



# Ecosystem-level effects of large-scale disturbance in kelp forests

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**ABSTRACT:** Understanding the effects of ecological disturbances in coastal habitats is crucial and timely as these are anticipated to increase in intensity and frequency in the future due to increasing human pressure. In this study we used directed kelp trawling as a scientific tool to quantify the impacts of broad-scale disturbance on community structure and function. We tested the ecosystem-wide effects of this disturbance in a BACI design using two 15 km<sup>2</sup> areas. The disturbance had a substantial impact on the kelp forests in this study, removing 2986 tons of kelp and causing a 26 % loss of total kelp canopy at trawled stations. This loss created a 67 % reduction of epiphytes, an 89 % reduction of invertebrates and altered the fish populations living within these habitats. The effect of habitat loss on fish was variable and depended on how the different species used the habitat structure. Our results show that large-scale experimental disturbances on habitat-forming species have ecological consequences that extend beyond the decline of the single species to affect multiple trophic levels of the broader ecosystem. Our findings have relevance for understanding how increasing anthropogenic disturbances, including kelp trawling and increased storm frequency caused by climate change, may alter ecosystem structure and function.

**KEY WORDS:** *Laminaria hyperborea* · Habitat loss · Community structure · Kelp trawling

## 1. INTRODUCTION

The scale, frequency and intensity of ecological disturbances are increasing with climate change (Turner 2010, Seidl et al. 2016). At the same time, direct human use, such as harvest and fishing, are intensifying and are disturbing many marine ecosystems, reducing their resilience (Filbee-Dexter & Scheibling 2014, Ling et al. 2015). As a result, it is increasingly critical to understand the community and ecosystem-level impacts of disturbances in marine ecosystems. Kelp forests are highly productive

and diverse marine ecosystems that extend along temperate and polar coasts (Wernberg et al. 2019). Recent human-driven changes in our oceans are impacting and destabilizing kelp forests at global scales, causing large-scale losses of kelp in many regions (Krumhansl et al. 2016, Wernberg et al. 2019). These impacts include kelp harvesting (Vázquez 2008), acute and chronic warming (Wernberg et al. 2016, Smale 2020), unusually cold periods (Norderhaug et al. 2015), storms (Filbee-Dexter & Scheibling 2012) and overgrazing (Ling et al. 2015). Harvesting and commercial use of seaweed is a rapidly expand-

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ing industry providing products such as alginate, fertilizers, agricultural feed and pharmaceuticals, and wild harvesting of kelp forests is intensifying in many regions (Buschmann & Camus 2019). Kelp forests are also ecologically valuable habitats. As foundation species, kelps create 3-dimensional habitats, which provide food for numerous species and modify the local environment to support distinct communities of plants and fish and invertebrates (Norderhaug et al. 2002, 2015, Teagle et al. 2017). Therefore, understanding impacts from ecological disturbances on kelps are particularly important because they may affect higher trophic levels that rely on these habitats. The impacts on associated communities and the recovery trajectory of the habitat should be shaped by both the spatial extent and intensity of ecological disturbance (Dudgeon & Petraitis 2001, Wernberg & Connell 2008). Yet, the consequences of spatially extensive disturbances in kelp forests are largely unknown and rarely tested experimentally. Such knowledge is essential to understand the role of kelp as foundation species, the broader implications of disturbance events and for sustainable management of kelp resources.

Manipulative experiments are powerful tools to study and test hypotheses on ecological processes. To date, experimental disturbances in kelp forests have been restricted to small-scale (meters) canopy clearings (e.g. 1.4 m<sup>2</sup>, Kennelly & Underwood 1993; 4–15 m<sup>2</sup>, Dayton et al. 1984; 1256 m<sup>2</sup>, Clark et al. 2004; 7 m<sup>2</sup>, Wernberg & Connell 2008). Exceptions are 'large-scale removal' experiments of *Macrocystis pyrifera* kelp forests in California and *Nereocystis luetkeana* in Alaska, but even these only covered 0.1 km<sup>2</sup> (Bodkin 1988) and 1500 m<sup>2</sup> (Siddon et al. 2008), respectively. The NE Atlantic is understudied and experiments on a large scale remain scarce (Smale et al. 2013). Therefore, there is a mismatch between the scale of localized experiments and the seascape structure of kelp forests, which can extend over hundreds to thousands of meters. As a result, experiments measuring the ecological impacts of kelp loss are generally limited to the fauna that use the habitat on these smaller scales (e.g. epiphytes, mesograzers), and do not capture impacts on the fauna that use the habitat on broad scales, such as large fish.

In this study, we used directed kelp trawling, a human activity that physically removes large quantities of kelp at scales of hundreds of meters using a bottom sledge (Vea & Ask 2011), as a scientific tool to quantify the impacts of broad-scale disturbance on community structure and function in kelp forest ecosystems. Quantitative data describing provision and

loss of ecosystem functions and services in kelp forests are typically hard to obtain and compare, and are therefore generally deficient (Bennett et al. 2015). Although a number of studies have shown how macroalgal and invertebrate communities respond to small-scale disturbances, fewer studies have been devoted to highly mobile fish and other species operating on larger scales (tens to hundreds of meters). An important reason for this is different catchability and visibility of fish assemblages in dense vegetation compared to open areas (e.g. continental shelf) (Duffy et al. 2019). To overcome such methodological challenges, we used new acoustic and visual methods in combination with traditional fishing methods. To our knowledge, ours is the first study focusing on benthic community response to experimental disturbance on such a large scale, and we therefore placed emphasis on responses in demersal fish assemblages that use these habitats on multiple scales. Specifically, we wanted to test how a large-scale directed kelp trawling affected: (1) the habitat structure of the kelp forest, (2) the available secondary habitat created by epiphytic algae on kelp stipes, (3) densities of invertebrates associated to epiphytes, (4) assemblages of fish associated with kelp, and (5) the use of kelp forests as nursery habitat for coastal fish (i.e. abundance of juvenile fish).

## 2. MATERIALS AND METHODS

### 2.1. Study area and design

The study was performed in the archipelago outside Vikna, Norway (64°47'N, 10°31'E; Fig. 1), which is a collection of shoals and islands that support extensive *Laminaria hyperborea* kelp forests (Fig. 2A). We defined 2 equally sized 'kelp forest areas' as polygons in GIS: one control area and one area that we opened for trawling. Both study areas are ~15 km<sup>2</sup> island groups that have comparable depth, topography and position, suggesting comparable environmental conditions (e.g. wave exposure levels). Although parts of the archipelago had been subjected to kelp trawling trials in the past, neither of the 2 areas had been trawled for at least 4 yr prior to the study.

This study was a collaboration with the Norwegian kelp harvest industry and resource managers (The Norwegian Directorate of Fisheries) designed to test the ecological impacts of kelp trawling, to provide advice on possible opening of an area that is closed for kelp trawling, and to assess the sustainability of

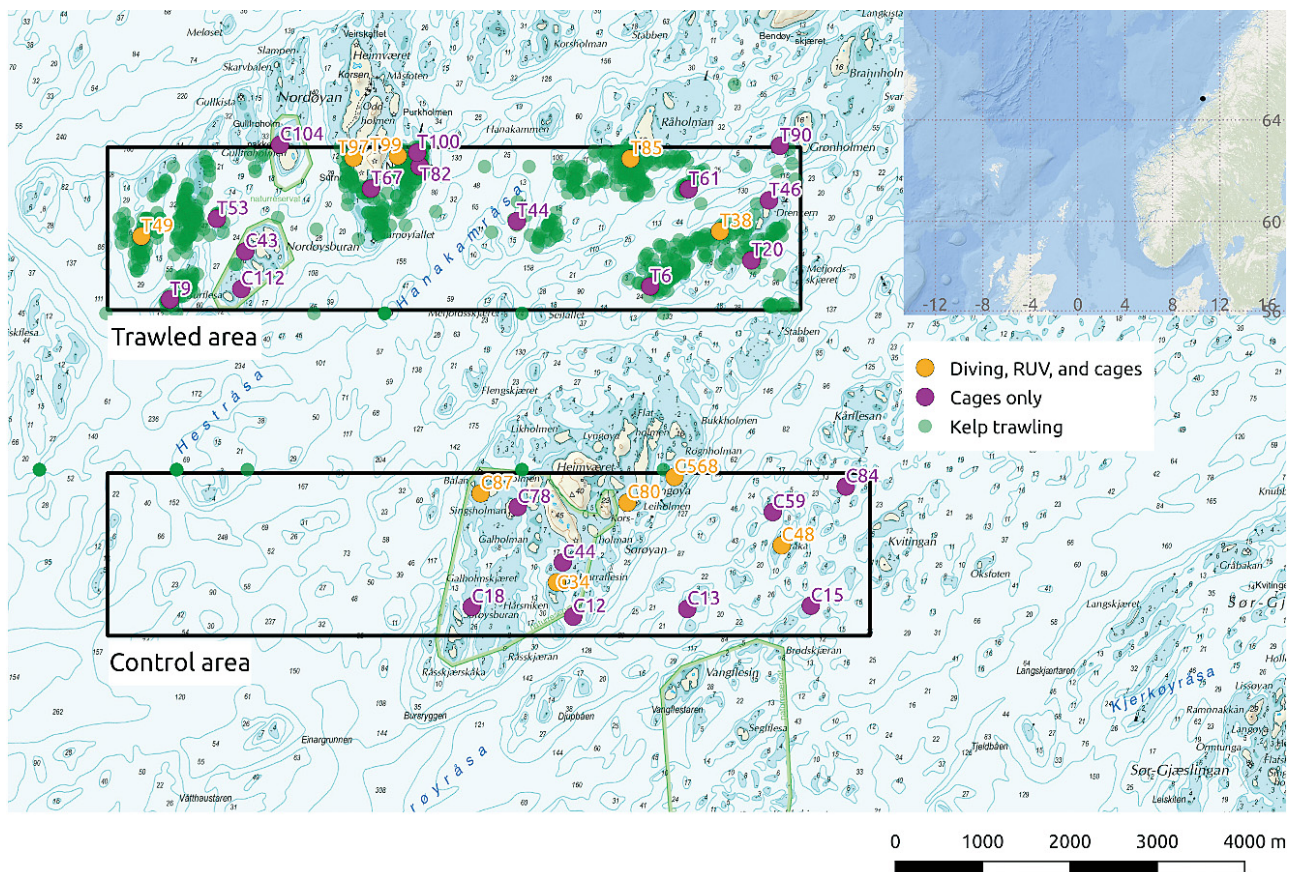


Fig. 1. Map of the study area, showing the 10 dive stations (diving, RUV and cages) and the additional 22 fish stations (cages only) in the impact and control areas. Note that 3 of the fish stations in the impact area were placed in seabird reserves, where kelp trawling was not performed, and served as control stations (C) inside the impact area

the industry. We used a controlled BACI (before–after, control–impact) design, to minimize the extent of unwanted effects outside the focus of the study and to comply with the issued permits for harvest. The impacted area was situated in the northern part of the archipelago and the control area in the southern part, with 2 small reserves in the northern area also used as controls (Fig. 1). The impacted and control areas were restricted to depths ranging between 5 and 20 m. Sites were selected within each area using a random stratified selection, stratifying on 3 levels of wave exposure: low (<0.6 m significant wave height), intermediate (between 0.6 and 0.9 m) and high (>0.9 m; Fig. 1). Three of the sites in the impact area were inside seabird reserves that were not trawled and were used therefore as control sites. A total of 16 sites were used as trawl stations and 16 as control stations (13 of these in the control area and 3 in the impact area; Table 1). At all selected sites we conducted drop camera transects to measure trawling intensity and used cages to catch fish and crabs

(Table 1). At 11 of these sites, divers swam transects to measure trawling intensity, sampled kelp, associated algae and invertebrates, and performed acoustic and visual measures. All sampling procedures are described below.

## 2.2. Kelp trawling

Field sampling was performed before (September 2017) and after (September 2018) controlled kelp trawling. In May 2018, kelp was removed from the impacted area by commercial kelp trawlers, creating large open clearings along the reefs at the sampling stations (Fig. 2C). The study area was then left to settle until the after-assessment 4 mo later. This avoided capturing initial trawling effects, e.g. attraction of fish to prey exposed by the trawling activity. Kelp trawling was performed by vessels dragging a pronged 3 m wide bottom sledge designed to hook kelp. The vessels operated at 3–20 m depth. The sledge cre-

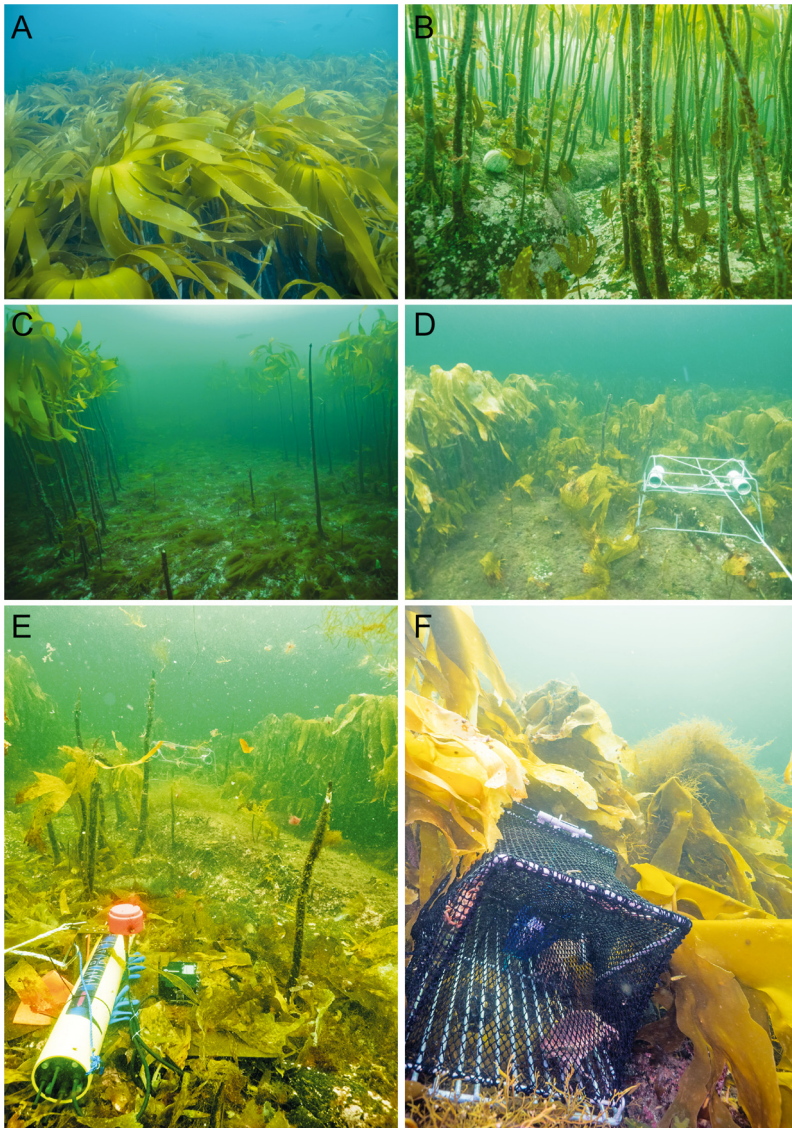


Fig. 2. (A) Pristine kelp forest, (B) kelp stipes with epiphytes under the canopy, (C) trawl track through dense kelp forest, (D) remote underwater video (RUV), (E) WBAT echosounder and (F) fish cage used in the study

ated 3 m wide and up to 100s of m long openings in the kelp forest when removing canopy kelps.

### 2.3. Disturbance intensity

Disturbance intensity was assessed at all sites before and after kelp trawling using a submersible video camera (drop camera) deployed from a fishing vessel along a 50 m long transect (one transect per cage station). In addition, in 11 of the sites, scuba divers swam a 50 m dive transect using a PARALENZ ([www.paralenz.com](http://www.paralenz.com)) video camera facing downwards with 1080 pixel resolution (one transect per dive station). The

percent kelp canopy cover in these videos was quantified from frame grabs and used to compare disturbance intensity before and after kelp trawling and between trawled and untrawled stations.

### 2.4. Primary and secondary producers

Kelp density and size was measured in both areas and before and after kelp trawling by SCUBA divers sampling all kelps in 4 replicate and haphazardly placed  $0.5 \times 0.5$  m quadrats in each site. Kelp age, stipe length and weight, lamina length and weight, holdfast weight and size, and total epiphyte weight were measured for each individual kelp. The age of kelps was estimated by counting cortical growth zones (Steen et al. 2016). An additional 3 kelps from each station were sampled in cotton bags to prevent mobile invertebrates from escaping. Epiphytic algae on kelp stipes (Fig. 2B) are the most important microhabitat for numerous amphipods, gastropods and other invertebrates, which are the main prey species for most kelp-associated fish (Norderhaug et al. 2005, 2007). All animals were rinsed out from the epiphytes using freshwater through a  $500 \mu\text{m}$  sieve and stored in plastic bottles. At the laboratory, they were identified and counted through a dissecting microscope and weighed (in g wet weight).

### 2.5. Fish assemblages associated with the kelp forest

#### 2.5.1. Acoustics and WBAT

Bottom-mounted, upward-facing echosounders were used to measure fish densities in the water column above the kelp canopy. The SIMRAD Wideband Autonomous Transceiver (WBAT, [simrad.com](http://simrad.com); Fig. 2E) is autonomous and constructed to reduce noise. Two WBATs with 200 kHz transducers were used to compare fish densities in the water column above trawled and untrawled kelp forest at night (from 20:00 to 08:00 h local time), when fish are expected to be most active. In 2017 (the first year), 2 EK15 with 200 kHz

Table 1. Sampling devices used at stations in the trawled and control areas. At dive stations, kelp cover was measured by diver transects, and kelps and the associated communities of algae and invertebrate fauna were sampled. Bottom-mounted echosounders (WBAT) and remote underwater video rigs (RUVs) were used. At cage stations, kelp cover was measured by drop camera transects and fish and crab cages were used. Three stations in the trawled area (C112, C43 and C104) were inside seabird reserves and therefore not trawled. These were used as control stations

	Station	Treatment	Dive stations				Cage stations		
			Kelp cover	Kelp, epiphytes, fauna	WBAT	RUV	Kelp cover	Fish cages	Crab cages
Trawled area	T49	Trawl	X	X	X	X	X	X	X
	T85	Trawl	X	X	X	X	X	X	X
	T99	Trawl	X	X	X	X	X	X	X
	T97	Trawl	X	X		X	X	X	X
	T38	Trawl	X	X	X		X	X	X
	T100	Trawl					X	X	X
	T20	Trawl					X	X	X
	T44	Trawl					X	X	X
	T46	Trawl					X	X	X
	T53	Trawl					X	X	X
	T6	Trawl					X	X	X
	T61	Trawl					X	X	X
	T67	Trawl					X	X	X
	T82	Trawl					X	X	X
	T9	Trawl					X	X	X
	T90	Trawl					X	X	X
	C112	Control					X	X	X
	C43	Control					X	X	X
	C104	Control	X	X	X	X	X	X	X
	Control area	C568	Control	X	X	X	X	X	X
C34		Control	X	X	X	X	X	X	X
C87		Control	X	X	X	X	X	X	X
C48		Control	X	X		X	X	X	X
C80		Control	X	X		X	X	X	X
C12		Control					X	X	X
C13		Control					X	X	X
C15		Control					X	X	X
C18		Control					X	X	X
C44		Control					X	X	X
C59		Control					X	X	X
C78		Control					X	X	X
C84		Control					X	X	X

transducers with cable to onshore boxes containing transceiver unit, PC and battery were used. To compare possible differences between data from the 2 systems (e.g. arising from variation in ping rate), one EK15 200 kHz transducer was used together with the WBAT 200 kHz at one station in the second year. From this, a correction factor of 0.529 was calculated and used for the EK15 counts. In both years, upward-facing GoPro cameras were used together with the echosounders to identify fish from the echograms (during daytime/light only). The echosounders were deployed from a boat and positioned on the seafloor by a diver. The diver arranged a line to a surface float with a weight to keep the line away from the transducer. Total fish densities per square meter were calculated using LSSS (Large Scale Survey System; Korneliussen et al. 2016).

### 2.5.2. Fish and crab cages

Two different types of cages were used for capturing fish and crabs. All cages were baited and therefore caught actively foraging fish searching for food (Fig. 2F). Two-chambered, cylindrical wrasse cages (each baited with  $\frac{1}{2}$  of a brown crab) were used to catch 10–30 cm large fishes, whereas rectangular crab cages (each baited with  $\frac{1}{2}$  of a saith) were used to catch crab (Bodvin et al. 2014). Five wrasse cages and 2 crab cages were deployed at 5–10 m depth at each site and hauled the following day. The catches were collected, identified to species, measured for length and weighed, before the cages were rebaited and redeployed at a new station. Each site was only sampled once per year.

### 2.5.3. Remote underwater video

We used unbaited remote underwater video (RUV; Fig. 2D) to collect data on fish occurring under the kelp canopy, including juvenile fish using the kelp forest as a nursery area. This sampling method does not attract fish and solves the problem of the influence of a diver on fish counts (Langlois et al. 2010). Stereo video provides depth vision and one can thus assess the amount of fish in a defined and limited water volume, thus overcoming the bias of different visibility of fish in dense kelp forest compared to open areas (Perry et al. 2018). Each of our RUV rigs carried 2 camera housings containing a GoPro Hero Black 5 with an extra battery pack for prolonged recordings. Three-dimensional calibration files for each camera pair were constructed using the SeaGIS software Cal ([www.seagis.com.au](http://www.seagis.com.au)) and the 1 × 1 × 0.5 m sized calibration cube 'Cal'. Videos were used to quantify fish densities and identify species inside trawled and untrawled kelp forests. In untrawled kelp forests, one video rig was placed by a diver on a horizontal surface below the canopy. At the trawled stations, one video rig was placed in the center of the trawl track and one was placed on the track margin facing the surrounding kelp forest to capture edge effects. The rigs were positioned by a diver and the kelps standing immediately in front of the cameras were removed to ensure the field of view was clear. At each station, a minimum of 1 h and maximum of 5.5 h of video was recorded during daytime. The difference in recording time was accounted for in analysis (see Section 2.7). Videos were analyzed with EventMeasure (SeaGis) on stereo mode, synchronizing screens from both the right and left cameras to obtain the same frames on the video sequences. All fish observed in the video were identified to species (or highest taxonomic level possible) and their size, position (distance to camera), entrance time and departure time were registered in order to calculate changes in fish density and community structure. The first 10 min were removed from the videos to remove any influence of disturbance from the divers from the analysis. We used a 1-m visual distance to obtain equal sampling water volume in dense kelp forests and open trawl tracks.

### 2.6. Trophic food web structure

Stomach contents from fish caught in the fish cages (to a maximum of 15 stomachs per species per station) were frozen direct after collection and analyzed under a dissecting microscope later the same day to mini-

mize decomposition. Stomach items were identified to species or the lowest taxonomic level possible. Fragments of prey were collected to estimate prey numbers as accurately as possible. Most of the collected stomachs were empty. Therefore, the data collected were suitable for identifying prey of different fish, which was used to infer feeding behavior, confirm which species were preying on kelp-associated fauna and calculate trophic level, but were not suitable for analyzing differences between areas and effects from trawling.

### 2.7. Statistical analyses

Generalized linear mixed models (GLMMs) were used to quantify the effect of trawling on kelp, epiphyte and fish communities. Models were fitted to the following response variables: percentage kelp cover, number of kelp plants per m<sup>2</sup>, total kelp biomass per m<sup>2</sup>, individual kelp length, individual kelp weight, kelp age, epiphyte and invertebrate weight per m<sup>2</sup>, fish density per m<sup>2</sup> (echosounder data), number of fish, number of crabs and number of fish species per site (fish cage data), and number of fish per h (RUV data). Trawling (impact, control) and period (before: 2017, after: 2018) were used as fixed factors, as well as their interaction (the BACI effect). Station was included as a random-effect variable to account for random variation between stations. Models took the following form:

$$\text{Response variable} = \alpha + \beta_1 \text{Trawling} + \beta_2 \text{Period} + \beta_3 \text{Trawling} \times \text{Period} + \alpha + \varepsilon \quad (1)$$

where the term  $\alpha$  is the model intercept and  $\beta_1$  to  $\beta_3$  are the model coefficients. The random intercept  $\alpha$  allows for a random variation around the intercept  $\alpha$ , and is assumed to be normally distributed with mean 0 and variance  $\delta^2$ . The term  $\varepsilon$  is independently normally distributed noise.

The following response variables were fitted using a Gaussian distribution: percentage kelp cover (logit transformed), total kelp biomass per m<sup>2</sup>, individual kelp length, individual kelp weight, kelp age, epiphyte weight per m<sup>2</sup> (log transformed) and fish density per m<sup>2</sup>. Count response variables were fitted using a Poisson distribution. For RUV data on number of fish per h, the number of video hours was entered as an offset in the models. Model validation was performed following Zuur & Ieno (2016) and indicated that some Poisson models were over-dispersed. These were later fitted with a negative binomial distribution, which solved the over-dispersion issues. Analyses were performed using the packages nlme and lme4 (Bates et

al. 2015) in the statistical program R (v. 3.5.1; R Core Team 2018).

### 3. RESULTS

#### 3.1. Disturbance intensity

A total of 2986 tons of kelp was removed from all the trawl stations (personal communication, Directorate of Fisheries, Norway) and resulted in a significant reduction of total kelp cover in the impacted area from  $88.6 \pm 13.5\%$  (mean  $\pm$  SD) before trawling to  $62.4 \pm 22.0\%$  after trawling (Fig. 3, Table 2). The resulting kelp matrix post trawl was a mix of patches of remaining kelps and open trawl tracks dominated by scattered young, small understory kelps with little epiphytes, reflected in the high variation in kelp and epiphyte size after trawling. Most kelps removed by trawling detached with the holdfast, and the trawl tracks also showed numerous scars of bare substrate where these holdfasts used to be attached. The kelp cover in the reference area was unchanged at  $89.0 \pm 12.5\%$  in the first year to  $89.8 \pm 13.2\%$  in the second year (Fig. 3, Table 2).

#### 3.2. Kelp and epiphytic macroalgae

The direct effect of removing the canopy by trawling was a significant decrease in kelp weight and length and kelp abundance and biomass per  $m^2$  (Fig. 3, Table 2). All registered kelps were *Laminaria hyperborea*.

Epiphytic fouling (measured as the total epiphytic weight per kelp stipe) was highly variable in both areas and years (Fig. 3D). Kelp canopies composed of the largest and oldest kelps had high epiphyte cover, while smaller and younger kelps had low epiphytic cover. Because the number of canopy kelps was reduced after trawling, a reduction of epiphytes from  $213 \pm 232$  to  $72 \pm 114$  g per  $m^2$  was observed in total at trawled stations.

#### 3.3. Invertebrate fauna

The invertebrate fauna on the epiphytes were dominated by gastropods (e.g. *Ansates pellucida*, *Lacuna vincta*, *Rissoa parva*) bivalves (e.g. *Mytilus edulis*, *Hiatella arctica*), amphipods (e.g. *Jassa falcata*), isopods (e.g. *Idotea granulosa*), decapods (e.g. *Galathea strigosa*), polychaetes (e.g. Nereidae) and echino-

derms (e.g. *Ophiopholis acuelata*). Their abundances and weights roughly correlated to the amount of epiphytes (abundance:  $7.54 \pm 4.53$  g<sup>-1</sup> WW epiphytic algae with  $R^2 = 0.66$  and  $0.23 \pm 0.09$  g WW invertebrates per g WW epiphytic algae with  $R^2 = 0.80$ ). From epiphytic volumes per  $m^2$  (Fig. 3D), their weights were shown to be significantly reduced from  $31.5 \pm 12.6$  before to  $3.4 \pm 1.6$  g  $m^{-2}$  after trawling (Fig. 4, Table 3).

#### 3.4. Fish and crabs

##### 3.4.1. Echograms

Echogram counts from WBAT indicated a decrease in the total density of fish above the canopy both in the trawled and the control areas between the first and second year (Fig. 5). There was no significant effect of trawling on fish densities in the water column over the kelp forest (Table 4). Cameras on the echosounders showed that records of fish were mainly schools of small saithe *Pollachius virens*.

##### 3.4.2. Fish and crab cages

Overall, there was no significant reduction after trawling in the total number of fish or in the total number of species per site, but there were significant effects on the species level (Fig. 6, Table 5). The number of goldsinny wrasse *Ctneolabrus rupestris* was significantly reduced by trawling, while its abundance increased in the control area from the first to the second year. Few cod were caught overall, and this could be the reason why no significant effect from trawling or between years was found. The catches of saithe (mainly small fish) in fish and crab cages were lower in both areas in the second year compared to the first, but this difference was larger in the reference area, so there was consequently a significantly positive effect of trawling on the number of saithe caught per site (Table 5). In total, more crabs and less fish were caught the second year compared to the first year in both areas.

##### 3.4.3. RUV trawl tracks and kelp margins versus control

The RUVs measured a significant decrease in the total number of fish per hour in the trawled area both in the trawl tracks (from  $118 \pm 132$  to  $64 \pm 71$  ind.  $h^{-1}$ ) and an even larger reduction along the kelp margins

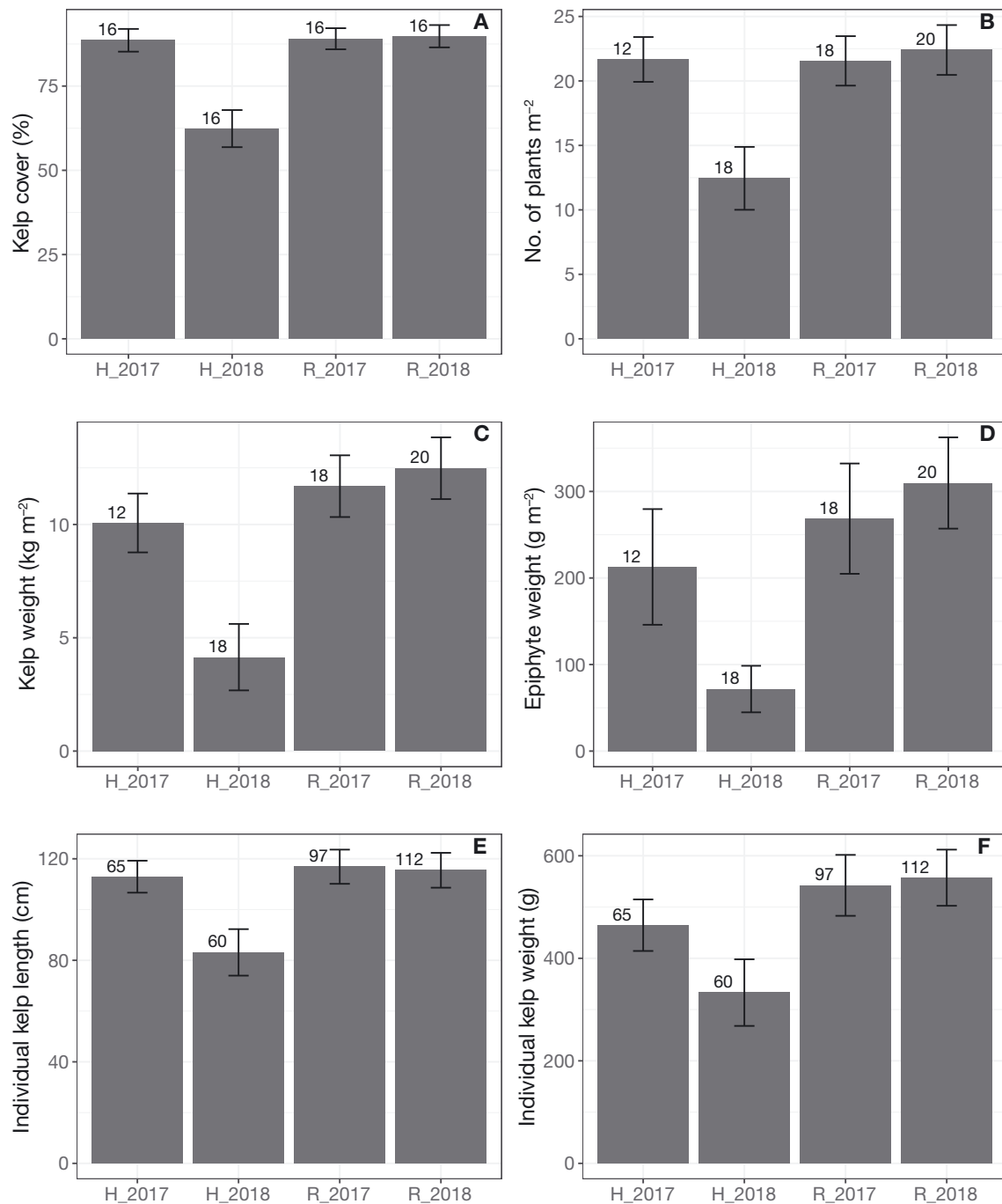


Fig. 3. (A) Average kelp cover (%) along 50 m dive and drop-camera transects, (B,C) average kelp density and biomass per m<sup>2</sup>, (D) average biomass of epiphytes per m<sup>2</sup> and (E,F) average length and weight of individual kelp in 0.5 × 0.5 m quadrats in trawled (harvested [H]) and control (reference [R]) stations before and after kelp trawling. Error bars are  $\pm$ SE; number of replicates is given above bars

(to  $12 \pm 10$  ind. h<sup>-1</sup>; Fig. 7, Table 6). On the species level, a large reduction in the number of goldsinny wrasse after trawling was observed, but few wrasses were identified in the control area both before and after trawling and this reduction was only significant

in the kelp margins (Table 6). Goldsinny wrasse were not very mobile and were closely associated with individual kelps in the video. The total number of observed cod was small (a total of 60 cod) and the model did not converge. A significant reduction



Table 2. Results from generalized linear mixed models comparing kelp cover, number and biomass of kelp per m<sup>2</sup>, biomass of epiphytes per m<sup>2</sup>, as well as length, weight and age of individual kelp in the control and trawled areas before (September 2017) and after (September 2018) kelp trawling. Model coefficients ( $\beta$ ), standard error (SE), degrees of freedom (DF),  $t$  (Gaussian distribution models),  $z$  (negative binomial model),  $p$ -values and model distribution are shown. Significance on a 0.05 level is indicated by **bold text**

Response variable	Term	$\beta$	SE ( $\beta$ )	DF	$t/z$	$p$
Kelp cover (%) (logit transformed)	Intercept	2.83	0.49	30	5.82	<b>&lt;0.001</b>
	Trawling[Impact]	0.33	0.69	30	0.47	0.64
	Period[After]	0.49	0.62	30	0.80	0.43
	Trawling $\times$ Period	-3.05	0.88	30	-3.47	<b>0.002</b>
No. of kelp plants m <sup>-2</sup>	Intercept	3.05	0.14		22.529	<b>&lt;0.001</b>
	Trawling[Impact]	0.08	0.22		0.372	0.71
	Period[After]	0.03	0.16		0.213	0.83
	Trawling $\times$ Period	-0.68	0.25		-2.723	<b>0.01</b>
Kelp weight (g m <sup>-2</sup> )	Intercept	11.69	1.71	55	6.82	<b>&lt;0.001</b>
	Trawling[Impact]	-0.44	2.67	9	-0.17	0.87
	Period[After]	1.11	1.74	55	0.64	0.53
	Trawling $\times$ Period	-8.35	2.67	55	-3.13	<b>0.003</b>
Epiphyte weight m <sup>-2</sup> (g; log transformed)	Intercept	5.14	1.02	55	5.03	<b>&lt;0.001</b>
	Trawling[Impact]	0.03	1.60	9	0.02	0.98
	Period[After]	0.32	1.12	55	0.28	0.78
	Trawling $\times$ Period	-8.22	1.71	55	-4.80	<b>&lt;0.001</b>
Kelp length (cm)	Intercept	120.42	11.51	317	10.46	<b>&lt;0.001</b>
	Trawling[Impact]	2.68	17.64	9	0.15	0.88
	Period[After]	-0.08	9.10	317	-0.01	0.99
	Trawling $\times$ Period	-45.01	15.76	317	-2.86	<b>0.005</b>
Kelp weight (g)	Intercept	565.47	93.04	317	6.08	<b>&lt;0.001</b>
	Trawling[Impact]	-35.24	142.58	9	-0.25	0.81
	Period[After]	52.03	73.67	317	0.71	0.48
	Trawling $\times$ Period	-278.27	127.63	317	-2.18	<b>0.03</b>

caused by trawling in the total number of juvenile *Pollachius* (pollack, saithe) was found both in the trawl tracks and in the kelp margins, from  $6.1 \pm 9.0$  to  $1.5 \pm 1.1$  in the trawl tracks and to  $1.8 \pm 0.8$  in the marginal kelp forest surrounding the trawl tracks (Table 6). The number was  $2.1 \pm 1.3$  in the first year and  $2.6 \pm 2.3$  in the second in the control area. A general reduction in the number of saithe occurred from the first to the second year, but the reduction was significantly larger in the control area compared to the trawled area after trawling, suggesting a positive effect of kelp trawling. Young saithe were observed in high abundances in the open trawl tracks. When regarding echosounder diagrams, RUV and cage data jointly, juvenile saithe using the water column above the canopy hardly seemed to be affected by trawling tracks, but they changed their vertical distribution, being distributed vertically all the way down to the sea floor after trawling.

There was a significant decrease in the number of adult pollack in the trawl area after trawling ( $2.1 \pm 1.9$  in the trawl tracks and  $1.7 \pm 0.4$  in the marginal

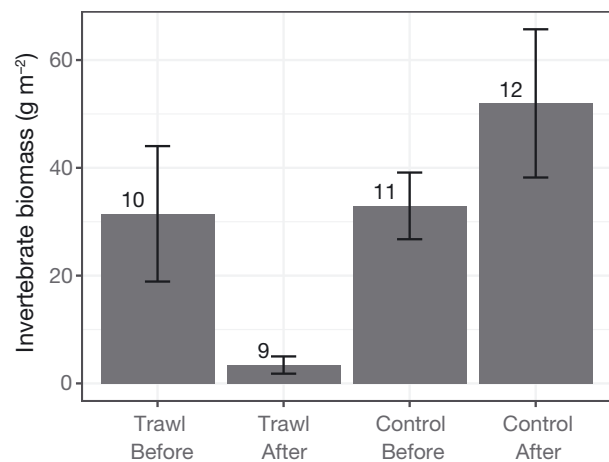


Fig. 4. The biomass of invertebrates (g m<sup>-2</sup>) living on epiphytes on kelp stipes at trawled and control stations before and after kelp trawling. Error bars are  $\pm$ SE; number of replicates is given above bars

kelp forest) compared to before in the intact forest ( $10.4 \pm 9.5$ ; Table 6). Both cod and pollack cruised through the kelp forest under the canopy in the RUV

Table 3. Results from generalized linear mixed models comparing biomass (g of invertebrate fauna per m<sup>2</sup>) in the trawled and control area before (September 2017) and after (September 2018) kelp trawling. Model coefficients ( $\beta$ ), standard error (SE), degrees of freedom (DF),  $t$  (Gaussian distribution models) and p-values are shown. Significance on a 0.05 level is indicated by **bold** text

Term	$\beta$	SE ( $\beta$ )	DF	$t$	p
Intercept	31.4	13.0	29	2.41	0.02
Trawling[Impact]	0.52	18.8	9	0.03	0.98
Period[After]	23.1	14.3	29	1.62	0.12
Trawling $\times$ Period	-58.8	19.9	29	-2.96	<b>0.006</b>

recordings. Trawling was associated with a significant decrease in the number of two-spotted gobies in the kelp margins (from  $11.2 \pm 10.8$  to  $1.8 \pm 2.7$ ), but no significant effect was found in the trawl tracks ( $20.5 \pm 27.6$  after trawling).

### 3.5. Trophic relationships and ecosystem structure

Many examined stomachs were empty (44% in 2017 and 43% 2018), and for all species, a substantial part of the stomach contents could not be identified. The contents that could be identified showed that cod mainly fed on decapods (*Cancer pagurus*, hermit crabs, *Galathea* sp.) and other fish, and goldsinny wrasse mainly fed on gastropods (e.g. *Ansatres pellucida*, *Rissoa parva*), which are associated with epiphytes on kelp stipes. Longspined bullhead mainly fed on different crustaceans, saithe on decapods and gastropods, shorthorn sculpin on other fish, and 3-bearded rockling preyed on decapods and fish.

## 4. DISCUSSION

The directed kelp trawling used as a large-scale experimental disturbance had a strong impact on the kelp forest ecosystems in the study area. It represented an acute disruption, which altered the physical kelp forest structure and affected 4 trophic levels, from primary producers to secondary producers and 2 levels of predatory fish. The effect was negative on low trophic levels and variable on higher trophic levels. Both positive and the most negative effects were found in higher trophic levels and could be linked to how different species used the individual kelps and the forest structure.

By removing 26% of the canopy-forming mature kelp plants, the disturbance created large openings

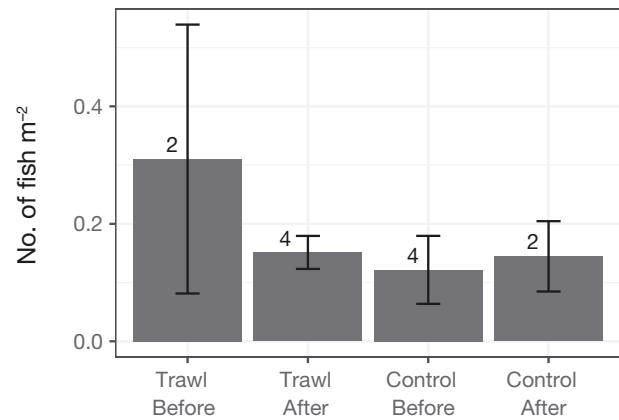


Fig. 5. Densities of fish (ind. m<sup>-2</sup>) above the kelp canopy estimated from echograms in trawled and control stations before and after kelp trawling. Error bars are  $\pm$ SE; number of replicates is given above bars

in the dense forest, which changed the kelp forest structure and its function as a macrohabitat. An ~46% reduction in the total abundance of fish living under the canopy was observed at trawled stations from RUVs (Fig. 7), but with interspecific differences that may correspond to habitat usage (Perez-Matus & Shima 2010). Loss of canopy cover will decrease light attenuation, which has consequences for shade-adapted understory algae, as well as for fauna and fish relying on the canopy for shelter (Bodkin 1988, Toohey et al. 2004). The consequent 67% reduction in total amount of epiphytes per m<sup>2</sup> associated with the loss of old plants inside the trawl tracks represents an additional loss of microhabitat. The invertebrates living on the epiphytes are the main prey for fish associated with the kelp forest (Schultze et al. 1990, Christie et al. 2003, Edgar & Aoki 1993, Norderhaug et al. 2005, stomach contents from the present study). Based on the biomass of these animals, this implies a reduction of 89% of invertebrates per m<sup>2</sup>. The loss of microhabitats and prey are important properties of the kelp forest as a nursery area that

Table 4. Results from the generalized linear mixed model (Gaussian distribution), showing differences in fish densities above the kelp canopy from echograms before (September 2017) and after (September 2018) kelp trawling and compared to control stations. Test statistics for  $\beta$ , standard error (SE), degrees of freedom (DF),  $t$  and p-values are shown

Term	$\beta$	SE ( $\beta$ )	DF	$t$	p
Intercept	0.226	0.109	7	2.075	0.08
Trawling[Impact]	-0.055	0.133	7	-0.411	0.69
Period[After]	-0.073	0.136	1	-0.538	0.69
Trawling $\times$ Period	0.025	0.167	1	0.152	0.90

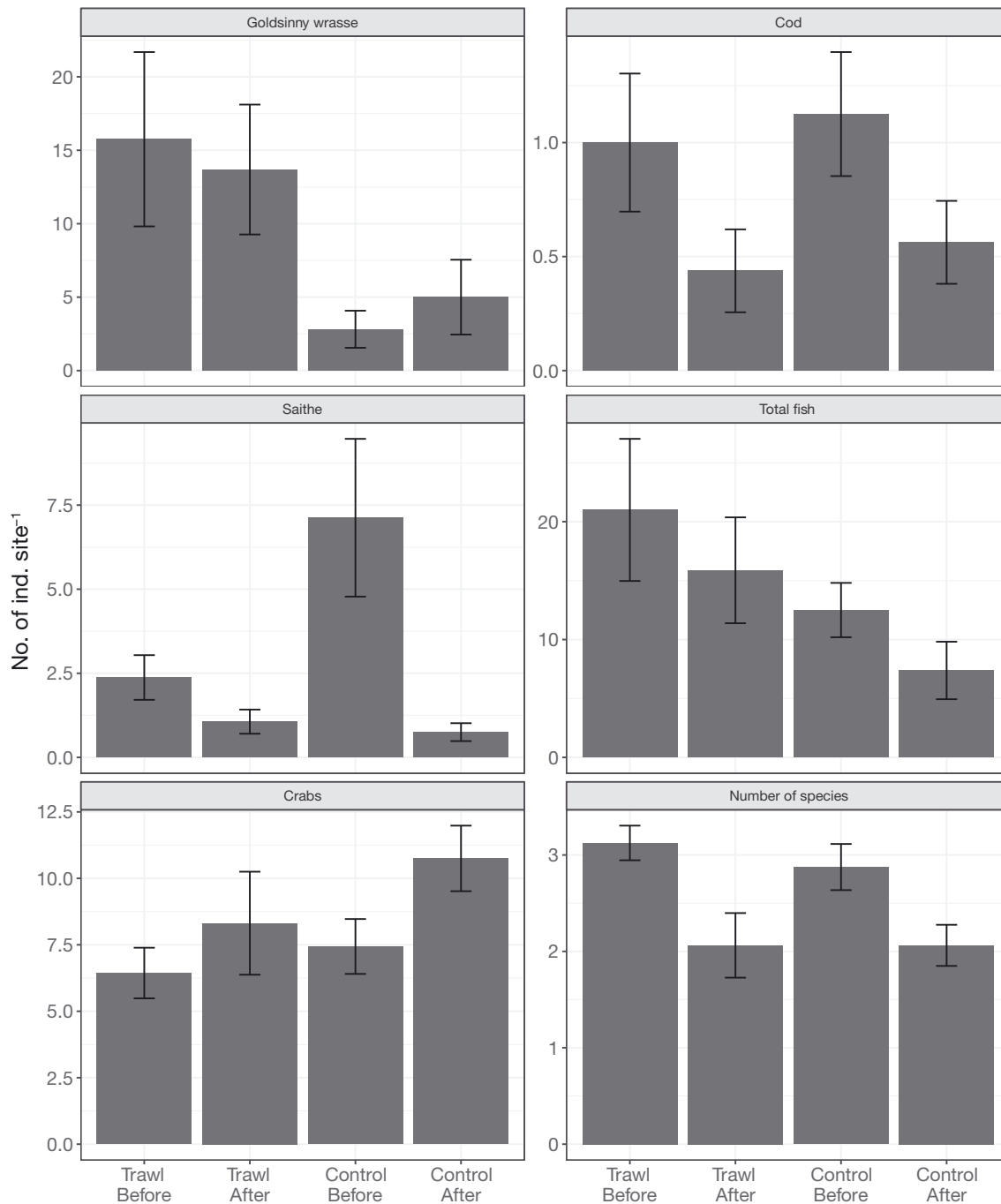


Fig. 6. Mean ( $\pm$ SE) number of individuals caught in the fish and crab cages per site, before and after kelp trawling and compared to the control area. Number of replicates (sites) in each area was 16 per year. Values are shown for goldsinny wrasse, cod, saithe, total number of fish, total number of crabs and total number of species per site

likely explains the corresponding strong reduction in abundances of juvenile *Pollachius* spp. (by some 75%). Our findings are consistent with small-scale experiments by Perez-Matus & Shima (2010) showing negative responses for small fish from a reduction in habitat heterogeneity, and variable responses of

larger fish to larger-scale habitat density. Research from other areas on the effects of reduced canopy cover on fish assemblages show mixed responses. Loss of kelp canopy has been shown to increase abundances of juvenile fish (Levin 1993), and increase schools of adult Gadidae fish, but reduce

Table 5. Results from generalized linear mixed models (Poisson and negative binomial distribution) on differences in cage catches per site for goldsinny wrasse, cod, saithe, the total number of fish, crabs and total number of species per site before and after kelp trawling and compared to the control area. Test statistics for  $\beta$  and corresponding standard error (SE),  $z$  and  $p$ -values are shown. Significance on a 0.05 level is indicated by **bold** text

Response	Term	$\beta$	SE( $\beta$ )	$z$	$p$
Goldsinny wrasse	Intercept	-0.99	0.74	-1.34	0.18
	Trawling[Impact]	2.23	0.94	2.37	<b>0.02</b>
	Period[After]	0.58	0.19	3.09	<b>0.002</b>
	Trawling x Period	-0.72	0.21	-3.44	<b>&lt;0.001</b>
Cod	Intercept	0.06	0.27	0.23	0.82
	Trawling[Impact]	-0.12	0.37	-0.33	0.74
	Period[After]	-0.69	0.41	-1.70	0.09
	Trawling x Period	-0.13	0.61	-0.22	0.83
Saithe	Intercept	1.43	0.27	5.30	<b>&lt;0.001</b>
	Trawling[Impact]	-0.85	0.39	-2.16	<b>0.03</b>
	Period[After]	-2.25	0.30	-7.42	<b>&lt;0.001</b>
	Trawling x Period	1.45	0.42	3.44	<b>&lt;0.001</b>
Total fish abundance	Intercept	2.39	0.24	10.04	<b>&lt;0.001</b>
	Trawling[Impact]	0.29	0.33	0.87	0.38
	Period[After]	-0.67	0.25	-2.65	<b>0.008</b>
	Trawling x Period	0.34	0.34	0.99	0.32
Crabs	Intercept	1.92	0.15	12.75	<b>&lt;0.001</b>
	Trawling[Impact]	-0.19	0.22	-0.87	0.39
	Period[After]	0.37	0.12	3.12	<b>0.002</b>
	Trawling x Period	-0.11	0.18	-0.64	0.52
Number of species	Intercept	1.06	0.15	7.16	<b>&lt;0.001</b>
	Trawling[Impact]	0.08	0.20	0.41	0.68
	Period[After]	-0.33	0.23	-1.46	0.15
	Trawling x Period	-0.08	0.32	-0.26	0.78

the abundance of juvenile demersal fish (Siddon et al. 2008), and both increase (Cole et al. 2012) and decrease fish diversity (Edgar et al. 2004) in relation to direct and indirect canopy effects and intraspecific and interspecific species interactions. Mixed responses in our study can also be related to the use of the kelp forest by different species.

The effect of kelp trawling on species (functional groups) on different levels in the kelp forest food web is summarized in Fig. 8. The figure also shows home range to indicate how different species use the kelp forest. The trawling effect was negative on the 2 lowest food web levels, including sessile species such as habitat-building kelp and epiphytic algae, as well as the small invertebrates with a small home range. Predators with a larger home range can escape or use the open patches created by trawling according to how they depend on prey associated with kelp, or use these habitats for shelter. This can explain the highly variable responses in higher trophic levels we found in the present study. *Cancer* crabs are predators more associated with the seafloor than the kelp vegetation itself, and commonly hide in crevices and

under stones (Steneck et al. 2013). This may explain the lack of effect on the abundances of crabs. Goldsinny was closely associated with kelps for food and shelter, which likely explained their reduction in abundance after trawling. Saithe swam in the water column above the canopy and may be little affected by removal of kelp patches except for a redistribution throughout the water column. RUVs and stomach contents showed that pollack hunt under the kelp canopy, which could explain the dramatic and significant reduction in abundance after trawling. Stomach contents from pollack and cod collected during this study, combined with existing research, demonstrate that predatory fish species survive on a diverse diet of decapods and other fish, which do not necessarily only live in kelp forests (Wennhage & Pihl 2002, Norderhaug et al. 2005, present study). Larger predatory fish also spend significant portions of their life cycle outside subtidal kelp forests, and when they do use these habitats it is over scales of several kilometers (Rogers et al. 2014), i.e. both inside and outside kelp forests. Species-specific responses from removing the canopy may also have arisen from the

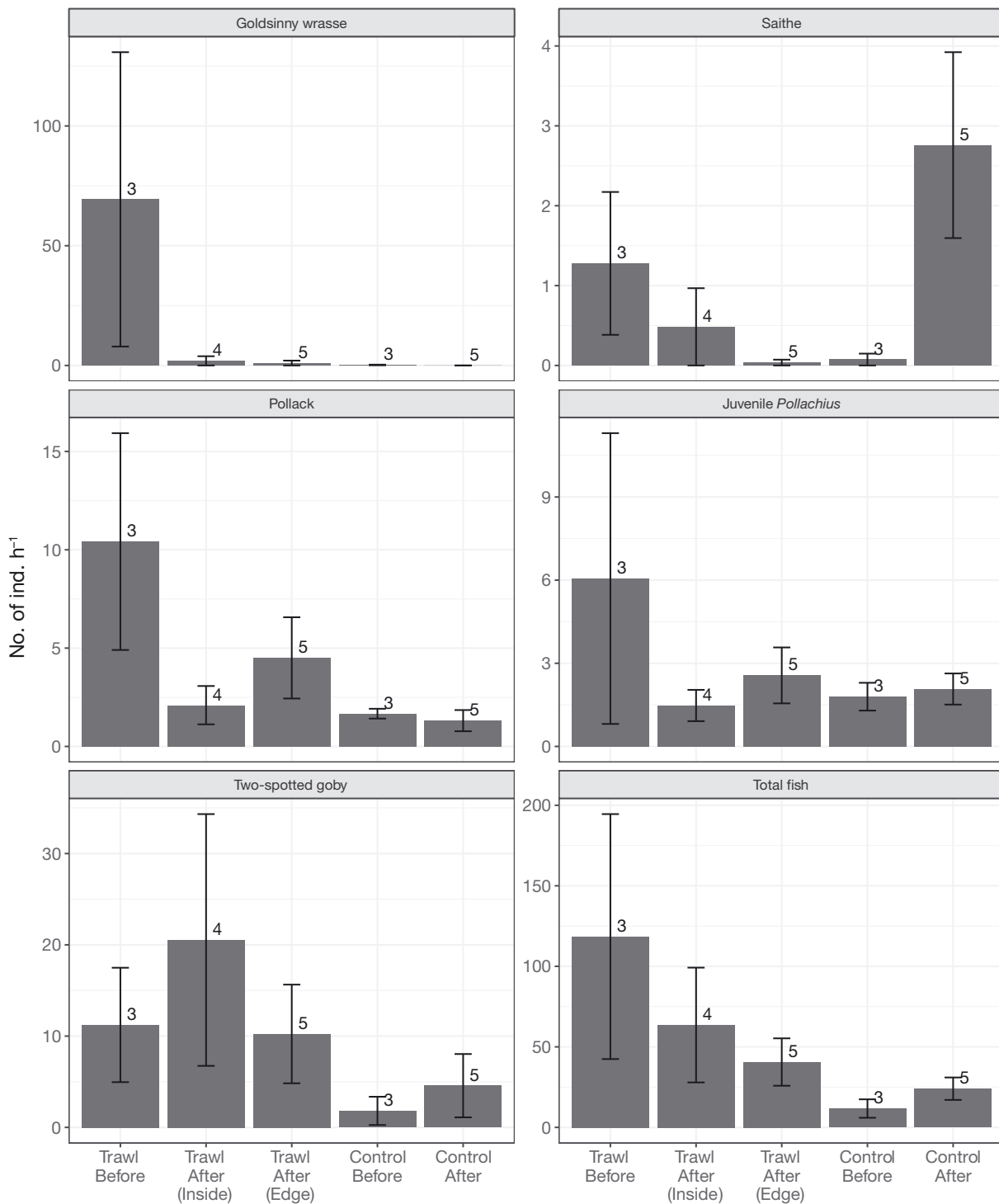


Fig. 7. Number of fish observed per hour (mean  $\pm$  SE) in the remote underwater videos (RUVs) in trawl stations (inside trawl track and along the trawl edge facing the kelp forest) and in control stations before and after trawling. The number of RUVs in each area is given above bars. Values are shown for goldsinny wrasse, cod, saithe, pollack, juvenile *Pollachius* (i.e. juvenile saithe and pollack <16 cm), two-spotted goby and the total number of fish

combined effects on both prey and the predator. RUVs facing the marginal kelp forests revealed edge effects and a significant reduction in abundances of

pollack and small fish including juvenile *Pollachius* spp. and gobies. Marginal kelp forests have sparser canopies and increased light attenuation, and thereby

Table 6. Results from generalized mixed effects models (Poisson and negative binomial distribution) used to compare the number of fish observed per h in the RUV videos from trawl tracks vs control (left) and edge effects i.e. RUVs in trawl tracks facing marginal surrounding kelp forest vs control (right). Results are shown for goldsinny wrasse, cod, saithe, pollack, juvenile *Pollachius* (i.e. juvenile saithe and pollack <16 cm), two-spotted goby and the total number of fish. Test statistics for  $\beta$ , standard error (SE), z and p values are shown. For adult cod the model did not converge. Significance on a 0.05 level is indicated by **bold** text

Term	Trawl track				Edge effects				
	$\beta$	SE ( $\beta$ )	z	p	$\beta$	SE ( $\beta$ )	z	p	
Goldsinny wrasse	Intercept	-33.08	110.10	-0.30	0.76	-28.83	0.01	-2234	<0.001
	Trawling[Impact]	36.27	110.10	0.33	0.74	30.11	0.01	2329	<0.001
	Period[After]	31.73	110.11	0.29	0.77	23.34	0.01	1813	<0.001
	Trawling $\times$ Period	-35.31	110.12	-0.32	0.75	-31.62	0.01	-2446	<0.001
Saithe	Intercept	-0.17	0.63	-0.28	0.78	-0.43	0.34	-1.25	0.21
	Trawling[Impact]	-0.59	1.06	-0.56	0.56	-0.44	0.65	-0.68	0.50
	Period[After]	-5.74	1	-3.84	<0.001	-5.36	1	-4.91	<0.001
	Trawling $\times$ Period	4	2	2.21	<b>0.03</b>	-1	2	-0.41	0.68
Pollack	Intercept	-1.48	0.66	-2.24	<b>0.03</b>	-1.04	0.60	-1.74	0.08
	Trawling[Impact]	2	0.97	1.64	0.10	2	0.85	2.78	<b>0.005</b>
	Period[After]	0.20	0.46	0.44	0.66	0.67	0.81	0.83	0.41
	Trawling $\times$ Period	-2.73	0.56	-4.90	<0.001	-5.10	1.19	-4.30	<0.001
Juvenile <i>Pollachius</i>	Intercept	-0.81	0.54	-1.50	0.13	-0.57	0.43	-1.32	0.19
	Trawling[Impact]	0.51	0.84	0.61	0.54	1.35	0.62	2.17	<b>0.03</b>
	Period[After]	-0.86	0.48	-1.80	0.07	-0.88	0.65	-1.37	0.17
	Trawling $\times$ Period	-1.73	0.61	-2.84	<b>0.005</b>	-3.06	0.91	-3.36	<b>0.001</b>
Two-spotted goby	Intercept	-0.06	1.05	-0.06	0.95	0.10	1.21	0.09	0.93
	Trawling[Impact]	1.43	1.39	1.03	0.30	1.26	1.53	0.83	0.41
	Period[After]	0.39	0.98	0.40	0.69	0.37	1.06	0.35	0.72
	Trawling $\times$ Period	-0.27	1.60	-0.17	0.87	-4.29	1.80	-2.38	<b>0.02</b>
Total fish abundance	Intercept	2.08	0.53	3.93	<0.001	2.08	0.49	4.23	<0.001
	Trawling[Impact]	2	0.86	1.94	<b>0.05</b>	2	0.79	2.09	<b>0.04</b>
	Period[After]	0.23	0.75	0.31	0.76	0.23	0.69	0.33	0.74
	Trawling $\times$ Period	-1.23	1.16	-1.06	0.29	-4.76	1.12	-4.24	<0.001

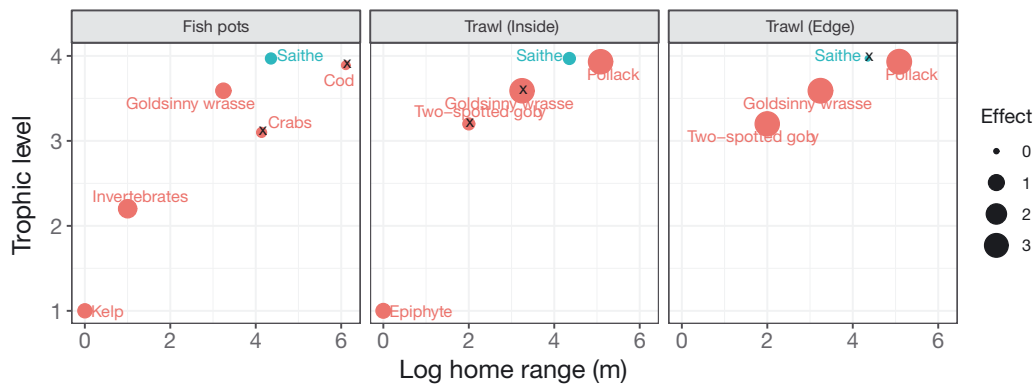


Fig. 8. The effect of kelp trawling on species (functional groups) on different levels in the food web and according to (log) home range, from fish pots (left) as well as remote underwater videos (RUVs) in the trawl tracks (middle) and facing the marginal kelp forest (trawl edge, right). The bubble size shows effect as % increase (blue) or decrease (red) in the trawled area minus the % change in the control area. Trophic levels were obtained for small invertebrates from Norderhaug & Christie (2011), *Cancer pagurus* from www.sealifebase.se, two-spotted goby from www.fishbase.se, and other fish species from stomach contents (present study). Home ranges for invertebrates are from Norderhaug et al. (2002), *C. pagurus* from Skajaa et al. (1998), two-spotted goby from www.marlin.ac.uk and Wacker et al. (2012), goldsinny from Hilldén (1981), Collins (1996) and Aasen (2019), cod from Espeland et al. (2007) and Aalvik et al. (2015), saithe from Rangeley & Kramer (1995) and pollack from Winge (2018). Very few goldsinny were observed on RUVs in the control area before trawling, producing spurious numbers; therefore, their bubble size is represented as the biggest size in the figure for illustration purposes only

increase the visibility of both predatory and prey fish. The open trawl tracks provide limited shelter for both prey and predatory fish. This may explain the different responses in abundance of gobies in open trawled tracks and in marginal kelp forests. Edge effects are known to alter abundances of large predators in terrestrial forests (Brodie et al. 2015) and to cause accumulation of fish larvae on kelp forest margins in Argentina (Bruno et al. 2018).

Natural variability is a striking feature of this ecosystem, as shown by high interannual variability in both study areas. This variability can be attributed to environmental conditions such as seasonal timing and temperature, disturbances such as storms, and biological variability such as year class strength of different species (Witman & Dayton 2001, Christie et al. 2003, Connell 2007, Bekkby et al. 2014). Kelp forests are generally resilient systems (Smale & Vance 2016, O'Leary et al. 2017). In Norwegian *L. hyperborea* kelp forests, removal of the canopy increases growth rates of the understory kelp and, consequently, the kelp biomass can recover quickly, in 3–4 yr (Steen et al. 2016). Epiphytic algae do not develop on kelp stipes until the kelps become large and the stipes develop a rough surface suitable for attachment. Consequently, it takes 6 or more years for the epiphytes and the mobile fauna inhabiting the epiphytes to recover (Christie et al. 1994, Norderhaug et al. 2012). These past studies and our current findings suggest that the function of the habitat as a feeding and nursery ground for fish will be reduced for 6 yr or longer following removal. Recovery rates for the ecosystem were not part of the present study, but are expected to decrease with trophic level (e.g. the kelps recovering faster than the associated primary and secondary consumers, and fish recovering only after these food sources become available again). In a future warmer climate, the recovery capacity and rate will also depend on the physiological response of kelps to warming, since the recovery rate in part depends on kelp growth rate (Wernberg et al. 2010). Kelp forest resilience and how it is affected by climate change and other human impacts should be taken into account when making decisions to commercially harvest kelp, for example, by using trawling strategies that only remove a portion of the kelp biomass and leave areas with pristine forests dominated by old kelps and abundant epiphytes to keep the ecosystem functions of kelp forests intact. Fish communities should also be monitored in harvested areas to track the effects of altered habitat to higher trophic levels.

Natural disturbances are challenging to predict and to test experimentally, and so studies such as ours,

combined with insights from large clearing experiments, are useful to understand the impacts of increased disturbance regimes in kelp forests. Natural disturbances are expected to effect kelp forests in similar ways to trawling by removing patches of kelp canopy. Therefore, our findings provide insight into possible consequences of increased natural disturbances on the functioning of this ecosystem. Larger storms can disrupt the kelp forest structure and create open patches (Ebeling et al. 1985, Connell & Irving 2008, Filbee-Dexter & Scheibling 2012). Both strong storms and trawling are expected to remove kelp more effectively on flat open seafloor and tend to be most severe in shallow compared to deeper waters, due to more efficient trawling and higher wave exposure in these areas (wave forces decrease with depth: Directorate of Fisheries trawling statistics). However, the fact that kelp was removed in corridors by trawls may have created more edge effects from trawling compared to natural disturbances and could influence how fauna use these disturbed habitats. Vessels operation is restricted to 3–20 m depth and our study was consequently limited to this depth range. Storm removal of kelp can occur all year round, but with highest frequency during autumn storms. But since kelp needs several years to recover (Steen et al. 2016), the seasonal timing of the trawling was expected to have little importance for our study.

The effects from expected future disturbance intensity and frequency have been explored through structural equation modeling (SEM) by Byrnes et al. (2011) in a study on Californian giant kelp systems. In line with Byrnes et al. (2011), we found a reduction in community complexity (kelp structure and epiphytic amount) if disturbance intensity and frequency increased. Using scenario modelling, Byrnes et al. (2011) showed how increased storm frequency may decrease ecosystem diversity because slowly recolonizing species became extinct. The SEM models also predicted that perturbations would track up the food web with increasing effects on higher levels. The variable effects on higher trophic levels in our study is therefore only partly consistent with predictions by Byrnes et al. (2011) and with general patterns in other ecosystems of higher trophic level species being more susceptible to habitat loss and fragmentation than lower trophic levels (Gilbert et al. 1998). Our results from a single disturbance event suggest that cascading effects are more consistent on lower than higher food web levels, but also indicate the potential for stronger cascading effects through the ecosystem, especially if the disturbance intensity and frequency increased.

In addition to being among the first experimental disturbance studies on a scale relevant for kelp-forest-associated fish, our study illustrates how different sampling techniques used in combination can provide a more complete picture of the responses within the fish assemblage than each technique alone. Fish cages catch actively foraging fish, RUVs quantify fish swimming under the canopy and echosounders quantify fish above the canopy. Bottom-mounted and upward-facing echosounders have been shown to be useful for fish studies at fixed stations (Kaartvedt et al. 2009), but to our knowledge, have never been used to study fish assemblages associated with kelp vegetation. Here, this tool provided an opportunity to perform non-intrusive assessments of fish assemblages in the water column. Importantly, the change in vertical distribution of saithe could only be fully understood when regarding data from the different sampling devices together.

In conclusion, our results show that large-scale experimental kelp trawling has ecological consequences that extend beyond the decline of the habitat-forming species to affect multiple trophic levels of the broader ecosystem. These effects include direct removal of food, diminished biogenic structure and indirect effects via altered fish assemblages across 4 ecosystem levels. Our findings also provide insights into the consequences of the increasing disturbance regimes predicted with climate change, such as increasing storm frequency and severity, which could create similar patterns of kelp loss and habitat fragmentation, and therefore lead to similar ecological consequences. Human disturbance such as kelp trawling may also amplify the effects of these new disturbance regimes by decreasing the resilience of ecosystems and making them more vulnerable to naturally occurring events such as storms (Ling et al. 2015). We suggest that management of coastal ecosystems should, consequently, focus on strengthening resilience and functional redundancy. Resilient ecosystems with high functional redundancy will be vital in order to withstand a future regime with increased disturbance frequency and intensity.

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