality in reef fishes. Coral Reefs 25, 19–22.

Andersen, N.G., 1999. The effects of predator size, temperature, and prey characteristics on gastric evacuation in whiting. J. Fish Biol. 54, 287–301.

Appelberg, M., Berger, H.-M., Hesthagen, T., Kleiven, E., Kurkilahti, M., Raitaniemi, J., Rask, M., 1995. Development and intercalibration of methods in Nordic freshwater fish monitoring. Water Air Soil Pollut. 85, 401–406.

Auster, P.J., Godfrey, J., Watson, A., Paquette, A., McFall, G., 2009. Behavior of prey links midwater and demersal piscivorous reef fishes. Neotropical Ichthyology 7, 109–112.

Bagge, O., 1977. Meal size and digestion in cod (*Gadus morhua* L.) and sea scorpion (*Myoxocephalus scorpius* L.). Medd Dan Fisk Havunders N S 7, 437–446.

Bailey, K.M., 1994. Predation on juvenile flatfish and recruitment variability. Neth. J. Sea Res. 32, 175–189.

Bailey, K.M., Houde, E.D., 1989. Predation on eggs and larvae of marine fishes and the recruitment problem. Advancesin Marine Biology 25, 1–83.

Beverton, R., Iles, T., 1992. Mortality rates of 0-group plaice (*Pleuronectes platessa* L.), dab (*Limanda limanda* L.) and turbot (*Scophthalmus maximus* L.) in European waters: III. Density dependence of mortality rates of 0-group plaice and some demographic implications. Neth. J. Sea Res. 29, 61–79.

Bogstad, B., Lilly, G.R., Mehl, S., Palsson, O.K., Stefansson, G., 1994. Cannibalism and year-class strength in Atlantic cod (*Gadus morhua* L.) in Arcto-boreal ecosystems (Barents Sea, Iceland, and eastern Newfoundland). ICES Mar. Sci. Symp. 198, 575–599.

Efron, B., Tibshirani, R.J., 1993. An Introduction to the Bootstrap. Chapman and Hall Inc., New York.

Espeland, S.H., Gundersen, A.F., Olsen, E.M., Knutsen, H., Gjosaeter, J., Stenseth, N.C., 2007. Home range and elevated egg densities within an inshore spawning ground of coastal cod. ICES J. Mar. Sci. 64, 920–928.

Fevolden, S.E., Westgaard, J.I., Pedersen, T., Praebel, K., 2012. Settling-depth vs. genotype and size vs. genotype correlations at the Pan I locus in 0-group Atlantic cod *Gadus morhua*. Mar. Ecol. Prog. Ser. 468, 267–278.

Gibson, R.N., Pihl, L., Burrows, M.T., Modin, J., Wennhage, H., Nickell, L.A., 1998. Diel movements of juvenile plaice *Pleuronectes platessa* in relation to predators, competitors, food availability and abiotic factors on a microtidal nursery ground. Mar. Ecol. Prog. Ser. 165, 145–159.

Gray, B.P., Norcross, B.L., Beaudreau, A.H., Blanchard, A.L., Seitz, A.C., 2017. Food habits of Arctic staghorn sculpin (*Gymnocanthus tricuspis*) and shorthorn sculpin (*Myoxocephalus scorpius*) in the northeastern Chukchi and western Beaufort seas. Deep-Sea Res. II Top. Stud. Oceanogr. 135, 111–123.

Haddon, M., 2001. Modelling and Quantitative Methods in Fisheries. Chapman & Hall, London.

Hallfredsson, E.H., Pedersen, T., 2009. Effects of predation from juvenile herring (*Clupea harengus*) on mortality rates of capelin (*Mallotus villosus*) larvae. Can. J. Fish. Aquat. Sci. 66, 1693–1706.

Hixon, M.A., Carr, M.H., 1997. Synergistic predation, density dependence, and population regulation in marine fish. Science 277, 946–949.

Holling, C.S., 1959. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. The Canadian Entomologist 91, 293–320.

ICES, 2018. Report of the Arctic Fisheries Working Group (AFWG), 18–24 April 2018, Ispra, Italy. ICES CM 2018/ACOM. (06:859 pp).

Ivanova, S.V., Kessel, S.T., Landry, J., O'Neill, C., McLean, M.F., Espinoza, M., Vagle, S., Hussey, N.E., Fisk, A.T., 2018. Impact of vessel traffic on the home ranges and movement of shorthorn sculpin (*Myoxocephalus scorpius*) in the nearshore environment of the high Arctic. Can. J. Fish. Aquat. Sci. 75, 2390–2400.

Jackson, S., Duffy, D., Jenkins, J., 1987. Gastric digestion in marine vertebrate predators: in vitro standards. Funct. Ecol. 287–291.

Jakobsen, T., 1987. Coastal cod in northern Norway. Fish. Res. 5, 223–234.

Jørgensen, L.L., Primicerio, R., 2007. Impact scenario for the invasive red king crab *Paralithodes camtschaticus* (Tilesius, 1815) (Reptantia, Lithodidae) on Norwegian, native, epibenthic prey. Hydrobiologia 590, 47–54.

Larsen, L.H., Pedersen, T., 2002. Migration, growth and mortality of released reared and wild cod (*Gadus morhua* L.) in Malangen, northern Norway. Sarsia 87, 97–109.

Laurel, B.J., Brown, J.A., 2006. Influence of cruising and ambush predators on 3-dimensional habitat use in age 0 juvenile Atlantic cod *Gadus morhua*. J. Exp. Mar. Biol. Ecol. 329, 34–46.

Laurel, B.J., Knoth, B.A., Ryer, C.H., 2016. Growth, mortality, and recruitment signals in age-0 gadids settling in coastal Gulf of Alaska. ICES J. Mar. Sci. 73, 2227–2237.

Laurel, B.J., Cote, D., Gregory, R.S., Rogers, L., Knutsen, H., Olsen, E.M., 2017. Recruitment signals in juvenile cod surveys depend on thermal growth conditions. Can. J. Fish. Aquat. Sci. 74, 511–523.

Lie, U., 1961. On the growth and food of 0-group coalfish, *Pollachius virens* (L.) in norwegian waters. Sarsia 3, 1–35.

Linehan, J.E., Gregory, R.S., Schneider, D.C., 2001. Predation risk of age-0 cod (*Gadus morhua*) relative to depth and substrate in coastal waters. J. Exp. Mar. Biol. Ecol. 263, 25–44.

Loken, S., Pedersen, T., Berg, E., 1994. Vertebrae numbers as an indicator for the recruitment mechanism of coastal cod of northern Norway. In: ICES Marine Science Symposia. 1991. International Council for the Exploration of the sea, Copenhagen, Denmark, pp. 510–519.

Lough, R.G., 2010. Juvenile cod (*Gadus morhua*) mortality and the importance of bottom sediment type to recruitment on Georges Bank. Fish. Oceanogr. 19, 159–181.

Luksenburg, J.A., Pedersen, T., 2002. Sexual and geographical variation in life history parameters of the shorthorn sculpin. J. Fish Biol. 61, 1453–1464.

Methven, D., Haedrich, R., Rose, G., 2001. The fish assemblage of a Newfoundland estuary: diel, monthly and annual variation. Estuar. Coast. Shelf Sci. 52, 669–687.

Michaelsen, C., 2012. Habitat choice of juvenile coastal cod: the role of macroalgae habitats for juvenile coastal cod (*Gadus morhua* L.) in Porsangerfjorden and Ullsfjorden in northern Norway. In: Master thesis. Department of Arctic and Marine Biology. University of Tromsø, Tromsø.

Modin, J., Pihl, L., 1994. Differences in growth and mortality of juvenile plaice, *Pleuronectes platessa* L., following normal and extremely high settlement. Neth. J. Sea Res. 32, 331–341.

Myers, R.A., Cadigan, N.G., 1993. Density-dependent juvenile mortality in marine demersal fish. Can. J. Fish. Aquat. Sci. 50, 1576–1590.

Nilsen, M., Pedersen, T., Nilssen, E.M., 2006. Macrobenthic biomass, productivity (P/B) and production in a high-latitude ecosystem, North Norway. Marine Ecology-Progress Series 321, 67–77.

North, B., Curtis, D., Sham, P., 2003. A note on the calculation of empirical P values from Monte Carlo procedures. Am. J. Hum. Genet. 72, 498–499.

Olsen, E., Aanes, S., Mehl, S., Holst, J.C., Aglen, A., Gjosaeter, H., 2010. Cod, haddock, saithe, herring, and capelin in the Barents Sea and adjacent waters: a review of the biological value of the area. ICES J. Mar. Sci. 67, 87–101.

Olson, R.J., Boggs, C.H., 1986. Apex predation by yellowfin tuna (*Thunnus albacarus*): independent estimates from gastric evacuation and stomach contents, bioenergetics, and cesium concentrations. Can. J. Fish. Aquat. Sci. 43, 1760–1775.

Pedersen, T., Pope, J.G., 2003. How may feeding data be integrated into a model for a Norwegian fjord population of cod (*Gadus morhua* L.). Sci. Mar. 67 (Suppl. 1), 155–169.

Pihl, L., Wennhage, H., 2002. Structure and diversity of fish assemblages on rocky and soft bottom shores on the Swedish west coast. J. Fish Biol. 61, 148–166.

Schwarz, C.J., Arnason, A.N., 1996. A general methodology for the analysis of capture-recapture experiments in open populations. Biometrics 860–873.

Sissenweine, M.P., 1984. Why do fish populations vary ?: Exploitation of marine communities. In: Dahlem Workshop Report. vol 32 Springer, Berlin, Heidelberg.

Strand, H.K., Pedersen, T., Christie, H., Moy, F., 2020. Synergism between cruising cod and ambush sculpin predators on 0-group gadoids is modified by daylight cycle and presence of agressive wollfish. J. Exp. Mar. Biol. Ecol. 526, 151356.

Sundby, S., Bjørke, H., Soldal, A., Olsen, S., 1989. Mortality rates during the early life stages and year class strength of the Arcto-Norwegian cod (Gadus morhua L.). In: Rapports et Procès-Verbaux des Réunions Conseil Permanent International pour l'Exploration de la Mer. 191. pp. 351–358.

Svenning, M.A., Borgstrøm, R., Dehli TO, Moen, G., Barett, R.T., Pedersen, T., Vader, W., 2005. The impact of marine fish predation on Atlantic salmon smolts (*Salmo salar*) in the Tana estuary, North Norway, in the presence of an alternative prey, lesser sandeel (*Ammodytes marinus*). Fish. Res. 74, 466–474.

Temming, A., Herrmann, J.P., 2003. Gastric evacuation in cod - prey-specific evacuation rates for use in North Sea, Baltic Sea and Barents Sea multi-species models. Fish. Res. 63, 21–41.

Temming, A., Floeter, J., Ehrich, S., 2007. Predation hot spots: large scale impact of local aggregations. Ecosystems 10, 865–876.

Tupper, M., Boutilier, R.G., 1995. Effects of habitat on settlement, growth, and postsettlement survival of Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 52, 1834–1841.

White, G.C., Burnham, K.P., 1999. Program MARK: survival estimation from populations of marked animals. Bird study 46, S120–S139.

Yaragina, N.A., Bogstad, B., Kovalev, Y.A., 2009. Variability in cannibalism in Northeast Arctic cod (*Gadus morhua*) during the period 1947-2006. Mar. Biol. Res. 5, 75–85.