

Synergism between cruising cod and ambush sculpin predators on 0-group gadoids is modified by daylight cycle and presence of aggressive wolffish

H.K. Strand^{a,*}, T. Pedersen^b, H. Christie^c, F. Moy^a

^a Institute of Marine Research, P.O. Box 1870, Nordnes, 5817 Bergen, Norway

^b Department of Arctic marine Biology, UiT, The Arctic University of Norway, P.O. Box 6050, Langnes, 9037 Tromsø, Norway

^c NIVA, Gaustadaleen 21, 0349 Oslo, Norway



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ABSTRACT

Shorthorn sculpin (*Myoxocephalus scorpius*) and large cod (300–400 g body weight) are important predators on newly settled 0-group cod (*Gadus morhua*) and saithe (*Pollachius virens*) in Porsangerfjorden in northern Norway. The Atlantic wolffish (*Anarhichas lupus*) used to be abundant but is now very rare in the fjord. Video recorded experiments showed that interactions between shorthorn sculpins, wolffish and large cod affected predation rates on small 0-group cod and saithe in tanks with a gravel, cobble and seaweed (*Fucus serratus*) substrate. We found that sculpins were unable to catch 0-group specimens when they were the only predatory species in the experimental tank and the lights were left on 24 h a day (to simulate the midnight sun), and that they did not even attempt to catch them. The addition of a large cod to the tank increased sculpin attack rates and predation success significantly.

The “cod effect” was due to 0-group specimens avoiding attacks by escaping into the cobbles or vegetation, where they could be more easily reached by the sculpins. When tanks were supplemented with a wolffish in addition to the cod, both sculpin and cod predation success was lowered by approximately 50% in the 24-h light regime. When the experimental setup was changed to a day/night light cycle, however, the wolffish presence had no effect. Also, sculpins in tanks without cod and wolffish went from consuming zero to 29% of the 0-group specimens in the tank when the light regime went from 24-h light to day/night. Sculpins and cod were most effective predators on 0-group cod and saithe at dusk/night/dawn, and the presence of a cruising predator like cod increased sculpin predation success and probably *vice versa*.

The experimental data indicate that rebuilding wolffish stocks in the fjord system may make the bottom substrate more protective for 0-group specimens of cod and saithe, by limiting the foraging volume of an effective bottom-dwelling 0-group predator like the sculpin. Further field and lab studies must be conducted before the reported findings optionally can be turned into a management advice.

1. Introduction

Norwegian coastal cod (CC) has unique population components in most Norwegian fjords, but their stocks north of 62°N collapsed in the 1990s, and have not subsequently recovered (ICES, 2018). The experimental study reported here is a follow-up of a three-year (2013–2015) field study in Porsangerfjorden within the CC collapse zone (Pedersen et al., in submission), where we sampled the shallow 0-group cod and saithe settlement areas and found that the bottom-dwelling predator shorthorn sculpin (*Myoxocephalus scorpius*) was surprisingly abundant. Shorthorn sculpins are bottom-dwelling predators that inhabit marine and brackish water and are widely distributed in the northern hemisphere between 40 and 83°N, including both the

Pacific and Atlantic oceans (Parin et al., 2002; Ray and Robins, 2016). On average, 10% of the sampled sculpin stomachs from Porsangerfjorden contained either a 0-group saithe or cod specimen. Cod caught in the settlement areas had a comparable frequency of occurrence to 0-group gadoids (9%), but they were four times less abundant in the gill net catches. While cod are generalist cruising predators (Laurel and Brown, 2006), shorthorn sculpins are generalist ambush predators (Atkinson and Percy, 1992), and both species are also previously known to consume 0-group cod in the settlement areas (Linehan et al., 2001; Laurel et al., 2003). Mid-water cruising and bottom predators have been shown to influence each other's predation success (Hixon and Carr, 1997; Stallings and Dingeldein, 2012; Auster et al., 2013).

The Atlantic wolffish (*Anarhichas lupus*) was previously common in

* Corresponding author.

E-mail address: hansk@hi.no (H.K. Strand).

the fjords of northern Norway, but currently the abundance is very low. The Atlantic wolffish is distributed on both sides of the North Atlantic at depths of 4 to 550 m (Falk-Petersen and Hansen, 1991). Its main prey items are sea urchins, crabs, gastropods and bivalves (Falk-Petersen et al., 2010).

There is growing evidence on temperate continental shelves that the removal of top predators causes mesopredator release (Baum and Worm, 2009). (Steneck and Sala, 2005) suggest that large carnivores in many instances heavily influence shallow benthic marine ecosystems. Thus, could the decline in the large, mainly non-piscivorous wolffish in the fjords potentially have “released” the shorthorn sculpin, making it a more important 0-group predator, for example through a more efficient interplay with cruising cod predators? Since the wolffish is mainly non-piscivorous, this might not seem likely, but these kinds of effects do not need to work exclusively through consumption, as predators can also exert their influence through non-consumptive effects on growth and behavior (Peckarsky et al., 2008). For example, under experimental conditions the mesopredator dottyback (*Pseudochromis fuscus*) continuously foraged and attacked juvenile damselfish (*Pomacentrus amboinensis*), but the visual stimulus of a top predator restricted the strike rate significantly (Palacios et al., 2016). Also, in Canadian waters it has been suggested that large piscivore fish are discouraged from entering the shallow-water cod nursery areas, due to the perceived predation risk from the river otter (*Lutra canadensis*) (Cote et al., 2008). While the reduced wolffish population may have increased sculpin predation efficiency on 0-group specimens, one could equivalently anticipate that the collapse in the piscivorous cod population in the fjord would have an opposite effect, as larger cod are known to predate on juvenile cod (Bergstad et al., 1987; Bogstad et al., 1994; Pedersen and Pope, 2003). However, the interplay between these two 0-group predators has not previously been studied.

Several studies show that predation risk for juvenile fish changes during the diurnal cycle. Predation on tethered 0-group cod was higher during the day and at dusk than at night (Linehan et al., 2001; Ruttenberg et al., 2011; Walsh et al., 2012; Davenport and Chalcraft, 2013; Campanella et al., 2019). When not tethered, predators elicit strong behavioral responses in prey in order to minimize their risk of being eaten, exemplified by young plaice (*Pleuronectes platessa*) that move shoreward in response to predators entering their habitat at dusk (Gibson et al., 1998). In Porsangerfjorden (approximately 70°N), where the current experiments took place, there are approximately two months of midnight sun during mid-summer, with day length decreasing significantly from August onwards. 0-group gadoids in this area experience both a 24-h light regime during mid-summer as well as a day/night light regime from early autumn onwards.

Behavioral studies have shown that 2+ cod foraging on 0-group juveniles were five times more active than sculpins pursuing the same matter and that the juveniles adjusted their behavior as a response to whether they were subjected to the cruising or bottom-dwelling predator (Laurel and Brown, 2006).

Since both sculpin ambush predators and cruising cod predators are simultaneously present in the 0-group gadoid settlement area, studying any dynamic interactions between them under biotic conditions like the presence/absence of wolffish and abiotic conditions like the diurnal

cycle will help us to understand how ecosystem interactions influence 0-group gadoid vulnerability. Here we investigate experimentally if shorthorn sculpin and large cod predation efficiencies on 0-group cod and saithe changed under different light conditions and with the presence or absence of wolffish.

2. Material and methods

2.1. Experimental fish

Shorthorn sculpins used in the experiments were caught with bottom-set multi-mesh gill nets that were 30 m long and 1.5 m deep (Appelberg et al., 1995). Red king crabs (*Paralithodes camtschaticus*) are attracted to and can damage sculpins within a few hours after they are entangled in the net. We also believe the sculpins to be more active during dusk and dawn. Thus, to minimize stress the nets were deployed from the afternoon until early next morning. Cod and wolffish were caught with pots measuring 95 cm × 65 cm × 80 cm (bought from www.froststad.no) and baited with herring. Caught fish were immediately transferred to a tank with running water supplemented with diffused oxygen onboard the boat. Within approximately 3 h of capture, fish were transported to the experimental facility (Porsangerfjorden field and experimental station), placed in larger tanks, and acclimatized for at least 7 days. Fish were not fed during acclimatization. Only fish that appeared to behave and move normally were used in the experiments. 0-group cod and saithe were caught close to the station with a beach seine at a depth of 0–4 m and transferred from the seine to 20 l buckets of water that were oxygenated and changed frequently. Batches of approximately 50–60 specimens were collected before being distributed to the experimental tanks in groups of five. The 0-group specimens were acclimatized for 2–3 days and specimens displaying abnormal behavior were exchanged with new fish before the start of the experiment. The wolffish and the 0-group specimens were transferred to the experimental tanks the day before the experiment started, and the large cod and sculpins were transferred simultaneously at startup. To minimize stress, weighing and measuring were conducted when the experiments were terminated after 96 h.

2.2. Experimental designs

The experiments were designed to evaluate if the presence of a naturally occurring cruising predator (cod) or wolffish would influence the 0-group predation success of a bottom-dwelling ambush predator (the sculpin). They were also designed to evaluate whether the sculpins were more successful in a day/night light regime than a 24-h light regime (Table 1). Since we would not be able to see behavior during dusk, night and dawn, only experiments run in the 24-h light regime were recorded and video-analyzed. The numerical ratio between 0-group cod and saithe used in the experiments (Table 2) was approximately as it appeared during collection on the settlement ground. In the field studies by Pedersen et al. (in submission), it was found that cod in the size range 24–38 cm predated on 0-group cod and saithe in shallow waters in a fjord in northern Norway. Thus, this size class cod was also implemented in the study.

Table 1

Average, minimum and maximum length (l) and weight (w) of experimental fish. 0-group juvenile values are based on values from tanks with zero mortality (Sculpin regime, 24-h light, Table 2).

	Sculpin		Large cod		Wolffish		Saithe 0-group		Cod 0-group	
	l (cm)	w (g)	l (cm)	w (g)	l (cm)	w (g)	l (cm)	w (g)	l (cm)	w (g)
Average	22	177	32	323	72	2937	9.0	5.8	6.6	2.0
Std	2.1	61	1.9	54	5.8	716	1.3	2.4	0.9	0.8
Min	19	93	29	232	64	2000	6.8	2.4	5.6	1.3
Max	27	335	35	406	80	4120	13.2	14.1	8.2	3.6

Table 2

Experimental regimes run with both a 24-h light and natural light regime. Number of specimens per experimental tank of the different species in the different regimes. All regimes were triplicated.

Regime	Sculpin/Cod/Wolffish	Sculpin/Cod	Sculpin
	Sculpin (#)	Sculpin (#)	Sculpin (#)
Sculpin (#)	2	2	2
Large cod (#)	1	1	
Wolffish (#)	1		
Cod 0-group (#)	3	3	3
Saithe 0-group (#)	20	20	20

The nine tanks used were $230 \times 60 \times 100$ cm deep, and each tank was supplemented with $18\text{--}20 \text{ l min}^{-1}$ ambient seawater. Two experiments, one with a 24-h light regime and one with a day/night light cycle, were conducted and both lasted for 4 days (96 h). The bottom of each tank was covered with gravel, 10 evenly distributed cobble stones (approximately 10×20 cm) and a bundle of seaweed (*Fucus serratus*) weighing approximately 600 g and approximately 40 cm across, weighted down centrally in the tank. It was possible for the sculpins to hide themselves from view underneath the seaweed bundle.

The 24-h light regime was arranged by placing one 400 W white light metal halide lamp between pairs of two tanks, 50 cm below the tank ridges, and pointing upwards towards the ceiling. Light was scattered from the white roof into the tanks. The day/night light regime was obtained by turning off all artificial light sources and letting ambient light into the room through doors and windows, open to 50 cm below tank level. Light intensity was logged every 30 s with HOBO MX2202 light loggers placed 10 cm below the water surface. Data shown are averages from three loggers (Fig. 1). The experiments were run over the period from 30 September to 8 October. The average temperature (SD) during the experimental period was $8.5 (0.4)^\circ\text{C}$.

For video recording, two cameras were mounted per tank, one on each short wall of the treatment tanks.

2.3. Statistics and measurements

At the end of the experiment, cod and sculpin predators were first removed from the experimental tanks, anesthetized with an overdose of MS-222 and killed by cutting the spinal cord behind the neck. They were then eviscerated, and their length and weight were measured. Gut contents (partly digested 0-group specimens) were counted and weighed. Due to some 0-group specimens being digested to a point beyond recognition as individuals, a limit was set at 1 g, and only solid

content heavier than this was counted as an individual prey item. This procedure led to a discrepancy between the number of 0-group specimens counted into the experimental tanks at the start of the experiment and the total number of individuals based on gut content and remaining live specimens at its end. The discrepancy varied from 0% in the three replicates in the regime where there was no predation (sculpin/24-h light), to between 7 and 16% in the two other regimes. Data are shown for predation rates based on counts from eviscerations of cod and sculpins, but statistical analysis of predation rates was only performed on data obtained from counting remaining 0-group specimens in the tanks at the end of the experiment (Fig. 1).

In the 24-h light regime the first 12 h were video analyzed for wolffish and sculpin behavior. The recordings from both cameras in each tank were analyzed at 1–4 \times natural speed, depending on the type of activity (attacks, threatening display, positioning). Each incident was replayed at normal speed for verification. An attack was defined as the attacker orienting itself apparently purposefully, and making a fast movement towards another fish, with the result that the attacked fish was either caught (0-group specimens) or escaped (0-group specimens, sculpin and large cod).

Also, in the 24-h light regime, cod were analyzed for attack rate on cod and saithe 0-group specimens, but only for the first 6 h, since recording these data was more resource-intensive. Since cod swim almost continuously, and 0-group specimens attempt to escape when the cod approach, the videos had to be played at normal speed to identify cod foraging behavior. Typically, the cruising cod would come to a halt when approaching a group of 0-group specimens, maneuvering with its pectoral fins and then suddenly increase speed during a pursuit phase. There were large variations in the duration of the pursuit phase, however, from short bursts, as if to test or habituate the prey, to consistent tracking of the 0-group specimens along their escape route. Also, cod could change from cruising to attack in a moment when an opportunity presented itself, for example when a 0-group specimen escaped an attack from a sculpin. It was typically not possible to verify whether a 0-group specimen was caught when attacked by a cod or sculpin whether a 0-group specimen attacked by a cod or sculpin was caught or not.

Differences in mortality rates between regimes were tested for significance using a Chi-squared test with Yates' continuity correction, in R (R., 2013). No significant differences between replicates were demonstrated and these were therefore pooled for further comparisons. Shapiro-Wilk's method was used for normality test of 0-group length and weight data. As some of the datasets did not meet the normality criteria ($p < .05$), further comparisons were conducted with the Mann-Whitney (M-W) test. Since there was no predation in the 24-h light regime with only sculpins present, 0-group specimens from these tanks

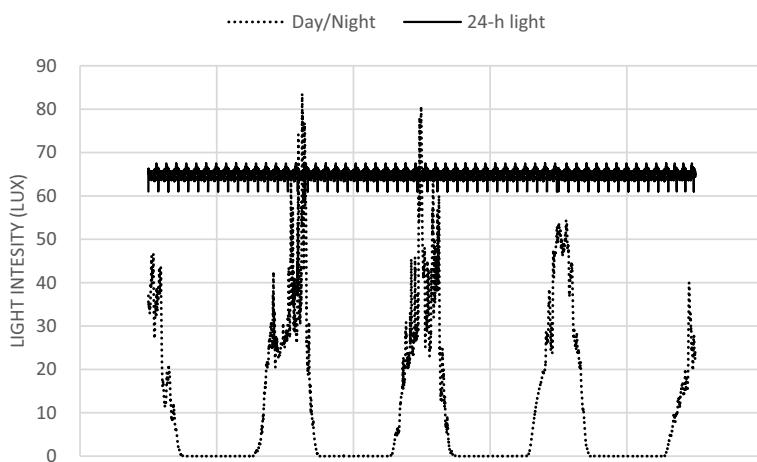


Fig. 1. Light intensity during the 96-h experimental period (from 12:00 pm to 12:00 pm). Day/night and 24 h light regimes are shown with dotted and solid lines respectively.

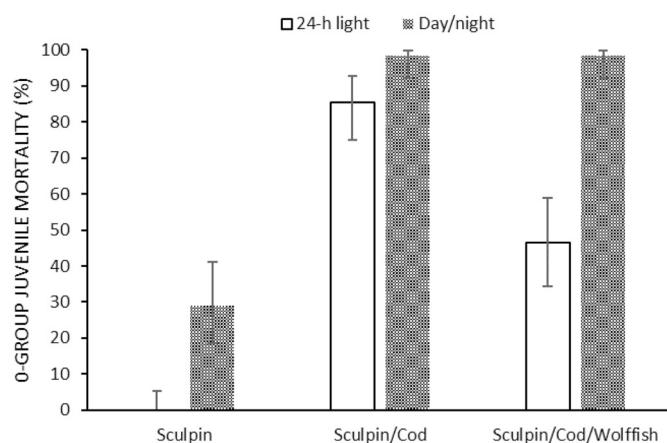


Fig. 2. Average 0-group mortality (saithe and cod combined) with Sculpin/Wolffish/Cod, Sculpin/Cod or only Sculpins in the tank, during 96 h with a 24-h or a day/night light regime. 95% confidence intervals shown as error bars.

represented the unpredated populations in the analyses. Confidence intervals for proportion mortality in various regimes were estimated assuming binomial error distribution and the function exactci in R. Generalized linear mixed models (GLM, glm function in R) with a Poisson error distribution or Quasipoisson option when data were overdispersed (*i.e.* variance > mean) were used to compare attack rates and estimate 95% confidence intervals for number of preys caught per predator.

3. Results

0-group specimens were captured by predators in all regimes (sculpins, sculpins + cod, sculpins + cod, sculpins, wolffish) and in a day/night as well as a 24-h light regime, except when sculpins were the only predators in the 24-h light regime (Fig. 2). When sculpins were the only predators, 0-group mortality increased from 0 at 24-h light to almost 30% in a day/night light regime ($\chi^2 = 18.5$, df = 1, p < .01). When both cod and sculpins were present, 0-group mortality increased significantly from zero to 86% in the 24-h light regime ($\chi^2 = 8.73$, df = 1, p < .01) and from 29% to 99% in the day/night light regime ($\chi^2 = 15.63$, df = 1, p < .01). When a wolffish was present in the tank in addition to sculpins and cod, 0-group mortality was reduced from 86% to 46% in the 24-h light regime ($\chi^2 = 15.09$, df = 1, p < .01) but its presence had no effect on mortality (99%) in the day/night light regime ($\chi^2 = 0$, df = 1, p = 1) (Fig. 2).

Significantly fewer 0-group cod (7%) survived the experimental period than 0-group saithe (33%) ($\chi^2 = 11.55$, df = 1, p < .01). At the start of the experiment the 0-group saithe were both longer (M-W, Z = 2.4, p < .05) and heavier (M-W, Z = 2.6, p < .01) than 0-group cod specimens. Surviving 0-group cod were on average longer (7.1 cm) and heavier (2.4 g) than those present at the start (6.6 cm and 2.0 g). The differences between the 0-group cod initial and final lengths and weights were, however, not significant (M-W, p > .05 and Z = -0.9 and Z = -0.1, for lengths and weights, respectively). 0-group saithe had similar initial lengths and weights as the survivors after 96 h, being on average 9.0 cm and 5.8 g at the start and 9.0 cm and 5.7 g at the end.

In the 24-h light regime, each large cod caught on average twice as many 0-group specimens as each sculpin did (Fig. 3 a). There were, however, two sculpins and one cod in each tank, and thus one could also view the result as approximately equal numbers of 0-group specimens being caught by cruising cod and ambush sculpin predators. Alternatively, since the cod weighed on average almost twice as much as the sculpins (Table 1), approximately equal numbers of 0-group specimens were consumed by cruising as by ambush predators per unit of biomass. When a wolffish was added to the tank in the 24-h light

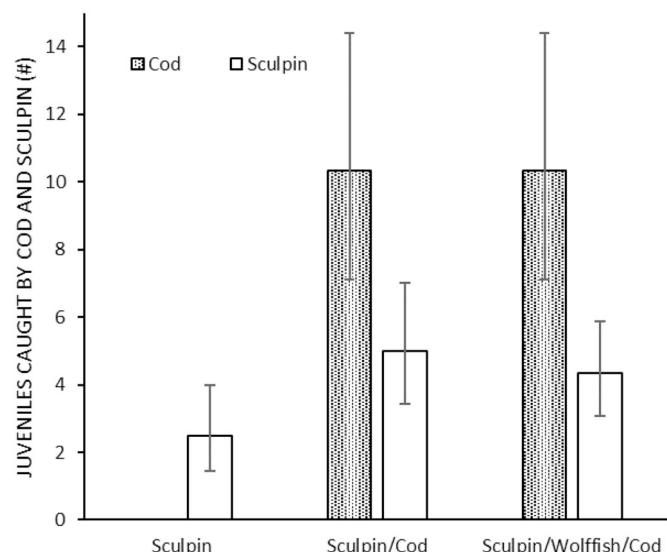
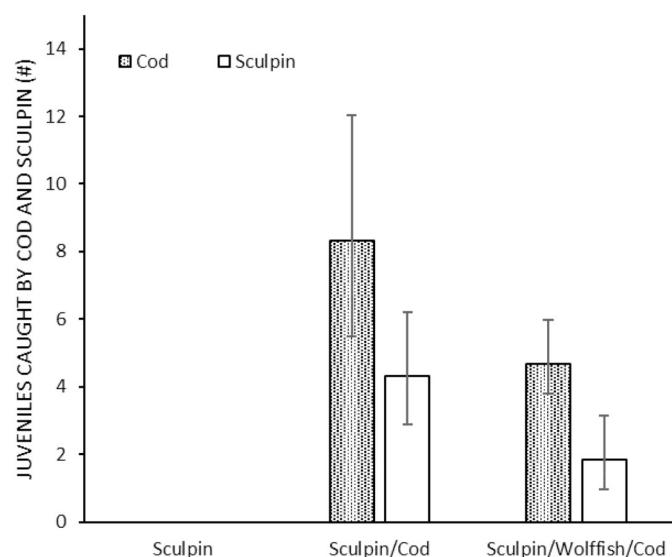


Fig. 3. Average sculpin and large cod predation rates on 0-group saithe and cod combined, based on eviscerated specimens after 96 h with a 24-h light (a) or a day/night light regime (b). 0 = zero mortality. 95% confidence intervals shown as error bars.

regime, the predation success of both sculpins and cod fell by approximately 50% (Fig. 3 a).

The most conspicuous effect of a day/night light regime compared to a 24-h light regime was that the presence of wolffish had no effect on 0-group predation by either cod or sculpins (Fig. 3 b).

The video analysis revealed that the sculpin attack rate on 0-group specimens was dramatically higher when a cod was added to the tank than when sculpins were either the sole predators or when a wolffish was present in the tank in addition to the cod (GLM, p < .01) (Fig. 4). On average only one attack per 12 h was observed when sculpins were the sole predators in the tanks (Sculpin), a number that increased to an average of 43 when a cod was added (Sculpin + Cod). The “cod effect” was nullified when a wolffish was added (Sculpin + Wolffish + Cod) (GLM, p > .05).

When sculpins were the only predators in the tank, 0-group specimens were loosely aggregated and spent most of their time in mid-water with occasional trips to the bottom or close to the surface. The 0-group specimens were never observed to swim very close to or into the centrally placed bundle of seaweed. Sculpins occasionally shifted position

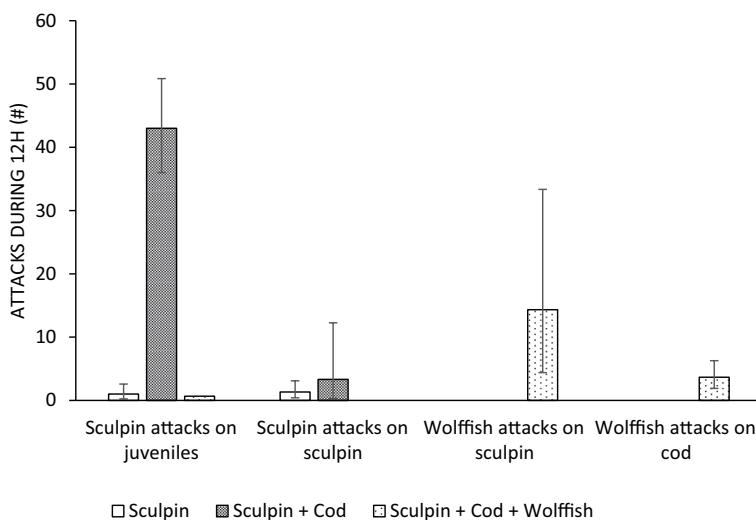


Fig. 4. Sculpin and wolffish attack rates based on video analysis of the first 12 h in the 24-h light regime. 95% confidence intervals shown as error bars.

and placed themselves under the main 0-group aggregations, but seldom launched attacks if the 0-group specimens did not come within a distance of approximately 1–1.5 sculpin body lengths. When a cod was added to the tank, the 0-group specimens changed behavior notably. Not only did they aggregate more closely, but they also started to swim ahead of the cod as it was cruising back and forth in the tank. The cod alternated between cruising and attacking 0-group specimens continuously throughout the observational period. The 0-group specimens escaped attacks by diving between cobble stones or into or behind the bundle of seaweed. Sculpins placed themselves strategically with respect to the main escape routes and launched several attacks on 0-group specimens during the observational period. Most attacks were launched from the bottom, but several attacks were launched from above or from within the bundle of seaweed.

When a tank contained a wolffish in addition to the large cod and sculpins, the average cod attack rate on 0-group specimens decreased by 38%, but the decrease in number of attacks was not significant (GLM, $p > .05$). The large cod generally alternated between cruising and attacking 0-group specimens, but sometimes inspected cobblestones and the bundle of seaweed more closely. When they tried to jolt hiding 0-group specimens out of the bundle of seaweed by pushing their snout into it, they were occasionally chased off by the wolffish. On average the wolffish attacked cod 3.7 (0.6) times during the 12-h observational period, but the large cod easily avoided contact by changing its swimming direction. The cod were also observed to engage in foraging behavior towards 0-group specimens just after a wolffish interaction.

The wolffish effect on the sculpins' behavior was much more pronounced. Not only did the wolffish attack the sculpins much more frequently than cod, the sculpins mainly lay still without launching attacks on 0-group specimens even when the large cod's behavior brought them within reach. Also, the sculpins were typically attacked by the wolffish when they tried to place themselves strategically with respect to the main 0-group escape routes. The sculpins could, however, shield themselves from observation by hiding under the bundle of seaweed.

Sculpins occasionally attacked other sculpins, either by chasing them off directly or by approaching sideways with undulating body movements. The behavior was never observed in the tanks with wolffish and it happened almost three times more often when a cod was also present than when sculpins were the only predators in the tanks (Fig. 4). The differences between sculpin-sculpin attack rates were, however, not significant (GLM, $p > .05$).

4. Discussion

Both sculpins and cod were effective 0-group predators in the current experiment. The presence of a cruising predator such as cod strongly increased the predation success of the bottom-dwelling sculpin ambush predator, even though the cod's own predation success reduced the number of available prey.

The presence of a wolffish reduced the predation success of both cod and sculpins, but only when the lights were on 24 h a day (midnight sun simulation). In the day/night light regime, the "wolffish effect" was nullified, indicating that the mere presence of a wolffish is not enough to cause behavioral changes in the cod and sculpin predators. Also, the much higher predation success in the day/night than the 24-h light regime indicates that a continuous light regime is more favorable to 0-group gadoid specimens' survival while dusk/night/dawn gives predators the advantage.

5. Sculpins increase their predation success in the presence of a cruising predator

In the current experiments 0-group specimens of cod and saithe were not particularly susceptible to sculpin attacks when the lights were on and the bottom-dwelling ambush sculpin was the only predator in the tank. Such circumstances will, however, rarely be the case in a natural setting. In field investigations we have found that on average 10% of sculpin stomachs contained a 0-group cod or saithe and stomachs of cod up to 35 cm had similar proportions (Pedersen et al. (in subm)). In the experimental regime with cod of this size class, however, cod stomachs contained twice the number of 0-group specimens as did the sculpins, indicating that the experimental setup was somehow to the advantage of cod. The most conspicuous effect of adding a cod was, however, that they induced a dramatic change in the 0-group behavior and vulnerability. Typically, in the presence of a large cod the 0-group specimens would aggregate more closely and approach cobble stones as well as dive behind the bundle of seaweed. In contrast, this behavior was absent in the sole presence of the sit-and-wait sculpin ambush predator. Under the latter circumstances the 0-group specimens would typically swim in the midwater and occasionally along the bottom or towards the surface, but they were never observed to swim into the vegetation. The changes in 0-group behavior induced by the presence of a cod not only increased the sculpin predation success, but also increased their attack rate on 0-group fish dramatically, from on average one to more than 40 attacks during the first 12 h. The ingestion rate went up, but the high number of attacks means that most attacks were

unsuccessful, and that escaping 0-group specimens returned to the water column where they would probably be susceptible to a second attack by the cod. Hence, the cruising and ambush predators probably amplified each other's predation success at the expense of 0-group cod and saithe survival.

While diving on a rocky reef in the Gulf of Mexico, Stallings and Dingeldein (2012) observed that prey in the absence of a cruising predator stayed just out of reach of the benthic-oriented gag (*Mycteroperca microlepis*), but when approached by the midwater-oriented greater amberjack (*Seriola dumerili*), they were pushed towards the reef where they became more vulnerable to attacks by the former. Similar observations have been made by Auster et al. (2013) who found that midwater predators caused prey species to approach the sea floor where they were attacked and consumed by demersal piscivores, where such interactions influenced the distribution and availability of prey over diel periods (Campanella et al., 2019). It has also been shown that predation on newly-settled *Chromis cyanea* was highly density-dependent only when they were simultaneously attacked by resident predators from below and transient piscivores from above, while largely density-independent in the presence of either kind of predator individually (Hixon and Carr, 1997).

During the field work period leading up to the experiments reported here, we sampled the cod and saithe settlement grounds in the wild for 3 years and found that approximately 10% of predator stomachs contained either a 0-group saithe or cod juvenile (Pedersen et al., 2020). Only rarely did we eviscerate more than one 0-group specimens from a predator stomach. In the current experiment both sculpins and large cod had captured several prey items on most occasions. Thus, our experiments were conducted in an artificial environment and should be interpreted with care. However, predators and prey often co-exist at high densities within the same habitat (Laurel and Brown, 2006) and we therefore conclude that modulations in the cod-sculpin predatory interaction revealed in our studies could have important bearings on the post-settlement 0-group gadoid survival rate in the fjord.

6. Sculpins reduce their predation success in the presence of an Atlantic wolffish

Both cod and sculpins saw their predation success reduced by 50% when a wolffish was present in the tank and the lights were on for 24 h a day. With a day/night light cycle, the wolffish effect was, however, not detected. This indicates that the wolffish was inactive during dusk/night/dawn and that cod and sculpin predation efforts are not influenced by its mere presence. Nighttime observations of wolffish that were not part of the experiment showed they sometimes laid still on their side, appearing almost dead, yet appeared healthy and accepted food the next day.

When cod were present in the tank, they induced 0-group specimens to swim closer to the cobble stones, from where the sculpins launched the lion's share of their attacks. The rate of observed attacks by sculpins on 0-group specimens plummeted when a wolffish was present. However, hidden from view under the bundle of seaweed, sculpins were probably still able to catch specimens escaping from the cod's attacks. The cod's attack rate was not significantly affected by the wolffish's presence, although its capture success rate was. The dramatically reduced attack rate of sculpins probably proportionally reduced the number of 0-group specimens returning back up the water column after an unsuccessful sculpin attack, where they would be vulnerable to a second and maybe more effective attack by the cod. In addition to some antagonism shown by the wolffish towards the cod, the decline in the number of "returns" probably explains why cod were less efficient 0-group predators when wolffish were present. Thus, in this case a cruising predator increased the predation success of an ambush predator and probably *vice versa*, and the wolffish affected both predators' success – one directly and one at least partly indirectly. A similar effect was seen when the mesopredator dottyback (*Pseudochromis fuscus*)

continuously foraged and attacked juvenile damselfish (*Pomacentrus amboinensis*), but the visual stimulus of a top predator restricted the dottyback strike rate significantly (Palacios et al., 2016). In this latter case, the top predator in question (coral trout, *Plectropomus leopardus*) is supposed to benefit from chasing off mesopredators in order to obtain better access to the resource itself.

7. The effect of prey size

Cod and saithe numerically accounted for 15 and 85% of the 0-group specimens in the tanks, respectively, which is the same ratio as they appeared in during collection from the settlement grounds. Daily mortality rates for fish are extremely high during their early development and then decrease with increasing age and size (Bailey and Houde, 1989). The fact that 0-group cod had a mortality rate that was about five times as that of 0-group saithe may be explained by cod being significantly shorter and lighter than the saithe at the start of the experiment. This seemingly contradicts observations and foraging models that predict predators should maximize prey size for energetic reasons (Werner, 1974; Gillen et al., 1981; Mittelbach, 1981; Stein et al., 1984; Perez and Munch, 2010). However, prey vulnerability is strongly affected by body size (Greene, 1983; Lundvall et al., 1999) and predator capture success is known to decrease with increasing prey size (Folkvord and Hunter, 1986; Miller et al., 1988; Rice et al., 1993; Juanes and Conover, 1994). In addition, coastal seine surveys show that both Atlantic and Pacific (*Gadus macrocephalus*) cod 0-group abundance predicts recruitment potential best when temperature conditions are favorable for optimal juvenile growth rates (Laurel et al., 2017).

If cod and saithe 0-group specimens had arrived at the settlement grounds approximately at the same time, the smaller 0-group cod would probably have been more vulnerable than 0-group saithe. However, saithe arrive at the settlement grounds before the cod (late April vs. mid-June to August on the Norwegian west coast) (Bergstad et al., 1987; Salvanes et al., 1994), and thus both species are probably exposed to predation from the two suites of predators described in this experiment when they are small and inexperienced. Saithe might, however, benefit more than cod from favorable light conditions when they arrive on the settlement grounds.

8. Diel changes in predation risk

The largest difference in regime effects from predator composition was the one observed between a 24-h light regime and a day/night light regime comprising day, dawn, night and dusk. The 0-group mortality rate was much higher with day/night light when sculpins were the only predators. If we consider the 24-h light regime as a proxy for continuous daytime, going from this regime to one including dusk/night/dawn doubled the predation success of both cod and sculpins. In apparent contradiction of these results, Anderson et al. (2007) suggested, based on 0-group cod schooling behavior, that the juveniles perceived the predation risk as higher during daytime than at night. Also, 0-group cod tethered to vegetated and unvegetated sites experienced higher predation mortality at dusk and during daytime than at night (Linehan et al., 2001). When prey is tethered, however, there are few opportunities for behavioral adjustments (Halpin, 2000). The un-tethered 0-group specimens in our experiments were frequently attacked in the 24-h light regime but were more successful at avoiding attacks than during the cycle that included dusk/night/dawn. When sculpins were the sole predators this was particularly obvious as the 0-group specimens stayed at a distance to not elicit attacks. Cod (28–33 cm in length) off Newfoundland have been shown to migrate into shallow waters to feed at night and return to less active behavior in deeper waters towards dawn (Clark and Green, 1990).

Also, with the experimental regime change from 24-h light to a day/night cycle the effect of adding a wolffish disappeared completely as 0-group mortality increased from 50% to almost 100%. If these results are

transferrable to natural conditions, the protection from increased wolffish abundance will only manifest itself during the hours where light levels are above a certain threshold, unless the wolffish's territorial behavior during daytime has an effect that lasts into the darker hours. The wolffish used to be abundant but is now rare in the Norwegian fjords. It is unknown, however, if and how far the eventual protective effect of a single wolffish would extend in the wild.

0-group specimens are younger, smaller and less skilled at predator avoidance in the summertime, but during this time of year they will reap the benefit of continuous light. Increased vulnerability from the full day/dawn/night/dusk cycle that comes with autumn might, to an unknown degree, be compensated by their increased size and experience.

Our results indicate that 0-group cod and saithe are more vulnerable to predation during a full diel cycle than under 24-h light, indicating that they are more susceptible during dusk, dawn or night than during daytime. However, our results are obtained from tank studies and are not on an equivalent scale to field conditions regarding predator-prey proximities and available area and volume and must be interpreted with care. Contradictory results obtained from tethered cod experiments or indirectly from behavioral studies likewise have their inherent limitations and must also be interpreted with care.

9. Implications for wild stocks and conclusions

Alterations in the saithe and cod 0-group mortality sources in the settlement and post settlement phase might translate into variation in recruitment to fisheries. For example, the determining factor for year class strength in walleye pollock (*Theragra chalcogramma*) not only shifted from the larval to the juvenile stage following an ecological regime shift resulting in high abundance of predatory Pacific cod (*Gadus macrocephalus*) and flatfishes (Bailey, 2000), but was generally lower when determined at the juvenile stage (Ciannelli et al., 2005).

It is not possible to determine whether sculpin abundance in Porsangerfjorden today is higher or lower than it was prior to the Coastal Cod (CC) collapse, but if for some reason sculpins have become more effective predators or their abundance have increased this might have influenced CC and saithe recruitment.

Atlantic wolffish stocks in the fjords of northern Norway fell to very low levels roughly in parallel with the decline in coastal cod stocks. Norwegian fishery statistics at present reveal a catch of less than 1000 t per year for the entire Norwegian coastline (Bakketeig et al., 2016).

It remains, however, to be verified whether these results from aquarium experiments repeat themselves in real world situations. Thus, we believe that the possible synergistic effect on newly settled cod and saithe juvenile mortality caused by bottom-dwelling and cruising predators operating in concert should be studied further. The ability of species cohabiting with the juveniles on the settlement grounds to influence such relationships would also be interesting to investigate further.

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Declaration of Competing Interest

None.

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