



## Multi-trophic consequences of kelp harvest

Svein-Håkon Lorentsen<sup>a,\*</sup>, Kjersti Sjøtun<sup>b,1</sup>, David Grémillet<sup>c,d</sup>

<sup>a</sup> Norwegian Institute for Nature Research, NO-7485 Trondheim, Norway

<sup>b</sup> Institute for Marine Research, P.O. Box 1870, Nordnes, 5817 Bergen, Norway

<sup>c</sup> Centre d'Ecologie Fonctionnelle et Evolutive, CNRS-UMR 5175, 1919 route de Mende, F-34293 Montpellier, France

<sup>d</sup> Perzy FitzPatrick Institute, DST/NRF Centre of Excellence, University of Cape Town, Rondebosch 7701, South Africa

### ARTICLE INFO

#### Article history:

Received 25 September 2009

Received in revised form 12 May 2010

Accepted 18 May 2010

Available online 9 June 2010

#### Keywords:

Coastal habitat

Cormorant

Ecosystem-based management

Fisheries

Gadid fish

Marine ecosystems

### ABSTRACT

Coastal kelp forest ecosystems provide important habitats for a diverse assemblage of invertebrates, fish and marine top-predators such as seabirds and sea mammals. Although kelp is harvested industrially on a worldwide scale little is known about the multi-trophic consequences of this habitat removal. We investigated how kelp fisheries, which remove feeding and nursery grounds of coastal fish, influence local food webs and the availability of food to a marine top predator, the great cormorant (*Phalacrocorax carbo*). We conducted experimental harvesting of the canopy-forming kelp (*Laminaria hyperborea*) during a 3 year period (2001–2003) in an area at the coast of Central Norway while synoptically monitoring fish occurrence and cormorant foraging parameters. Our results demonstrate that cormorants preferentially foraged within kelp-forested areas and performed significantly more dives when feeding in harvested versus un-harvested areas suggesting lower foraging yield in the former case. In kelp areas that were newly harvested the number of small (<15 cm) gadid fish was 92% lower than in un-harvested areas. This effect was persistent for at least 1 year following harvest. To our knowledge, this is the first time that the ecological consequences of kelp harvesting have been tested at a multi-trophic level. The results presented strongly suggest that kelp harvesting affects fish abundance and diminishes coastal seabird foraging efficiency. Kelp fisheries are currently managed in order to maximize the net harvest of kelp biomass, and the underlying effects on the ecosystems are partly ignored. This study calls for re-assessment of such management practices.

© 2010 Elsevier Ltd. All rights reserved.

### 1. Introduction

Trophic relationships structure food webs via complex suites of interactions. Within marine ecosystems, both bottom-up and top-down trophic control occur, whereby the prevalence of each type of mechanism varies in time and space (Frank et al., 2007). Bottom-up control is resource driven, from primary producers onto high trophic levels including top-predators, whereas top-down control is consumer driven, from top-predators onto lower trophic levels. Both operate naturally, and/or can be forced by man-made changes of local and/or global extent.

In kelp forests (brown algae of the order Laminariales) both top-down and bottom-up processes occur and they can operate at various times and have huge effects on the ecosystem. In the Aleutian archipelago, for instance, heavy exploitation of sea otters

(*Enhydra lutris*) by aboriginals and fur traders nearly drove the population to extinction in the 1800s. Sea otters were important predators on sea urchins (*Strongylocentrotus polyacanthus*) which subsequently increased, causing a trophic cascade whereby the kelp forests were grazed down (e.g. Jackson et al., 2001; Steneck et al., 2004; Reisewitz et al., 2006). Legal protection of sea otters reversed this scenario during the 20th century but later kelp forests were again depleted because of increased predation on sea otters by killer whales (*Orcinus orca*, Estes et al., 1998).

Kelp are harvested worldwide as a source of alginate; a biopolymer widely used in the food and cosmetics industry. In Norway, for example, approximately 150,000 tonnes of the canopy-forming kelp (*Laminaria hyperborea*) is harvested annually, providing 5500 tonnes of alginate (e.g. Steen, 2009). These fisheries may strongly affect bottom-up control of marine food webs because they remove feeding and nursery grounds of coastal predatory fish, thereby influencing local food webs and the availability of food to top-predators such as seabirds.

Kelp forests are often viewed as the marine equivalent to terrestrial rain forests due to their great biodiversity of epiphytic flora and macrofauna (e.g. Steneck et al., 2002; Christie et al., 2003, 2009). For instance, Christie et al. (2003) found, on average, 7762 invertebrate

\* Corresponding author. Tel.: +47 73 80 14 00; fax: +47 73 80 14 01.

E-mail addresses: [shl@nina.no](mailto:shl@nina.no) (S.-H. Lorentsen), [kjersti.sjotun@bio.uib.no](mailto:kjersti.sjotun@bio.uib.no) (K. Sjøtun), [david.gremillet@cefe.cnrs.fr](mailto:david.gremillet@cefe.cnrs.fr) (D. Grémillet).

<sup>1</sup> Present address: University of Bergen, Department of Biology, P.O. Box 7800, 5020 Bergen, Norway.

individuals (range 2 to >82,000) on single (*L. hyperborea*) kelp along the Norwegian coast, with a total of 238 mobile macrofaunal taxa. Many of these invertebrates are important food for a number of fish species (Nelson, 1979; Kennelly, 1983; Holmlund et al., 1990; Fosså, 1995; Norderhaug et al., 2005) which use the kelp forests as feeding and nursery areas, and as shelter from larger predators (e.g. Bodkin, 1988; Norderhaug et al., 2005; Reisewitz et al., 2006; Vanella et al., 2007). This is the case for gadid fish, which are particularly common in Norwegian kelp forests (Norderhaug et al., 2005).

Gadid fishes are important for Norwegian coastal fisheries and fishermen often complain about kelp harvest removing important nursery and feeding habitats for these fishes. Up to now very little research has been conducted to test this hypothesis, but studies in *Macrocystis pyrifera* forests (an ecological equivalent to *L. hyperborea*) have shown that removal of kelp reduces fish biomass (Ebeling and Laur, 1985; Bodkin, 1988; Carr, 1989).

If the kelp harvest significantly influences fish abundance by removing important resources like feeding and nursery grounds, effects should be evident for top marine consumers such as large predatory fish, seabirds, and marine mammals, whose distributions are tightly linked to kelp forests (Røv et al., 1990; Fosså, 1995; Bustnes et al., 1997; Steneck et al., 2002; Estes et al., 2004; Graham, 2004). For instance, Røv et al. (1990) demonstrated a close, spatial-overlap between feeding areas of breeding great cormorants (*Phalacrocorax carbo carbo*, hereafter termed cormorants) and kelp forests within their feeding range at the coast of Central Norway. This was also confirmed by Fredriksen (2003) who found that 37% of cormorant carbon originated from local kelp. Cormorants are opportunistic predators that usually search for prey at depths of 10–15 m (Grémillet et al., 1999). They are sensitive to fluctuations in prey availability, as demonstrated in an experimental study on the closely related double-crested cormorant (*Phalacrocorax auritus*) where efficient foraging was not maintained at low levels of prey availability (Enstipp et al., 2007). Consequently, cormorants should be suitable when tracking the potential impact of kelp harvesting on seabirds.

In this study we tested the following hypotheses; (a) kelp harvest reduces the abundance of juvenile gadids through removal of key habitat and/or feeding grounds and (b) if kelp harvest reduces gadid abundance, cormorant feeding performance should be modified in the harvested areas. To test these hypotheses we conducted experimental kelp harvesting during a 3 year period (2001–2003) in an area at the coast of Central Norway while synoptically monitoring fish occurrence and cormorant feeding ecology. We specifically wanted to test the following predictions: (1) numbers of juvenile gadids are lower in harvested kelp areas than in un-harvested areas, (2) numbers of juvenile gadids are positively correlated with the re-growth of kelp in the harvested areas, (3) numbers of cormorants feeding in areas with different harvesting regimes are positively correlated with the number of juvenile gadids, and (4) numbers of cormorant feeding dives should be positively correlated with the number of juvenile gadids.

To the best of our knowledge, this is the first time that the ecological consequences of kelp harvesting have been investigated experimentally at a multi-trophic level.

## 2. Material and methods

### 2.1. Study area, mapping of kelp distribution and kelp harvesting

The study was carried out in the Sula archipelago, Sør-Trøndelag County in Central Norway (63°50'N, 8°20'E). The study area consists of vast shallow areas less than 30 m deep between sub-sea “valleys” at depths of 100–150 m. The shallow water areas in the study area consist of kelp (*Laminaria* spp.) forested areas inter-

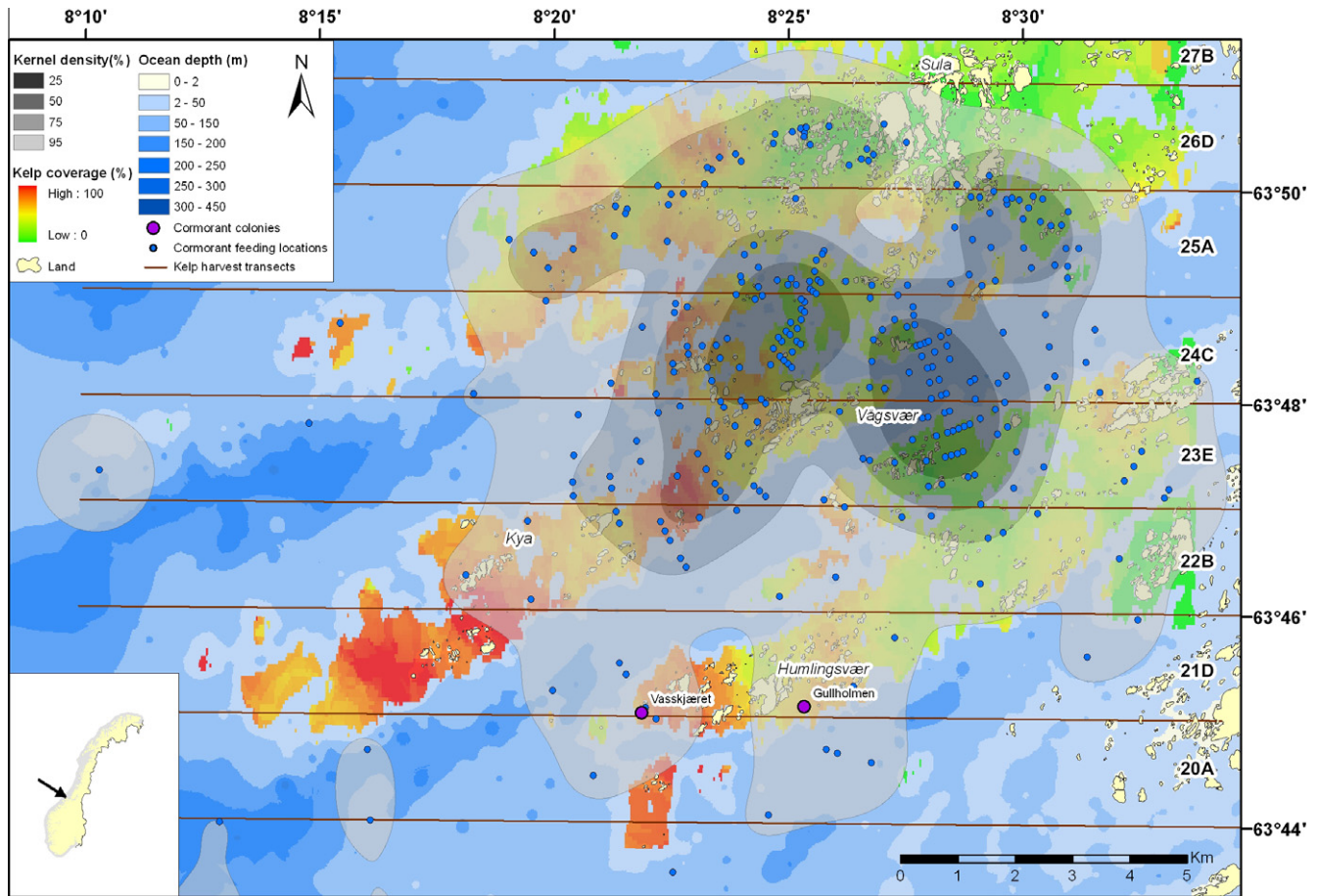
rupted by soft and hard bottom areas with no kelp (Lorentsen, 2001) (Fig. 1).

Kelp distribution in the study area was mapped during 18–27 June 2000 using a grid of sampling points with 300 m east–west and north–south separation. Sampling points within 0–30 m water depths (the maximum depth of kelp growth, e.g. Fosså, 1995) were selected giving a total of 403 points within the study area. An underwater camera (Seavision SVUH-95 with a 2.8 mm Cosmicar lens), attached to a 60 × 80 cm steel frame and coupled to a video recorder (Sanyo TLS 1500P VHS) through a 50 m cable (Bennex Transmark) was lowered to the seafloor at each of the sampling points. The seafloor substrate and kelp coverage was provisionally estimated in true-time from what was seen on a 4” monitor. Back in the office the video recordings were used to verify the initial estimates of substrate and kelp coverage. Kriging ([http://resources.esri.com/help/9.3/ArcGISDesktop/com/Gp\\_ToolRef/3d\\_analyst\\_tools/how\\_kriging\\_3d\\_analyst\\_works.htm](http://resources.esri.com/help/9.3/ArcGISDesktop/com/Gp_ToolRef/3d_analyst_tools/how_kriging_3d_analyst_works.htm)) was used to interpolate the surveyed kelp density sampling points.

We estimated the total area of different cormorant feeding habitats within the home range of the cormorants by constructing a convex polygon around the outermost feeding locations obtained from the radio telemetry study (see Section 2.2). Cormorant feeding habitats were split into three groups; kelp vegetated areas (containing >5% kelp), shallow (and sandy) areas with no kelp, and pelagic areas (>30 m depths) and their total coverage was then estimated in ArcView by combining the data on kelp abundance and coverage (cf. Fig. 1). For the study of fish and cormorant abundance and feeding behaviour the same map was used to select four study plots representing different habitat categories (see Section 2.3). Kernel density estimates of cormorant feeding locations were obtained using the software Animal Movement (Hooge and Eichenlaub, 2000).

Kelp harvesting was initiated within the study area in 2000. Prior to allowing kelp harvesting the management authorities divide the harvestable coastal section into one nautical mile (1852 m) wide latitudinal transects numbered from north to south (Fig. 1). These transects are again arranged in groups of five transects labelled from A to E. The kelp harvest follows a 5 year cycle and each year one of the letter-labelled transects in this group are harvested (see below for an overview of which transects were harvested in the study area during the study period). The kelp is harvested with a rake-type dredge which is pulled by the boat along the bottom, and which rips the kelp plants from the rock. Kelp harvest removes all canopy-forming kelp plants in a 4-m wide track, leaving either a barren track or a track that is vegetated by small remaining kelp plants (Waage-Nielsen et al., 2003). This procedure is repeated until as much as possible of the kelp plants within the harvested transect are removed.

A total of 15,303 metric tonnes (wet mass) of kelp were harvested in the study area during 2000–2003. In the first year (2000) the D-transects were harvested (21D: 4485 tonnes) in the autumn, in 2001 no transects were harvested due to the experimental set-up as we wanted to get sufficient background data on cormorant feeding behaviour (feeding habitats, dive durations and foraging success) using radio-tracking and electronic balances placed under their nests (see below). In 2002 and 2003 the E- and B-transects were harvested (23E: 1419, 22B: 2607 and 27B: 710 tonnes, respectively), at the end, and before the field seasons, respectively. These transects were not those that were scheduled to be harvested according to the kelp harvesting industry's ordinary plan but were chosen specifically for the experimental set-up because they contained much kelp and were suitably positioned within the study area. The harvesting procedure itself, and the amount of kelp harvested were set by the industry according to procedures followed during “normal” harvest. There were strong and positive correlations between the number of sampling plots



**Fig. 1.** Location of the study area along the Norwegian coast (inserted map of Norway), kelp coverage (green to red shading), cormorant feeding habitats (blue dots) and Kernel cormorant feeding density distribution (light to dark grey shading). Kelp harvest transects, labelled 20A–27B are indicated as well as the two cormorant breeding colonies used in 2001 and 2002 (pink dots). Depth contours are indicated by light to dark blue shading.

with >50% kelp coverage within the respective transects and the amount of kelp harvested within the same transects;  $r^2 = 0.96$  (SHL unpublished data) indicating that the classification of kelp distribution was in agreement with real kelp abundance.

## 2.2. Cormorant radio-tracking, food consumption and catch per unit effort

In order to obtain data on cormorant feeding locations 11 individuals (3 in 2001 and 8 in 2002) were equipped with VHF-radio transmitters (Biotrack TW-3). The transmitters were attached underneath the two central tail feathers with cable ties. The birds were captured at the nest following Grémillet and Wilson (1998), and the capture and attachment procedure took less than 10 min.

In 2001 and 2002 birds were radio-tracked simultaneously from 21 June–8 July and 8 June–10 July, respectively, more or less daily from 6 am to 9 pm from two tracking stations situated 1.7 km from each other, at approximately 25 m above sea level (the two highest islands within the study area). Both tracking stations were equipped with two six element Yagi aerials mounted on a 4 m mast and connected through a null peak combiner (Telonics TAC-5) to a Televilt RX900 receiver. The bearing of the transmitters was determined at least every 10 min with 1° accuracy. The activities of the birds (nesting, flying, resting, diving) were registered, as well as the duration of at least one consecutive dive cycle (dive and recovery) if the bird was diving (cf. Wanless et al., 1991). All information was stored on a Husky Hunter field computer. The second tracking station was used to determine the position and the foraging range of

birds at sea by triangulation (cf. Grémillet et al., 1996) at least every 30 min, and to collect activity data in the same way as the primary station. Individual cormorants normally perform 1–4 feeding trips/day (e.g. Grémillet et al., 2004), and a total of 347 feeding locations were obtained, with a mean of 32 locations (range 6–63) from each individual.

In order to estimate cormorant catch per unit effort (CPUE) we used nest balances to determine the amount of food caught during each foraging trip following Grémillet et al. (1996). Briefly, electronic balances were placed underneath the nests of five cormorant pairs raising young chicks and the total nest mass was registered every 10 s by the mass difference when adults entered and left the nest. Since females have a lower body mass than males we were able to distinguish between the pair members allowing us to calculate for each of them; the duration of each foraging trip, the amount of food brought back to the nest after each foraging trip, and the number of foraging trips per day. The mass of this food load was corrected for digestion occurring during the foraging trip following Grémillet et al. (1996).

Finally, catch per unit effort (CPUE  $\text{g min}^{-1}$ ) was estimated using the ratio of the amount of food caught per foraging trip (from the nest balances) to the time spent underwater per foraging trip (from the radio-tracking data).

## 2.3. Impact of kelp harvesting on fish and cormorants

In order to study the impacts of kelp harvesting on fish and cormorant abundance and feeding behaviour we selected four study

plots representing different habitat categories from the maps of kelp-distribution and abundance (Fig. 1): (1) un-harvested, <25% kelp coverage (sea area 1.7 km<sup>2</sup>), (2) un-harvested >50% kelp coverage (sea area 1.16 km<sup>2</sup>), (3) newly harvested (1.5 months prior to the study), >50% kelp coverage prior to harvesting (sea area 0.74 km<sup>2</sup>), and (4) harvested 1 year before the study (2002), >50% kelp coverage (prior to harvesting, sea area 0.51 km<sup>2</sup>). Due to the spatial distribution of kelp and the need for a nearby island to do the observations from, this selection process was not random. Also, these sites were not replicated. The fish counts were performed using a mini-ROV (Remote Operated Vehicle, VideoRay Pro, see below). While performing these counts in the cormorant study plot within the newly harvested transect we found that the kelp was insufficiently harvested and therefore (cormorant) observations from this plot were discarded. Additional fish observations for this transect were performed in a nearby (newly harvested) area. However, this area contained no islands from which we could perform direct observations of the cormorants. This information is therefore lacking for this particular habitat type.

From the 8–22 June 2003 visual observations of cormorants were performed in each of these habitat categories over 10 observation periods of 4.5 h each. The observation periods were rotated so that each habitat category was observed during morning (normally between 7 and 11) and afternoon hours (normally between 13 and 17) and between high and low tide every other time. Observation periods thus lasted from 2 h before high or low tide to 2 h after high or low tide. Two observers performed the observations in each area. Number of cormorants, and their behaviour (feeding, resting at sea or on land) within the habitat categories were registered once every hour (maximum time underwater per foraging trip is 54 min in cormorants Grémillet et al., 2004), thus avoiding counting the same individual several times. If a flock of foraging individuals arrived within the habitat categories we counted the number of individuals and timed their arrival and departure. In order to correct for different sizes of the habitat categories cormorant numbers (numbers observed per time unit) were adjusted according to the area of sea surface within each of the habitat categories (see above). Dive times, recovery periods at the sea surface as well as total diving bout time; i.e. from when that the individual in focus arrived into the study plot and until it left the area, including pauses of up to 5 min were recorded (following Grémillet et al., 2005) using a Husky Hunter field computer.

Fish occurrence was recorded from 20 to 29 June 2003 at 12 stations, one to four in each of the habitat categories (see above), using a mini-ROV fitted to a video recorder (LG TVCR). This study were mainly aimed at investigating the effects of kelp harvesting on breeding cormorants, and we, thus, assume that fish movements within this period is limited. The stations selected for the fish recordings were the same as those used for recording kelp coverage in 2000, thus eliminating small scale variations in kelp coverage within the habitat categories. Arriving at the stations the ROV was lowered to the seafloor, or to the top of the kelp bed, before it was manoeuvred in a direct line and at a constant speed (0.5–1 m/s) away from the boat until the cable was fully extended (c. 50 m). This was repeated 3–5 times at the same station and in different directions away from the boat, an operation that normally lasted 20–40 min. Fish abundance estimates were obtained from video tapes while the ROV was in motion just above the kelp canopy or the seafloor. These estimates were recorded as fish numbers per unit time for a total of 44 observation periods lasting between 5 and 20 min. Fish observed could usually be identified to family level by means of their appearance (shape, colour), and behaviour. Gadid fish were split in two groups according to their size; juvenile (small) fish <15 cm, and larger fish >15 cm.

Estimates of fish biomass in the different habitats was obtained using the following assumptions: (1) Only cod (*Gadus morhua*) and

saithe (*Pollachius virens*) were available (these two species consisted 78% of the cormorant diet in the study area in 2003, Lorentsen et al., 2004), (2) An “average fish” taken by cormorants consists of 83% saithe and 17% cod (Lorentsen et al., 2004), (3) The average mass of fish taken by cormorants is 17.3 g for a fish <15 cm, and 98.7 g for a fish >15 cm (Lorentsen et al., 2004), (4) The estimated volume of water scanned by the ROV min<sup>-1</sup> is 385 m<sup>3</sup> for the minimum and 246 m<sup>3</sup> for the maximum biomass estimates obtained (depending on the vertical and horizontal extension of the scanned area). The ROV moved with an average speed of 0.5 knots, covering 15.4 m min<sup>-1</sup>, and the vertical area of water in sight (from the camera when the fish was counted) was estimated to 5 × 5 m for the minimum and 4 × 4 m for the maximum estimates, respectively).

Estimates of cormorant foraging success in different habitats were calculated following the assumptions that: (1) cormorant CPUE as determined using nest-balances and radio-tracking in 2001–2002, 9.76 g min<sup>-1</sup> (Grémillet et al., 2004), were obtained from a un-harvested area with >50% kelp cover, and (2) that the CPUE obtained by the cormorants are directly proportional to the fish abundance estimates obtained using the ROV surveys (Fig. 3A). Thus, for this purpose, we used the fish abundance for an un-harvested area with kelp cover >50% as the reference point (100% fish abundance). Following this, an area with 50% fish abundance compared with un-harvested areas allows cormorants to forage with a CPUE of 4.88 g min<sup>-1</sup>. Thus, the reductions in CPUE and the estimated cormorant foraging success are assumed to be directly related to the reductions in fish availability in the other habitats.

#### 2.4. Statistical analysis

We used Chi-square goodness-of-fit tests (Neu et al., 1974) to analyse whether radio-tracked cormorants utilized feeding habitats in proportion to their availability (null hypothesis of no habitat selection). If a significant result was detected, Bonferroni Z-statistics were used to determine habitat use in relation to the expectations (Neu et al., 1974). A GLM with a quasi-Poisson distribution and a log-link function was used to test the effects of fish and cormorant numbers on harvesting regime. For fish we used the actual count and survey time was declared as an offset. Mann–Whitney U test was used to test whether cormorant numbers varied with tidal level (low or high). Observations of feeding cormorants and ROV surveys of fish abundance could not be performed at exactly the

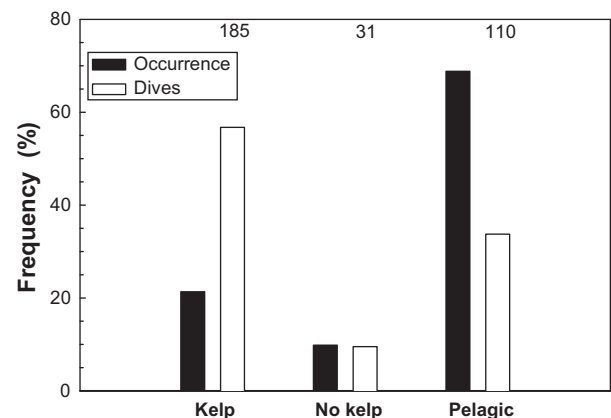
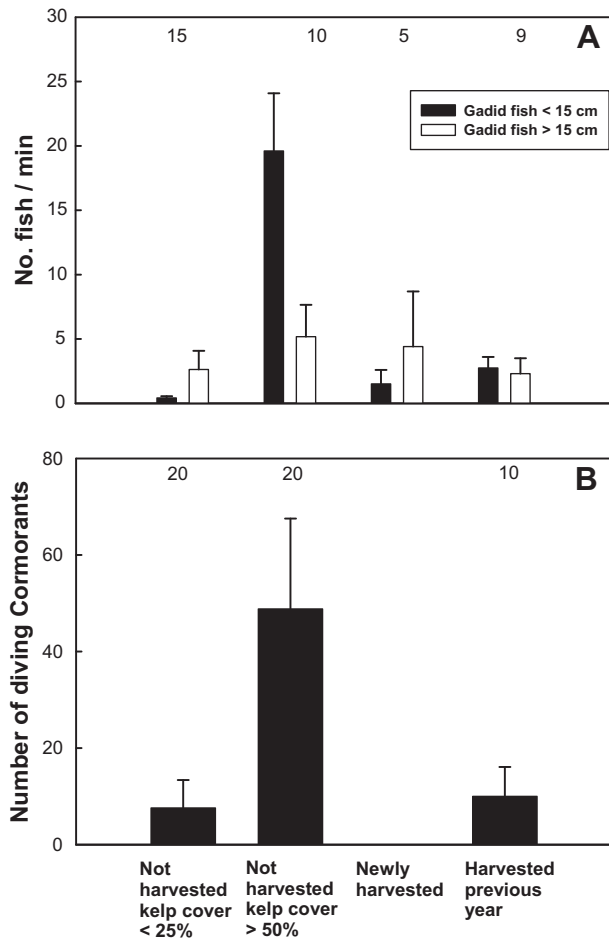


Fig. 2. Habitat use (frequency of feeding dives) of great cormorants in relation to the total availability of the different habitat types within the feeding area of the radio-tagged cormorants. The numbers above the white bars indicate the numbers of dives ( $n$ ).



**Fig. 3.** (A) Number of gadid fish (and SE) in habitat categories (study plots) with different kelp harvesting history and kelp cover. Black bars = fish <15 cm, white bars = fish >15 cm. (B) Mean number (and SE) of Great Cormorants in habitat categories with different kelp cover and harvesting history. Differences between the habitat categories un-harvested but with <25% and >50% kelp cover, respectively, were statistically significant. The numbers above the bars indicate the numbers of observation periods (*n*).

same time due to the disturbance caused by the ROV itself and by the vessel from which the ROV was operated. In order to test the combined effects of kelp harvest on the number of feeding cormorants and fish we therefore used a bootstrap procedure whereby we first resampled all relevant observations 1000 times and then  $\log(x + 1)$  transformed averages of the observations in order to achieve a normally distributed sample. Assuming a negative correlation between fish and cormorant numbers in harvested versus un-harvested areas *P* values were calculated using the number of negative slopes between observations from the two habitats (un-harvested and harvested in the previous year) assuming that kelp harvesting did not change numbers of cormorants or fishes, and if there was a change it would not be positive.

### 3. Results

#### 3.1. Kelp distribution and cormorant feeding habitats

Kelp had a westerly distribution within the study area, with the most pronounced kelp forests in rocky parts and areas most exposed to ocean swell, i.e. directed westwards (Fig. 1). The eastern parts of the study area were dominated by soft and sandy bottoms with very little kelp. Cormorant feeding areas were situated in the

central and the eastern sections of the study area, with 21% of these zones within kelp vegetated areas, 10% within sandy and shallow areas without kelp, and 69% over waters deeper than 30 m (Fig. 2). Cormorant use of these habitats was statistically different from their natural availability ( $\chi^2 = 250.08$ , *df* = 2, *p* < 0.001, Fig. 2) and birds clearly favoured kelp vegetated areas ( $\chi^2 = 191.76$ , *df* = 1, *p* < 0.001). Sandy and shallow areas were used as expected from their availability ( $\chi^2 = 0.04$ , *df* = 1, *p* > 0.05), and pelagic areas less than expected ( $\chi^2 = 58.28$ , *df* = 1, *p* < 0.001).

#### 3.2. Fish numbers

The number of small gadids (<15 cm body length) varied greatly between the habitat categories, from less than one individual observed per minute in the un-harvested area with less than 25% kelp cover, to nearly twenty individuals per minute in the un-harvested area with more than 50% kelp cover, whereas for the number of larger gadids (>15 cm body length) there were much less variation (Fig. 3A). A GLM was used to test the effect of kelp harvest regime and fish size/age on the number of fish observed. The model used two factors, one 4-level factor describing harvest regime and kelp coverage (cf. Fig. 3A), and the other the size/age of the fish. Small gadids but not larger ones were positively correlated with kelp cover and showed a strong association with the un-harvested areas (Table 1A, coefficient = 3.2612, *p* = 0.0124).

#### 3.3. Cormorant numbers

There were no significant differences in the number of cormorants feeding in the individual habitat categories with respect to tidal level (Mann–Whitney, all *p* > 0.05) so count data were collapsed into one group for each habitat category. A GLM was used to test the effect of kelp harvest regime on the number of cormorants observed in the study plots. The model used one 4-level factor describing harvest regime and kelp coverage (cf. Fig. 3B). Cormorant numbers were strongly correlated with kelp cover and showed a strong association with the un-harvested areas (Table 1B, coefficient = 1.8592, *p* = 0.0162). The bootstrap procedure showed that numbers of cormorants and small fish in the un-harvested area with more than 50% kelp coverage were higher than in the area harvested 1 year earlier (Fig. 3, *p* = 0.009). Such patterns were not found for larger fish (*p* = 0.126).

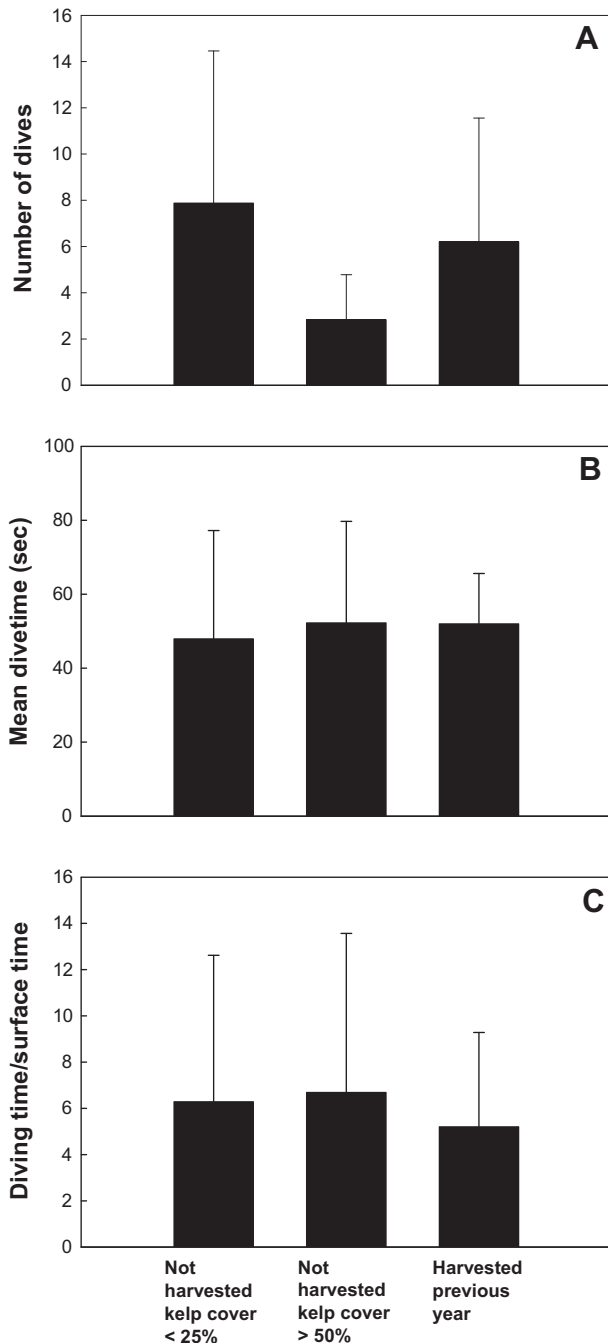
**Table 1**

Values for a GLM with a quasi-Poisson distribution with a log-link function testing the association between A. Fish numbers and kelp harvest regimes (kelp B = not harvested, kelp C = harvested previous year, and kelp D = newly harvested) and the size/age of the (fish, small vs. larger) and their interactions. Null deviance = 827.11, residual deviance = 428.83, *n* = 39. B. Cormorants numbers and kelp harvest regimes (same categories as for fish). Null deviance = 3861.9, residual deviance = 3057.7, *n* = 50.

	Parameter	Estimate	SE	<i>t</i> -Value	<i>P</i>
A	<i>Fish numbers</i>				
	Intercept	1.0464	0.4230	2.473	0.0158
	Kelp B	0.5806	0.5737	1.012	0.3150
	Kelp C	-0.2712	0.7551	-0.359	0.7206
	Kelp D	0.4576	0.7202	0.635	0.5272
	Small fish	-1.9396	1.1933	-1.625	0.1086
	Kelp B*small fish	3.2612	1.2705	2.567	0.0124
	Kelp C*small fish	2.1513	1.4601	1.473	0.1451
	Kelp D*small fish	0.8436	1.6674	0.506	0.6145
	B	<i>Cormorant numbers</i>			
Intercept		2.0289	0.8132	2.495	0.0162
Kelp B		1.8592	0.8742	2.127	0.0387
Kelp C		0.2735	1.2912	0.212	0.8331

### 3.4. Cormorant diving and feeding behaviour

Cormorants performed significantly different number of dives within the three habitat categories (ANOVA,  $F_{2,38} = 3.35$ ,  $p = 0.046$ ). Significantly fewer dives per foraging trip were performed in the un-harvested areas with kelp cover more than 50% than in the un-harvested areas with kelp cover less than 25% ( $p = 0.035$ , Tukeys test for differences between groups). No such differences were found between the other combinations of comparisons between numbers of dives per foraging trip in the different habitat categories (Fig. 4A).



**Fig. 4.** Cormorant diving behaviour in habitat categories with different kelp cover and kelp harvesting history. (A) Number of dives, (B) mean duration of dives, (C) ratio between time under water and the following surface time (until the next dive), an index of work load.

Mean dive times and the ratio between diving and surface time (an index of work load) showed no significant variation between the different habitat categories, or any individual differences between any of the habitat categories (Fig. 4B and C).

In order to assess whether the diving and feeding behaviour of the cormorants was related to possible foraging success, fish availability was estimated for the different habitat categories. Although cormorants performed more dives in areas with little kelp, the estimated foraging success was less than half of that experienced in the un-harvested areas with >50% kelp cover (Table 2). In the un-harvested area with <25% kelp cover, and the area harvested 1 year earlier, fish biomass estimates ranged between 0.7 and 1.1 g m<sup>3</sup> (minimum and maximum estimates, cf. Table 3). This corresponds to approximately 30% of the fish biomass estimate for areas with kelp cover >50% that were un-harvested.

## 4. Discussion

### 4.1. Kelp harvest reduces the abundance of juvenile gadids

Reductions of fish numbers after kelp removal have been demonstrated for *Macrocystis* kelp forests (e.g. Ebeling and Laur, 1985; Bodkin, 1988; Carr, 1994; Vanella et al., 2007), as well as *Laminaria* kelp forests (e.g. Reisewitz et al., 2006). In our study the number of small (<15 cm) gadid fish was more than 90% lower in the newly harvested area than in nearby un-harvested areas with >50% kelp cover. In an area that had been harvested 1 year earlier the fish numbers were around 85% lower than in un-harvested areas with >50% kelp cover. These numbers are similar to those found in areas with little, or no, kelp. For large (>15 cm) gadids fish numbers were similar in harvested and un-harvested areas indicating that these were not severely influenced by the harvest. Reduction in the number of small fish was similar to what Bodkin, (1988) found after experimental removal of *Macrocystis* from a 1-ha area off central California (63%), but much higher than what Ebeling and Laur (1985) observed in the same area after loss of a kelp habitat due to storm damage and urchin grazing (20%). This suggests that fish respond differentially to industrial harvest of kelp than to the “natural” removal through storms and benthic grazers, maybe because the amount of kelp removed during industrial harvest is larger.

Kelp harvest leave the small understory plants undisturbed (e.g. Christie et al., 1998), but ROV video-data collected during this study showed a more or less complete harvest (see also Christie et al., 2003). Such massive removal obviously triggered a dramatic reduction in the abundance of small-sized gadids which lost shelter and food. This was also demonstrated by Ebeling and Laur, (1985) and Vanella et al. (2007) who selectively removed kelp blades from plants. These thinning experiments clearly showed that juvenile fish avoided open spaces, but that adult fish were not severely affected.

The fate of small fish after kelp harvest is unclear and at least two outcomes are possible. First, they will become an easy target for predatory fish and birds (e.g. cormorants) and will be predated as soon as their hiding places are removed. Second, they will migrate or re-group to the nearest kelp-forested areas due to lack of shelter in the harvested areas. Bodkin (1988) suggested that fish that were displaced by kelp forest removal did not relocate to the nearest available kelp area, but may have dispersed over an area larger than the study site. The fate of larger gadids (>15 cm) is also unknown. Their numbers appeared unaffected by kelp harvest, although previous dietary studies clearly show that cormorants can target fish up to 55 cm in length (Lorentsen et al., 2004).

The number of juvenile fish was two times higher in the area that had been harvested 1 year earlier than in the area that had been newly harvested, but was still 15% of the fish numbers found

**Table 2**  
Estimated cormorant foraging success in different habitats. Fish availability in the un-harvested area with kelp cover >50 is 1 (=100%), and in the other areas relative to the estimated reductions in CPUE.

	Mean number of dives	Mean dive time (s)	Fish availability	CPUE (g min <sup>-1</sup> )	Estimated foraging success (g fish/dive bout)
Un-harvested, kelp cover <25%	7.9	48.0	0.12	1.17	7.4
Un-harvested, kelp cover >50%	2.8	52.3	1	9.76	23.8
Harvested previous year	6.2	52.0	0.21	2.0	10.7

**Table 3**  
Estimated fish biomass in different habitats.

	Estimated fish biomass (g m <sup>-3</sup> )	
	Minimum	Maximum
Un-harvested, kelp cover <25%	0.69	1.08
Un-harvested, kelp cover >50%	2.21	3.45
Harvested previous y	0.72	1.12

in un-harvested areas. In a study of kelp re-growth [Christie et al. \(1998\)](#) found that 5 years after the harvest mean canopy height was still 30% lower and the holdfast volume only one third of the pre-harvest level. The density of juvenile fish seems to be strongly influenced by kelp habitat characteristics (i.e. availability of shelter). [Christie et al. \(1998, 2009\)](#) show that kelp forests need many years to fully recover after the harvest and assuming that juvenile fish re-establish accordingly our results suggest that fish numbers might be low for several years after the harvest. Thus, in a kelp harvested area consisting of multiple transects harvested during a 5-year interval, as used in Norway, fish numbers might be considerably reduced compared to un-harvested areas. Although, our findings can only be verified through long-term studies the results might, in the long run, impose severe implications for gadid populations along the coastal sections that are being harvested.

#### 4.2. Kelp harvesting impacts cormorant feeding behaviour

Results from this study clearly confirm the importance of kelp-forested areas as feeding grounds for cormorants.

The numbers of feeding cormorants reflected the numbers of small fish found in the respective habitat categories demonstrating their unique capability of tracking even small fish densities ([Grémillet et al., 2004](#)). Seabird distribution in the open seas is often correlated with oceanographic features and fish abundance (e.g. [Fauchald et al., 2000](#)). For coastal, shallow water ecosystems which are less accessible to research vessels, such correlations have been more difficult to assess. By using ROVs and video surveillance this obstacle is partly avoided, but is still associated with methodological difficulties (see e.g. [Willis et al., 2000](#)). For instance estimates of fish abundance from the present study probably underestimate real numbers. Indeed, the present study was set to estimate fish numbers within the upper layer of kelp forests. When used in areas with little or no kelp, before or after harvest, the ROV was manoeuvred just above the seafloor or the canopy of the kelp present. Under these conditions well-camouflaged fish like flatfish and sculpins (*Cottidae*) might have been overlooked by the ROV (e.g. [Norderhaug et al., 2005](#)). On the other hand, direct underwater observations (DG pers. obs.) suggest that cormorants do not feed within dense kelp forests due to propulsion problems. Therefore estimates obtained for this habitat likely mirror prey availability to the birds, if not overall abundance.

[Enstipp et al. \(2007\)](#) investigated the functional link between prey abundance and double-crested cormorant foraging performance under controlled conditions. They suggested that fish densities of 2–3 g m<sup>3</sup> represented a threshold density below which

sustainable foraging is compromised. In our study, estimated fish densities were above this threshold only within un-harvested areas with kelp cover >50%, and below for all other habitats ([Table 3](#)). Moreover, the cormorants performed significantly more dives in the low density areas (un-harvested areas with kelp cover <25% and areas harvested the previous year) than in the high density areas suggesting they used more time to find prey. These results partly support findings by [Enstipp and colleagues](#), and suggest that kelp harvesting may strongly compromise cormorant foraging efficiency. Indeed, our estimates based on fish availability and cormorant feeding behaviour indicated a significant decrease in CPUE in harvested areas and areas with low kelp cover ([Table 2](#)). Although the relative difference between CPUE estimates in the different habitats is likely to be correct, these figures should be treated as indicative as they feature an average for several individuals that might have foraged in different habitats (both un-harvested and harvested areas with different kelp coverage). Thus, the CPUE used as a reference value in this study might have been too low for cormorants feeding in un-harvested kelp-forested areas, and too high for individuals feeding in harvested areas.

Beyond a reduction in gadid abundance, kelp harvesting also drastically modifies the underwater landscape familiar to foraging cormorants. Since such long-lived marine predators most probably use memorized information to optimize their foraging yield ([Grémillet et al., 1999](#); [Elliot et al., 2008](#)) they will most probably need time to familiarize with the alterations of their feeding habitats and the concurrent reductions in fish abundance.

#### 4.3. Conclusions and implications for the management of kelp harvest

Kelp harvest is currently managed in order to maximize the net harvest of kelp biomass and the underlying effects on the whole ecosystem are thus partly ignored. Kelp harvest removes all canopy-forming kelp plants, leaving either a barren track or a track that is vegetated by small kelp plants that ensure re-growth ([Waage-Nielsen et al., 2003](#)). In Norway kelp harvest follows a 5 year cycle which does not allow kelp plants to fully re-grow before the next harvest ([Christie et al., 1998, 2009](#)). Kelp epiphytes do not fully recover during this short period of time, neither do resident populations of amphipods and isopods ([Christie et al., 1998, 2009](#)), important food resources for gadid fishes ([Norderhaug et al., 2005](#)).

Kelp harvest removes the habitat for coastal fish and their food base, and our results strongly suggest that the number of juvenile fish remains low for several years following kelp harvest. Also, we suggest that in a coastal landscape with multiple kelp harvest transects of different age, the number of small gadids might be considerably lower than the numbers found in un-harvested areas. Although the long-term ecological consequences of these trends are still to be evaluated, they obviously impose severe threats to gadid populations along the coastal sections which are being harvested. The coastal population of Cod is classified as endangered on the Norwegian red list ([Kålås et al., 2006](#)), and all threats to this population should be avoided.

Kelp harvest compromises individual cormorant foraging efficiency and a significant decrease in CPUE is probably experienced

in harvested areas. How this reduced foraging efficiency affects cormorant populations is still unclear. In the study area and period, the number of breeding cormorants decreased by 35%, compared with 7% in a nearby, un-harvested area. However, for the period 2001–2008 population development were similar in these areas (The Norwegian monitoring programme for seabirds, unpubl. data), suggesting that the population decrease in the harvested area in the first years could be an initial effect of the harvest and that the cormorants, in the long run, are able to adapt to the changed feeding conditions. Nevertheless, this should be investigated further, together with the effect on other marine top-predators such as e.g. black guillemots (*Cephus grylle*) and otters (*Lutra lutra*), which are confined to nearshore kelp-forested habitats all the year around (e.g. Cramp and Simmons, 1977; Kruuk et al., 1990; Reisewitz et al., 2006).

Reduction of juvenile fish abundance due to the removal of their feeding and hiding grounds by kelp harvesting is by nature a bottom-up process, although driven by human exploitation. However, these fish, especially medium sized and large cod, are important predators of early pelagic and settled juvenile stages of sea urchins (e.g. Steneck et al., 2002, 2004). In our study gadids of the size that are considered important predators on sea urchins did not seem to be severely affected by kelp harvest. However, if this had been the case, it could have had a strong negative effect on sea urchin predation (and density) and might have strengthened kelp-forest susceptibility to grazing, especially because kelp forests are also strongly reduced and fragmented due to the harvest itself (e.g. Sjøtun et al., 2006). The kelp harvesting industry is familiar with the risk of increased sea urchin abundance after kelp harvest due to the “opening of barren areas” (Steneck et al., 2002). In a recent study (Byrnes et al., 2006) predator diversity in kelp forests was found to be negatively correlated with herbivore abundance and positively correlated with kelp abundance. Also, Steneck et al. (2002, p. 441) concluded that “predators... are the single most important agent controlling sea urchin populations” and that fragility in kelp forest ecosystems may depend on local biodiversity. Kelp harvest reduces local biodiversity (Christie et al., 2009) and might, thus, reduce kelp forest ability to resist to changes in herbivore abundance. The effects of kelp harvesting on other kelp-associated fish species (e.g. labrids and sculpins) which are important predators of invertebrate herbivores, and important food to kelp-forest-associated top-predators, remain to be studied to complement our understanding of kelp forest natural and anthropogenic dynamics.

The present study suggests that the kelp harvesting regimes used, and the kelp harvest itself, might have serious impacts on the marine community, including populations of Cod that are currently endangered. We suggest that the ecological impact of such harvest should be evaluated at the ecosystem level, taking into account its combined effects on all trophic levels. The present study is a first essential step towards this goal.

## Acknowledgements

This study was part of a 3 year Research Council funded Project addressing the ecological effects of kelp harvesting. Funding was also received from the Directorate for Nature Management, the County Governor in Sør-Trøndelag, and the Norwegian Institute for Nature Research.

Permissions to catch, handle and attach radio transmitters to the cormorants was obtained from the Directorate for Nature Management and the Animal Research Authorities. All handling of the birds was in accordance with the animal welfare act and other legal requirements in Norway.

We are indebted to Steinar Engen for help with the bootstrap analysis, to Grégoire Certain for help with the GLM, and to Stein Ar-

ild Hoem and Frank Hansen for help with preparing Fig. 1. Jostein Veia, FMC Biopolymer administered the contact with the kelp harvesters regarding the experimental harvest. The following persons contributed very much during the field work: Halvor Asper, Jan Ove Bustnes, Manfred Enstipp, Brage Bremset Hansen, Ann Harding, Karen Margrete Okstad, Svein Hustrulid, Jørgen Haarstad and Ragnar Lian, as did also the people at Sula, especially Edvin Paulsen.

## References

- Bodkin, J.L., 1988. Effects of kelp forest removal on associated fish assemblages in central California. *Journal of Experimental Marine Biology and Ecology* 117, 227–238.
- Bustnes, J.O., Christie, H., Lorentsen, S.-H., 1997. Seabirds, kelp beds and kelp trawling: a summary of knowledge. NINA Oppdragsmelding 472, 1–43 (in Norwegian with English summary).
- Byrnes, J., Stachowicz, J.J., Hultgren, K.M., Hughes, A.R., Olyarnik, S.V., Thornbert, C.S., 2006. Predator diversity strengthens trophic cascades in kelp forests by modifying herbivore behaviour. *Ecology Letters* 9, 61–71.
- Carr, M.H., 1989. Effects of macroalgal assemblages on the recruitment of temperate zone reef fishes. *Journal of Experimental Marine Biology and Ecology* 126, 59–76.
- Carr, M.H., 1994. Effects of macroalgal dynamics on recruitment of a temperate reef fish. *Ecology* 75, 1320–1333.
- Christie, H., Fredriksen, S., Rinde, E., 1998. Regrowth of kelp and colonization of epiphyte and fauna community after kelp trawling at the coast of Norway. *Hydrobiologia* 375 (376), 49–58.
- Christie, H., Jørgensen, N.M., Norderhaug, K.M., Waage-Nielsen, E., 2003. Species distribution and habitat exploitation of fauna associated with kelp (*Laminaria hyperborea*) along the Norwegian coast. *Journal of the Marine Biological Association of the United Kingdom* 83, 687–699.
- Christie, H., Norderhaug, K.M., Fredriksen, S., 2009. Macrophytes as habitat for fauna. *Marine Ecology Progress Series* 396, 221–233.
- Cramp, S., Simmons, K.E.L., 1977. *The Birds of the Western Palearctic*, vol. I. Oxford University Press, Oxford.
- Ebeling, A.W., Laur, D., 1985. The influence of plant cover on surfperch abundance at an offshore temperate reef. *Environmental Biology of Fishes* 12, 169–179.
- Elliot, K.H., Woo, K., Gaston, A.J., Benvenuti, S., Antonia, L.D., Davoren, G.K., 2008. Seabird foraging behaviour indicates prey type. *Marine Ecology Progress Series* 354, 289–303.
- Enstipp, M.R., Grémillet, D., Jones, D.R., 2007. Investigating the functional link between prey abundance and seabird predatory performance. *Marine Ecology Progress Series* 331, 267–279.
- Estes, J.A., Tinker, M.T., Williams, T.M., Doak, D.F., 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* 282, 473–476.
- Estes, J.A., Danner, E.M., Doak, D.F., Konar, B., Springer, A.M., Steinberg, P.D., Tinker, M.T., Williams, T.M., 2004. Complex trophic interactions in kelp forest ecosystems. *Bulletin of Marine Science* 74, 621–638.
- Fauchald, P., Erikstad, K.E., Skarsfjord, H., 2000. Scale-dependent predator-prey interactions: the hierarchical spatial distributions of seabirds and prey. *Ecology* 81, 773–783.
- Fosså, J.H., 1995. Management of Kelp. Prioritized Research Activities. Institute of Marine Research (in Norwegian with English summary).
- Frank, K.T., Petrie, B., Shackell, N.L., 2007. The ups and downs of trophic control in continental shelf ecosystems. *Trends in Ecology and Evolution* 22, 236–242.
- Fredriksen, S., 2003. Food web studies in a Norwegian kelp forest based on stable isotope ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) analysis. *Marine Ecology Progress Series* 260, 71–81.
- Graham, M.H., 2004. Effects of local deforestation on the diversity and structure of southern California giant kelp forest food webs. *Ecosystems* 7, 341–357.
- Grémillet, D., Wilson, R.P., 1998. A remote-controlled net trap for ground nesting cormorants. *Seabirds* 20, 44–47.
- Grémillet, D., Dey, R., Wanless, S., Harris, M.P., Regel, J., 1996. Determining food intake by great cormorants and European shags with electronic balances. *Journal of Field Ornithology* 67, 637–648.
- Grémillet, D., Wilson, R.P., Gary, Y., Storch, S., 1999. Three-dimensional space utilization by a marine predator. *Marine Ecology Progress Series* 183, 263–273.
- Grémillet, D., Kuntz, G., Delbart, F., Mellet, M., Kato, A., Robin, J.-P., Chaillon, P.-E., Gendner, J.-P., Lorentsen, S.-H., Le Maho, Y., 2004. Linking the foraging performance of a marine predator with local prey abundance. *Functional Ecology* 18, 793–801.
- Grémillet, D., Kuntz, G., Woakes, A.J., Gilbert, C., Robin, J.-P., Le Maho, Y., Butler, P.J., 2005. Year-round recordings of behavioural and physiological parameters reveal the survival strategy of a poorly insulated diving endotherm during the Arctic winter. *Journal of Experimental Biology* 208, 4231–4241.
- Holmlund, M.B., Peterson, C.H., Hay, M.E., 1990. Does algal morphology affect amphipod susceptibility to fish predation? *Journal of Experimental Marine Biology and Ecology* 139, 65–83.
- Hooge, P.N., Eichenlaub, B., 2000. Animal movement extension to Arcview. Ver. 2.0. Alaska Science Center. Biological Science Office, US Geological Survey, Anchorage, AK, USA <<http://www.absc.usgs.gov/glb/gistools/>>.
- Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlanson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange,



- C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J., Warner, R.R., 2000. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293, 629–638.
- Kålås, J.A., Viken, Å., Bakken, T., 2006. 2006 Norwegian Red List. Artsdatabanken, Norway.
- Kennelly, S.J., 1983. An experimental approach to the study of factors affecting algal colonization in a sublittoral kelp forest. *Journal of Experimental Marine Biology and Ecology* 68, 257–276.
- Kruuk, H., Wansink, D., Moorhouse, A., 1990. Feeding patches and diving success of otters, *Lutra lutra*, in Shetland. *Oikos* 57, 68–72.
- Lorentsen, S.-H., 2001. Mapping of kelp *Laminaria* spp. And Cormorant *Phalacrocorax carbo carbo* at Sula, Frøya municipality, Sør-Trøndelag county. NINA Oppdragsmelding, 683 (in Norwegian).
- Lorentsen, S.-H., Grémillet, D., Nymoen, G.H., 2004. Annual variation in diet of breeding great cormorants: does it reflect varying stock recruitment of Gadids? *Waterbirds* 27, 161–169.
- Nelson, W.G., 1979. Experimental studies of selective predation on amphipods: consequences for amphipod distribution and abundance. *Journal of Experimental Marine Biology and Ecology* 38, 225–245.
- Neu, C.W., Byers, C.R., Peek, J.M., 1974. A technique for analysis of utilization-availability data. *Journal of Wildlife Management* 38, 541–545.
- Norderhaug, K.M., Christie, H., Fosså, J.H., Fredriksen, S., 2005. Fish-macrofauna interactions in a kelp (*Laminaria hyperborea*) forest. *Journal of the Marine Biological Association of the United Kingdom* 85, 1279–1286.
- Reisewitz, S.E., Estes, J.A., Simenstad, C.A., 2006. Indirect food web interactions: sea otters and kelp forest fishes in the Aleutian archipelago. *Oecologia* 146, 623–631.
- Røv, N., Christie, H., Fredriksen, S., Leinaas, H.P., Lorentsen, S.-H., 1990. A preliminary investigation on the possible effects of seaweed trawling in Sør-Trøndelag county. NINA Oppdragsmelding 52, 1–20 (in Norwegian with English summary).
- Sjøtun, K., Christie, H., Fosså, J.H., 2006. The combined effect of canopy shading and sea urchin grazing on recruitment in kelp forest (*Laminaria hyperborea*). *Marine Biology Research* 2, 24–32.
- Steen, H., 2009. Kelp forests in the Norwegian coastal zone. In: Agnalt, A.-L., Bakketeig, I.E., Haug, T., Knutsen, J.A., Opstad, I., (Eds.), *Coast and Aquaculture. Fisken og Havet, særnr. 2–2009* (In Norwegian with English summary).
- Steneck, R.S., Graham, M.H., Bourque, B.J., Corbett, D., Erlandson, J.M., Estes, J.A., Tegner, M.J., 2002. Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environmental Conservation* 29, 436–459.
- Steneck, R.S., Vavrinec, J., Leland, A., 2004. Accelerating trophic-level dysfunction in kelp forest ecosystems of the western north Atlantic. *Ecosystems* 7, 323–332.
- Vanella, F.A., Fernandez, D.A., Romero, M.C., Calvo, J., 2007. Changes in the fish fauna associated with a sub-Antarctic *Macrocystis pyrifera* kelp forest in response to canopy removal. *Polar Biology* 30, 449–457.
- Waage-Nielsen, E., Christie, H., Rinde, E., 2003. Short-term dispersal of kelp fauna to cleared (kelp-harvested) areas. *Hydrobiologia* 503, 77–91.
- Wanless, S., Harris, M.P., Morris, J.A., 1991. Foraging range and feeding locations of shags *Phalacrocorax aristotelis* during chick rearing. *Ibis* 133, 30–36.
- Willis, T.J., Millar, R.B., Babcock, R.C., 2000. Detection of spatial variability in relative density of fishes: comparison of visual census, angling, and baited underwater video. *Marine Ecology Progress Series* 198, 249–260.