Norges miljø- og
biovitenskapelige
universitet

NMBU

Great cormorant *Phalacrocorax carbo* diet related to the supply of marine shallow-living fish species in southeastern Norway; opportunistic or selective foraging?

Fredrik Gustavsen
Master in Natural Resource Management

Preface

Growing up and participating in the industry and culture of coastal, small scale fishing, my consideration of ensuring continuation in this activity has always been substantial. In light of this interest, favorable management actions should be implemented. Considering the expansion of nesting great cormorants along the coast of southeastern Norway, further knowledge on the subject of cormorant impact on fish populations was gathered in this study.

Ås, 12.05.2017

_____

Fredrik Gustavsen

Summary

The diet of wintering and nesting great cormorants in a marine, coastal ecosystem located in southeastern Norway was studied by analyzing stomachs of shot individuals and regurgitations collected at a nesting colony. Additionally, data on the fishery supply were gathered by initiating test fishing from May to September in the study area, covering a wide range of shallow marine habitats. In both cormorant diet and the test fishing catches, the proportions of cod and wrasses were prominent, whereas considerable differences in other fish species occurrences were disclosed. Subsequently, dividing prey fish species into three groups, "cod", "wrasses" and "other", were considered expedient for the statistical analyses.

The proportions of cod in cormorant diet were 8% and 31% of total number and total biomass, respectively. By comparison, corresponding percentages in the test fishing catches were 6% and 22%. Furthermore, wrasses in cormorant diet constituted 35% and 32% of total number and total biomass, respectively. In the test fishing catches, wrasses represented 69% of the total number fish individuals and 30% of the total fish biomass. Considering the group of fish species represented in both cormorant diet and test fishing catches, the proportions differed significantly among species. In cormorant diet, excluding cod and wrasses, the shorthorn sculpin dominated in both number (70%) and biomass (50%). In contrast, the European eel dominated in both number (46%) and biomass (75%) in the test fishing catches, when excluding cod and wrasses.

The occurrences of cod and wrasses in cormorant diet and test fishing catches differed significantly in both number and biomass, indicating selective cormorants and/or selective fishing gear. No significant differences were observed between the weight distribution of wrasses and other fish species found in stomachs and those regurgitated at the nesting colony, defined as the cormorant winter and summer diet, respectively. However, a slight difference was observed for the proportion of cod, suggesting more frequent larger cod individual occurrence in cormorant winter diet. Overall, cormorants preyed most frequent on fish individuals less than 100 grams. Nevertheless, the wide range of shallow-living prey fish species, contrastive in their behaviors and traits, found in cormorant stomachs and regurgitations, indicates highly opportunistic foraging. Moreover, cormorant diet might reflect the relative proportions of several fish prey species present in this marine ecosystem, hence an indicator of fish stock fluctuations.

Considering the ongoing expansion of breeding great cormorants of the *P. c. subspecies*, and the considerable fish biomass needed to sustain these cormorant populations, more intensive management actions in terms of population decline should be implemented when experiencing depleted fish populations in threshold fiords and inner archipelago, applicable to parts of the marine ecosystem studied in this thesis.

Sammendrag

Dietten til storskarv langs deler av Sørlandskysten (Norge) ble undersøkt ved å analysere magesekker fra skutte individer og oppgulpet fisk fra en stor hekkekoloni. Et prøvefiske ble samtidig utført fra mai til september for tilegnelse av relative estimater på tilbudet av fisk i dette marine kystøkosystemet. Andelen torsk og leppefisk dominerte både i skarvens diett og i fangstene gjennom prøvefisket. Fordelingen av de resterende fiskeartene, både i antall og vekt, varierte imidlertid sterkt mellom skarvens byttefisk og det estimerte tilbudet av fisk. På grunnlag av disse observasjonene ble det vurdert hensiktsmessig å gruppere samtlige individer fisk under "torsk", "leppefisk" og "andre" for de statistiske analysene.

Andelen torsk i antall og vekt utgjorde henholdsvis 8 % og 31 % av skarvens diett. Tilsvarende andeler av torsk i prøvefisket var 6 % og 22 %. Videre utgjorde arter i leppefiskfamilien 35 % og 32 % av henholdsvis det totale antallet og den totale vekta av skarvens byttefisk. Tilsvarende andeler av leppefisk i prøvefisket var 69 % og 30 %. Andelene av de resterende fiskeartene felles for både skarvens diett og prøvefisket varierte betraktelig mellom arter. I skarvens diett dominerte vanlig ulke i antall (70 %) og vekt (50 %), sett bort ifra torsk og leppefisk. I fangstene gjennom prøvefisket utgjorde imidlertid europeisk ål den største andelen, både i antall (46 %) og vekt (75 %), sett bort ifra torsk og leppefisk.

Forekomsten av torsk og leppefisk i skarvens diett skilte seg signifikant fra forekomstene i prøvefisket, både i antall og vekt. Det kan tyde på selektive skarver og/eller selektivt fiskeredskap. Ingen signifikant forskjell ble observert mellom vektfordelingen av leppefisk og andre fiskearter funnet i magesekkene og de funnet som oppgulp i hekkekolonien, definert som henholdsvis skarvens vinter- og sommerdiett. En liten forskjell ble imidlertid observert for vektfordelingen av torsk, og det kan dermed tyde på at skarven preferererer større torskeindivider om vinteren. Majoriteten av fiskeindividene i skarvens diett var mindre enn 100 gram. Det store spekteret av forskjellige arter byttefisk, ulike i adferd og med varierende

egenskaper, gir uansett grunnlag for å karakterisere storskarven som en typisk generalist. Mengdeforholdet av ulike arter byttefisk i skarvens diett kan dermed gjenspeile de relative andelene fisk som representerer tilbudet i dette marine økosystemet, i så fall også variasjoner i de ulike fiskebestandene over tid.

Tatt i betraktning den fortsatt økende utbredelsen av hekkende storskarv, gjeldende for underarten *P. c. sinensis*, og den betydelige biomassen av fisk som trengs for å opprettholde disse skarvepopulasjonene, burde ytterligere forvaltningstiltak med sikte på bestandsreduksjon iverksettes når utarmede fiskepopulasjoner observeres. Spesielt vil dette gjelde for indre skjærgård og terskelfjorder, overførbart til deler av studieområdet i denne oppgava.

Content

1 Introduction

The complexity of marine ecosystems and their interactions within avian and aquatic species have been comprehensively studied through decades, covering a wide range of food webs in all parts of the world. In particular, understanding the causalities of depleted fish populations has been of substantial interest when shaping harvest regimes in both small and large scale fisheries (Cury et al. 2003). As commonly suggested, top predators might limit prey populations and, subsequently, reduce catches of commercially important fish species (Steven 1933; Cowx 2003; Heithaus et al. 2008; Steffens 2010). However, the overall impact of top predators on prey populations is widely debated and continuously a subject of great disagreement among scientists. Several seabird-fish interactions have been illustrated by collapse in seabird populations following low densities of specific prey species populations, highly indicating bottom-up mechanisms in such marine food webs (Barrett & Krasnov 1996; Cury et al. 2011). Nevertheless, in Norway, great increases in populations of the fish-feeding great cormorant *Phalacrocorax carbo* have been observed, simultaneously with declining fish stocks. Hence, questions concerning cormorant impact on coastal fisheries have arisen.

During the last two–three decades, the great cormorant subspecies *Phalacrocorax carbo sinensis*, which utilize both freshwater and marine ecosystems, increased rapidly in number along the Norwegian coast, counting more than 5000 breeding pairs in 2012 (Lorentsen 2013). From 2010 to 2012, the increase of nesting cormorants of this subspecies was 32% (Lorentsen 2013). By comparison, the Danish population of the *P. c. sinensis* subspecies increased by 1700 breeding pairs from 2011 to 2012, reaching a total number of 27 237 pairs in 2012 (Bregnballe et al. 2013). Analyses of regurgitated pellets collected at nesting colonies from Rogaland to Sør-Varanger along the Westcoast of Norway indicated that cormorants subsist largely on cod (*Gadus morhua*) and saithe (*Pollachius virens*), which represent commercially important gadoids (Barrett et al. 1990). These results were supported by surveys conducted along the coast of central Norway in 2001–2003 (Lorentsen et al. 2004). Based on analyses of 608 diet samples representing 1013 fish individuals from nesting colonies, 75% of the number and 86% of the biomass was gadoids (Lorentsen et al. 2004).

From the middle of the 1990s to the beginning of the 2000s, the Norwegian spawning population of coastal cod decreased by approximately 70% (Michalsen 2003). The causality of this decline might, however, be complex. Warmer ocean temperatures due to climate

change (Clark et al. 2003), overexploitation (Botsford et al. 1997) and eutrophication (Lekve et al. 1999) might constitute an explanation to the previous and current status of several fish populations in marine ecosystems. Also, the use of fishing gear which selects on fish over a given minimum size, for a certain period, might lead to evolutional changes, such as slower growth rates and earlier spawning age, causing lower overall fish production (Hutchings & Myers 1993). Moreover, the importance of keystone habitats as an explanatory factor to fish population growth is probably underestimated, as they constitute important spawning and nursery areas (Bustnes et al. 1997). The group of species forming marine keystone habitats along the Norwegian coast, including the study area of this thesis, is dominated by brown algae (*Phaeophyceae*) forming kelp forests, which was harvested by nearly 165 000 tons annually around Millennium (Sjøtun & Lorentsen 2003). The harvest of kelp did in some areas lead to disappearance of juvenile gadoids, highlighting the importance of this habitat to fish recruitment (Sjøtun & Lorentsen 2003). Moreover, the fluctuations in cod and pollack (*Pollachius pollachius*) densities along the coast of southeastern Norway have been related to temporal changes in the coverage of eelgrass (*Zostera marina*) (Fromentin et al. 1998).

The daily food intake by great cormorants has been calculated using a time-energy budget method (Gremillet et al. 2000). This method revealed different food requirements of nesting great cormorants dependent on their type of activity through the nesting season. The fish requirement of male birds in the period of incubation and rearing of small and large chicks, was 690 g, 1050 g and 1350 g, respectively (Gremillet et al. 2000). The requirements of female birds were 200–400 g lower for each breeding activity. However, linking these estimates to the numerous populations of great cormorants, a significant amount of fish biomass is needed to sustain the current cormorant numbers. The prey size selectively in foraging cormorants, revealed by dietary studies, might add helpful disclosures when estimating the impact on fish communities. Diet samples from nesting great cormorants along the Norwegian west coast indicated an average fish weight of 52 grams, and approximately 90% of all fish individuals eaten had weight less than 100 grams (Lorentsen et al. 2004). Larger fishes seem to be taken in the winter months, possibly due to cold temperatures and corresponding prey behavior (Čech et al. 2008).

The numerous expansion of breeding great cormorants in Øra nature reserve, located in the archipelago of Fredrikstad (Norway) close to shallow saltwater habitats, has been an object of dietary studies using fish prey otoliths for species determination (Skarprud 2003; Sørensen 2012). In both studies, diverse diet compositions were disclosed, suggesting no selective

foraging strategies in breeding great cormorants of this colony. Still, the impact of cormorant predation on fish species of cultural and economic interests were considered substantial compared to coastal, small-scale fishery catches. This is in contrast to results from an extensive research in South Sweden where a total of 15 lakes were surveyed in order to examine the effects of the *P. c. sinensis* subspecies expansion on local fisheries (Engström 2001). Overall, neither the biomass nor the number of different fish species was significantly related to cormorant density, suggesting that the local freshwater fish populations were nearly unaffected by the cormorant invasion (Engström 2001). In northern Italy, the relation between great cormorant diet, prey availability and fish harvest in two freshwater lakes was examined (Gagliardi et al. 2015). No relationship between the proportions of different fish species consumed by wintering cormorants was detected, suggesting that species-specific availability is determinative to explain the diet composition (Gagliardi et al. 2015).

In a European perspective, the massive population of great cormorants has been accused to "result in serious ecological damage to fish populations and in remarkable economic and socio-cultural losses to fishery" (Steffens 2010). In Sweden, management actions have been implemented by local authorities in an attempt to slow down the great cormorant population growth, involving extended hunting and pricking of eggs (Engström 2001). From 1994 to 2000, up to 4000 cormorants were reported shot annually. Furthermore, in a period of 15 years, egg-pricking actions have been executed in 19 nesting colonies (Engström 2001). However, more knowledge of the real impact caused by cormorants on marine fish communities is needed to provide support for implementing more intensive management models.

Due to the concern of possible negative effects of increasing cormorant populations on fish stocks, a series of studies have been published worldwide. However, most of these studies examine effects of cormorant predation in brackish and fresh water systems housing less species and habitats compared to marine coastal ecosystems. Although there also are several studies on cormorant diet composition in saltwater systems, disclosing a wide range of prey species of contrastive behavior and traits in the diet, a minority of these studies has incorporated estimates of fish community compositions in their analyses. In this thesis, data on great cormorant diet based on stomachs and regurgitation pellets are compared to estimates of prey fish species supply gained by performing test fishing in shallow marine habitats of the Skagerrak coast in southeastern Norway. My prediction is that cormorants, including both *P. c. carbo* and *P. c. sinensis* subspecies, do not favor on fish species when foraging. Rather, I

suggest that fish availability, fish size and species-specific catchability are essential factors determining great cormorant diet in a marine ecosystem. From this I predict that the effect of great cormorant predation on a certain fish stock depends on the fish species and their behavior or traits, as well as the ecosystem forming the foraging terms. To what extent cormorant predation might impact fish populations is carefully questioned, and favorable management actions/perspectives in terms of fishery sustainability, fish population recovery and viability are discussed.

2 Methods

2.1 The study area

The study area is located in Grimstad, Arendal and Tvedestrand municipalities in the County of Aust-Agder, representing the coast of Skagerrak in southeastern Norway. It is characterized as an archipelago, stretching from 58°13'38N, 8°29'31E in west to 58°39'7N, 9°12'24E in east (Fig. 1). This 63 km long Norwegian coastline of shallow water involves several marine habitats of great importance for a certain number of spawning fish species. Keystone plant species forming these habitats include eelgrass, sugar kelp (*Saccharina latissimi*), cuvie (*Luminaria hyperborean*) and oarweed (*Luminaria digitate*). In isolated shallow water areas, such as coves and inlets, eelgrass occurs frequent and creates underwater meadows. At sites more exposed to waves and currents, species like oarweed and sugar kelp within the group brown algae are forming kelp forests closely to the sea surface. Within the study area (Fig. 1), marine protected areas of various restriction levels (e.g. no-take marine reserves and lobster reserves) have been implemented and, in December 2016, the third marine national park in Norway was established, covering approximately 607 square kilometers of the coast (Fig. 1).

Fish species of significant economic value, such as gadiformes and wrasses, use these marine kelp and eelgrass habitats as spawning, nursery and living areas (Sjøtun & Lorentsen 2003), hence such habitats constitute keystone importance to fish recruitment in the ecosystem. Additionally, several freshwater habitats like rivers, streams and lakes are connected or closely related to this coastline. Generally, these freshwater habitats are characterized as humus rich and turbid, both high and poor in nutrients. Carps, like rudd (*Scardinius erythrophthalmus*), tench (*Tinca tinca*) and minnow (*Phoxinus phoxinus*) occur in high concentrations in a large proportion of these freshwater systems. Furthermore, brown trout (*Salmo trutta*), salmon (*Salmo salar*) and perch (*Perca fluviatilis*) are widespread species living in these coastal related freshwater habitats. Hence, these species might constitute a substantial part of cormorant diet in the study area.
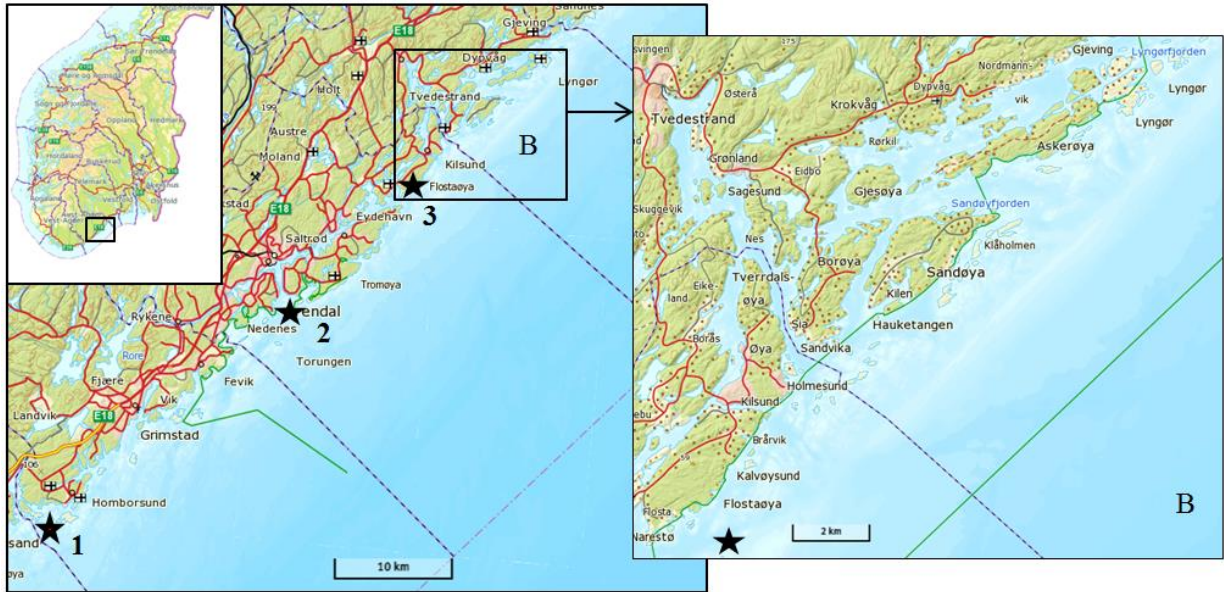
Fig. 1: The study area along the coast of southeastern Norway, more specifically the coastline stretching trough three municipalities (Tvedestrand, Arendal and Grimstad) in the County of Aust-Agder, housing three great cormorant nesting colonies (black stars). The collection of regurgitation pellets was conducted on the most numerous nesting colony of great cormorants, Rivingen nature reserve, located in Grimstad (star number 1). However, both hunting of cormorants and test fishing are carried out widespread in the archipelago of Arendal and Tvedestrand municipalities (map enlargement B). In map enlargement B, the green solid line represents parts of the border of Raet national park; the third marine national park in Norway, established in December 2016.

2.2 Great cormorant diet analyses

The data collection of great cormorant diet samples involved two different methods; 1) shooting of great cormorants during the hunting season and the winter months, and 2) collection of regurgitation pellets at a nesting colony during summer. To obtain great cormorant stomachs, the birds have to be shot or found dead. Since choice of prey may differ between months, the Norwegian environment agency approved my application of killing 40 great cormorants beyond the ordinary hunting season stretching from October 1 to November 31, more specifically from December 1, 2015 to March 1, 2016. Similarly, this kind of application was approved for the period January, 1, 2017 to March 1, 2017, adding another 40 cormorant stomachs for the diet analyses. Taking this into consideration, the stomach content analyses are based on birds shot between October and February (five months).

During the ordinary hunting season in 2015 I shot 28 individuals of great cormorants. These individuals were shot from islets using entice birds of wood, cut as silhouettes and painted in black. Apparently, this method of attracting the birds seemed to be efficient. However, a great number of these individuals were shot during sunrise, and by dissecting the birds their stomachs turned out to be empty. In contrast, the majority of cormorants shot in the afternoon had fish in their stomachs. Nevertheless, the determination of prey species individuals was restricted to visual identifying, highly dependent on fish skin remainings, excluding stomachs containing highly digested prey species (Fig. 2).

The collection of cormorant stomachs through the ordinary hunting season in 2015, more specifically from October 14 to November 23, resulted in 28 stomachs for analyses. However, 13 of these stomachs were empty. A large proportion of the cormorants shot during sunrise (before 12:00 AM) had empty stomachs; 10 out of 15. In direct opposition, only three out of 12 cormorants shot during sunset (after 12:00 AM) had empty stomachs, indicating low hunting activity during night hours and high metabolism. Learning from this observation, all remaining 80 cormorants were shot in the afternoon in both licensed periods December 1, 2015 to March 1, 2016 and January 1, 2017 to March 1 2017, and the number of empty stomachs was limited to 7 out of 80.

Fig. 2: The determination of prey species in cormorant stomachs (N=84) was restricted to those possible identifying not using otoliths or other species determination methods (A–E), excluding a significant proportion of the collected stomachs containing highly digested prey species (F).

As the collection of another 40 individuals in the period December 1, 2015 to March 1, 2016, and similarly for the period January 1, 2017 to March 1, 2017 were not constrained by rules concerning the use of motorized boat during hunting activities, it was possible to shoot the cormorants on site while they were fishing. Based on my experiences, the cormorants were reluctant to fly right after swallowing a fish, probably because of weight issues. This made it easy to shoot them on the water surface. However, a large proportion of the cormorants regurgitated the recently swallowed fish when I approached by boat, subsequently they escaped by wings out of shooting range. In total, 84 great cormorant stomachs were usable for prey identification.

Furthermore, on June 27, I entered Rivingen nature reserve, representing a large/numerous nesting colony of the *P. c. sinensis* subspecies with 207 nests, located along the coast outside Grimstad in Aust-Agder County (Fig. 1). Geographical positions of this colony are 58°14'39N, 8°28'13E. Permissions were not granted for entering the less numerous colonies of nesting great cormorants further east (Fig. 1), also representing nature reserves, considering the vulnerability of disturbance in some nesting seabird species. The collection of regurgitations at Rivingen may indicate great cormorant choice of prey during the summer months, considering the feeding activity of more than 400 adults this season. However, even though regurgitation pellets analysis is a widely used method in dietary studies of cormorants (Barrett et al. 1990; Suter 1997; Leopold et al. 1998; Lorentsen et al. 2004; Ostman et al. 2012; Heikinheimo et al. 2015), there might be some limitations associated with this method regarding non-representative results caused by variations in fish species digestion rates and otolith erosions (Barrett et al. 1990). Most likely, by using both stomach content and regurgitation pellets from different parts of the year, these limitations will be minimalized.

2.3 Test fishing

From May to September I initiated test fishing scattered widespread in the archipelago defined by map enlargement B (Fig. 1). However, the test fishing was concentrated in areas where the cormorants were shot most frequent for stomach analyses. Expediently, in terms of covering a wide range of shallow marine habitats, this caused a lumpy distribution of the surveys (including both fishing and hunting) within the refinements of the study area. The fishing gear used for the test fishing consisted of 10 classical eel traps, which currently are used to catch wrasses for the salmon farming industry (Fig. 3). These traps catch any fish size from a few grams up to 3–4 kilograms, approximately, thus including close to all fish sizes up to 1000 grams caught by the great cormorant (Čech et al. 2008). The locations of these fishing traps considering depth were in shallow water, covering a representative selection of different marine habitats as previously described in "The study area" section. It is reasonable to assume that the cormorants use these depth sites frequently when searching for fish during the nesting season, especially in close proximity to their nesting grounds. The traps were emptied approximately twice a week during the period May 25 to August 31, constituting close to 130 effective fishing days in total (Fig. 4).
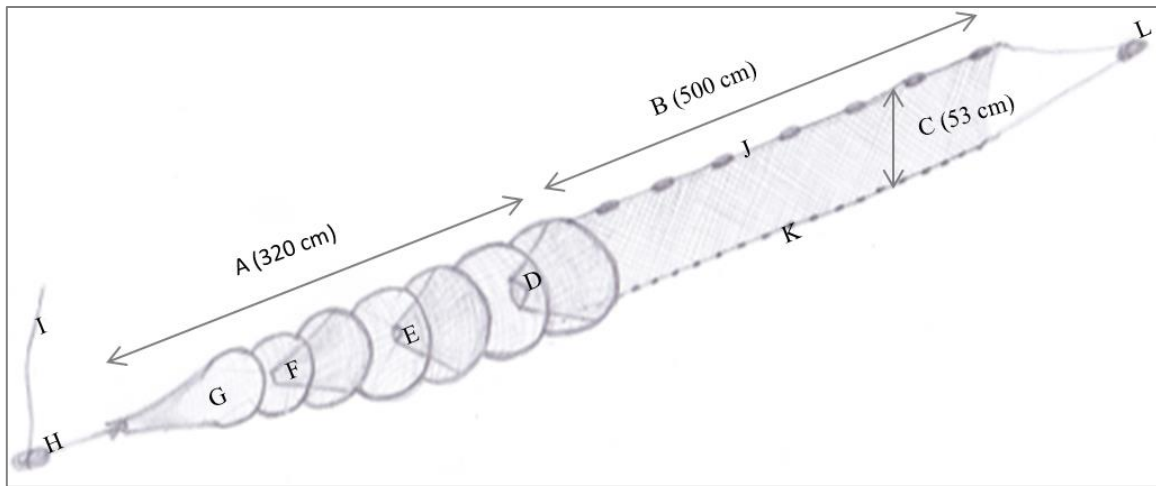
Fig. 3: Classical eel trap used for test fishing. This type of passive fishing gear consists of two parts/components; A) metal-rings making the skeleton of the trap, connected to B) a leading net. The leading net, made by fine-meshed nylon, a floating line (J) and a sinking line (K), stretches approximately 53 cm above seabed, leading colliding organisms toward the first wide open entrance (D). When passing the next even smaller opening (E), the chance of escaping is reduced. Finally, when passing the third, slim opening of 17 cm (F), made as a "flap solution", the organisms are held captive in the final "room" (G). Critical for the function of the trap are some kind of heavy weighted objects tied to each end (H, L) to ensure that the trap is properly stretched on the seabed. Any kind of rope tied to the end of the trap (I), connected to a floating object on the sea surface, is needed to empty as well as stretching this type of fishing gear.

Fig. 4: When emptying the fishing gear, all individuals representing each species present in the catch was sorted separately and weighted collectively using a net and a digital fish weight, giving an average weight on each species individual. Consecutively, all species were released after weighted and, finally, the trap was reestablished at a new spot.

2.4 Statistics and data restrictions

All fish individuals gathered in cormorant stomachs, regurgitation pellets and test fishing were added to the program "JMP®Pro 13.0.0", using logistic regression for the data analyses. The response variables were defined as "1" and "0" for fish individuals in stomachs/pellets and the test fishing catch, respectively. A chi-square test was considered suitable to test if the cormorant diet differs from what to expect of a random selection from the fishery supply. The proportion of data representing summer diet (regurgitation pellets) was considered disproportionate to the proportion representing winter diet (stomach content), thus both datasets were aggregated to define an overall cormorant diet in the multiple logistic regression model.

Certain species of numerous occurrences in the test fishing catches were represented in relatively constant weight classes through the whole period, applicable to the goldsinny

wrasse (*Ctenolabrus rupestris*), the rock cook (*Centrolabrus exoletus*) and the corkwing wrasse (*Symphodus melops*), in particular. Hence, calculating average weights of a major part of these fish species individuals, 20 grams (goldsinny wrasse), 19 grams (rock cook) and 46 grams (corkwing wrasse), based on some of the first catches were considered expedient.

All species of shellfish were excluded from the analyses, involving the European green crab (*Carcinus maenas*), European lobster (*Homarus gammarus*), shrimps, edible crab (*Cancer pagurus*), toad crab (*Hyas coarctatus*) and *Galathea strigosa*, due to no or insignificant occurrence in the cormorant diet. Additionally, exclusively freshwater living fish species represented by the common rudd and perch in the cormorant diet were excluded. Furthermore, lower individual fish weight included was set to 10 grams, excluding sticklebacks (*Gasterosteidae)* only found in the cormorant diet.

In test fishing catches, fish individuals more than 1000 grams (n=59) were excluded from the model, constituting 83544 grams distributed among 1,28% pollack (n=1), 92,73% cod (n=54) and 5,99% European eel (*Anguilla anguilla*) (n=4). Moreover, broadnosed pipefish (*Syngnathus typhle*), lumpfish (*Cyclopterus lumpus*), common sole (*Solea solea*), turbot (*Scophthalmus maximus*), common topknot (*Zeugopterus punctatus*) and the European plaice (*Pleuronectes platessa*) were excluded from the model due to no occurrence in the cormorant diet. Finally, saltwater fish species only found in the cormorant diet and in small numbers; greater weever (*Trachinus draco*), common dragonet (*Callionymus lyra*), whiting (*Merlangius merlangus*), common dab (*Limanda limanda*) and brown trout, were excluded.

Collectively, these restrictions on data inclusion leaves cod, wrasses and the remaining species present in both cormorant diet and test fishing catches for the nominal logistic regression analyses. Dividing fish species into families was not considered expedient due to considerable differences in species behavior and traits within families. However, all species present in both cormorant diet and test fishing catches were divided into three groups; "cod" (the species), "wrasses" (the family) and "other" (remaining species of all families), considering their proportions in data scope as well as their economic and cultural significance in coastal small scale fisheries. Furthermore, prey fish species in both the subspecies *P. c. carbo* (only stomachs from wintering individuals) and *P. c. sinensis* (stomachs and regurgitations) diet are represented in the analyses, aggregated to represent an overall great cormorant diet.

3 Results

3.1 Stomach analysis

Overall, 259 individuals of 20 different prey fish species were found in the 84 investigated cormorant stomachs, constituting a total weight of 21 269 grams (Table 1). In percentage of total biomass, cod dominated by 36%, followed by the shorthorn sculpin (*Myoxocephalus scorpius*) (21%) and the ballan wrasse (*Labrus bergylta*) (16%). In percentage of total number, the shorthorn sculpin outnumbered remaining prey species, constituting 45% of all fish prey individuals found in the stomachs. Also, species of shellfish were found in the stomachs, represented by the European green crab (n=2), Arctic lyre crab (*Hyas coarctatus*) (n=1), squat lobster (*Galathea strigosa*) (n=5) and the caridean shrimp (*Caridea*) (n=5), constituting 290 grams in total. The mean weight of all prey fish individuals was calculated to approximately 125 grams (Table 1).

Table 1: Great cormorant diet revealed by analyzing 84 stomachs from cormorants shot in winter months, October–March. Total number (N) of each fish species is given. Furthermore, total weight (W_{tot}) in grams and mean weight (W_{mean}) of all species are calculated.

Species	N	W_{tot}	W_{mean}
Cod (*Gadus morhua*)	24	7710	321
Pollack (*Pollachius pollachius*)	3	755	252
Saithe (*Pollachius virens*)	4	998	250
Poor cod (*Trisopterus minutus*)	16	840	53
Tadpole fish (*Raniceps raninus*)	1	60	60
Ballan wrasse (*Labrus bergylta*)	14	3520	220
Goldsinny wrasse (*Ctenolabrus rupestris*)	30	480	16
Corkwing wrasse (*Symphodus melops*)	5	125	25
Cuckoo wrasse (*Labrus mixtus*)	4	480	120
Shorthorn sculpin (*Myoxocephalus scorpius*)	123	4571	37
Lemon sole (*Microstomus kitt*)	1	350	350
European flounder (*Platichthys flesus*)	2	480	240
Rock gunnel (*Pholis gunnellus*)	6	127	21
Black goby (*Gobius niger*)	6	60	10
Stickleback (*Gasterosteidae*)	8	32	4
Common rudd (*Scardinius erythrophthalmus*)	4	135	34
Not represented in test fishing catches			
Whiting (*Merlangius merlangus*)	1	70	70
Common dab (*Limanda limanda*)	1	185	185
Brown trout (*Salmo trutta*)	1	156	156
Perch (*Perca fluviatilis*)	2	140	70
SUM	**259**	**21269**	**125**

3.2 Collection of regurgitation pellets

In total, 95 prey individuals distributed among 16 different fish species were found in the regurgitation pellets analyses, constituting a total estimated weight of 5890 grams (Table 2). The mean weight of all prey fish individuals was calculated to 62 grams. In univariate tests, there was no difference between winter diet (stomachs) and summer diet (regurgitation pellets) with regard to weight distribution of wrasses or other fish species, but there was a significant higher weight of cods in the winter diet (Table 3).

Table 2: Fish species found in regurgitation pellets on the nesting colony Rivingen nature reserve, June 27. Number (N), total weight (W_{tot}) in grams and mean weight (W_{mean}) of each species are given.

Species	N	W_{tot}	W_{mean}
Cod (*Gadus morhua*)	3	300	100
Saithe (*Pollachius virens*)	6	360	60
Ballan wrasse (*Labrus bergylta*)	20	2200	110
Goldsinny wrasse (*Ctenolabrus rupestris*)	25	350	14
Corkwing wrasse (*Symphodus melops*)	5	260	52
Rock cook (*Centrolabrus exoletus*)	1	25	25
Cuckoo wrasse (*Labrus mixtus*)	6	720	120
Shorthorn sculpin (*Myoxocephalus scorpius*)	5	125	25
European eel (*Anguilla anguilla*)	5	570	114
Viviparous eelpout (Zoarces viviparus)	1	120	120
Black goby (*Gobius niger*)	3	55	18
Not represented i test fishing cathes			
Greater weever (*Trachinus draco*)	4	175	44
Brown trout (*Salmo trutta*)	6	300	50
Perch (*Perca fluviatilis*)	1	60	60
Common dragonet (*Callionymus lyra*)	3	130	43
Common dab (*Limanda limanda*)	1	105	105
SUM	**95**	**5890**	**62**

Table 3: The output values when running separate nominal logistic regression analyses on the biomass of cod, wrasses and other fish species, with cormorant winter diet revealed by stomach analyses (y=1) or cormorant summer diet revealed by regurgitation pellets (y=2) as the response variable. No difference in the weight distribution of wrasses and other fish species were observed. For cod, the individuals were smaller in the summer diet than in the winter diet.

Source	Estimate	Std Error	DF	SciSquare	Prob>ChiSq
biomass[cod]	0.018523	0.014330	1	5.49	0.0191
biomass[wrasses]	0.002680	0.002237	1	1.56	0.2117
biomass[other]	-0.001846	0.002877	1	0.37	0.5438

3.3 Estimated relative number of prey species from test fishing

In total, 23 different fish species were represented in the test fishing catches (Table 4). Dominating species were cod and European eel, constituting 35% and 30% of total biomass, respectively. The percentage of wrasses was 24% of total biomass, distributed among the ballan wrasse (10.5%), the corkwing wrasse (6.5%), the cuckoo wrasse (4.1%), the goldsinny wrasse (1.9%) and the rock cook (1.2%). Wrasses were the overall dominating group in number, constituting 66.4% (n=1700), with 26.5% corkwing wrasse, 15.8% goldsinny wrasse, 11.4% rock cook, 7.3% ballan wrasse and 5.3% cuckoo wrasse. The European eel, cod and the shorthorn sculpin constituted 11.7% (n=299), 7.6% (n=195) and 6.2% (n=159) of total number individuals (n=2562), respectively. Remaining fish species (n=15) in the test fishing catches occurred in minor proportions (Table 4).

Table 4: All fish species caught during test fishing in summer months, May–August 2016. Total number (N), total weight (W_{tot}) in grams and mean weight (W_{mean}) are given for each species. Additionally, the fish species not represented in cormorant diet are sorted out, based on the findings in both the stomach analyses and the regurgitation pellets.

Species	N	W_{tot}	W_{mean}
Cod (*Gadus morhua*)	195	165407	848
Saithe (*Pollachius virens*)	13	1641	126
Pollack (*Pollachius pollachius*)	49	17150	350
Poor cod (*Trisopterus minutus*)	9	522	58
Tadpole fish (*Raniceps raninus*)	4	1420	355
Goldsinny wrasse (*Ctenolabrus rupestris*)	406	8981	22
Ballan wrasse (*Labrus bergylta*)	188	49489	263
Rock cook (*Centrolabrus exoletus*)	293	5605	19
Corkwing wrasse (*Symphodus melops*)	678	30680	45
Cuckoo wrasse (*Labrus mixtus*)	135	18461	137
European flounder (*Platichthys flesus*)	3	1330	443
Lemon sole (*Microstomus kitt*)	7	2870	410
European eel (*Anguilla anguilla*)	299	142324	476
Viviparous eelpout (*Zoarces viviparus*)	73	12001	164
Shorthorn sculpin (*Myoxocephalus scorpius*)	159	9413	59
Black goby (*Gobius niger*)	21	425	20
Rock gunnel (*Pholis gunnellus*)	2	73	37
Not represented in cormorant diet			
Broadnosed pipefish (*Syngnathus typhle*)	15	510	34
Lumpfish (*Cyclopterus lumpus*)	1	460	460
Common sole (*Solea solea*)	2	875	438
Turbot (*Scophthalmus maximus*)	1	800	800
Common topknot (*Zeugopterus punctatus*)	1	190	190
European plaice (*Pleuronectes platessa*)	8	1520	190
SUM	**2562**	**472151**	**184**

3.4 Cormorant diet in relation to prey supply

As specified in the method section, some restrictions on data inclusion when comparing both cormorant diet and test fishing catches were made. Expediently, the fish species not represented in the test fishing catches (n=6) (Table 1, 2) and the fish species not represented in cormorant diet (n=6) (Table 4) were excluded in the logistic regression analyses, constituting 4.8% (1321 grams) and 0.9% (4355 grams) of total biomass, respectively. Consequently, 321 fish individuals (25643 grams) representing cormorant diet and 2475 fish individuals (384244 grams) representing the prey fish species supply were included.

In both cormorant diet and test fishing catches, the dominating species was cod, representing 31% and 22% of total biomass consumed/caught, respectively (Fig. 5). Wrasses, including goldsinny wrasse, ballan wrasse, rock cook, corkwing wrasse and cuckoo wrasse, constituted 32% of cormorant diet and 30% of test fishing catches (Fig. 5). In both cormorant diet and the test fishing catches, the ballan wrasse dominated in biomass by 70% and 44% of total wrasse biomass, respectively (Fig. 6). Most significantly, the proportion in both biomass and number of the corkwing wrasse was lower in cormorant diet (4.7% and 8.9%, respectively) than in the test fishing catches (27.1% and 39.9%, respectively) (Fig. 6).

In univariate tests, the weight distribution differed between cormorant diet and test fishing catches for cod and other fish species, whereas the weight distribution of wrasses did not differ (Table 5). For both cod and other species, the individuals were smaller in the cormorant diet than in the test fishing catches.

Table 5: The output values when running separate nominal logistic regression analyses on the biomass of cod, wrasses and other fish species, with cormorant diet (y=1) or test fishing catches (y=0) as the response variable. For cod and other fish species, individuals were smaller in cormorant diet than in test fishing catches. For wrasses, there was no difference.

Source	Estimate	Std Error	DF	ChiSquare	Prob>ChiSq
biomass[cod]	0.007313	0.001384	1	45.36	<0.0001
biomass[wrasses]	-0.000639	0.000937	1	0.43	0.5091
biomass[other]	0.012858	0.001452	1	253.59	<0.0001

In a multiple logistic regression model, the proportions of cod/wrasses in number and biomass differed significantly between cormorant diet and test fishing catches (Table 6). The proportion of cod was higher and fish weights lower in the cormorant diet than in the test fishing catches. There also was an interaction effect, meaning that the impact of biomass was dependent on whether the prey species was cod or wrasses.

Table 6: The output values when running a nominal logistic regression analysis, with cormorant diet (y=1) or test fishing catches (y=0) as the response variable, and "cod/wrasses" and "biomass" as the explanatory variables. Highly significant values were observed, indicating fish species and biomass preferences in cormorant diet and/or selective fishing gear.

Source	Estimate	Std Error	DF	ChiSquare	Prob>ChiSq
Intercept	0.561897	0.293300			
biomass	0.003337	0.000836	1	21.0794	<0.0001
cod/wrasses	1.766044	0.227468	1	62.1039	<0.0001
cod/wrasses*biomass	-0.003976	0.000836	1	23.1947	<0.0001

All remaining species, categorized as "other" fish species, constituted approximately 37% of total biomass in cormorant diet and 48% in the test fishing catches, respectively (Fig. 5). In cormorant diet, the shorthorn sculpin was dominant, constituting 49.58% of total biomass (Fig. 7). It was followed by saithe, poor cod (*Trisopterus minutus*) and pollack, constituting 14.34%, 8.87% and 7.97% of total biomass, respectively. The European eel, European flounder (*Platichthys flesus*), lemon sole (*Microstomus kitt*), viviparous eelpout (*Zoarces viviparus*), black goby (*Gobius niger*), rock gunnel (*Pholis gunnellus*) and tadpole fish (*Raniceps raninus*) were represented in less significant amounts (Fig. 7). In test fishing catches, however, the proportion of European eel was prominent, constituting 75% of total biomass (Fig. 7). When excluding the European eel from the analysis, wrasses and cod represented 46% and 36% of total biomass, respectively, leaving a minor percentage on remaining species in the catch (19%). Similar to cormorant diet, the remaining species were represented in less significant amounts. Considering the number of fish individuals distributed among species, 57% of total number in the cormorant diet was represented in "other" fish species (Fig. 5). More specifically, the shorthorn sculpin dominated superiorly by 70% of total number in this group (Fig. 7). In the test fishing catches, however, the species of wrasses constituted 69% of total number fish individuals caught.
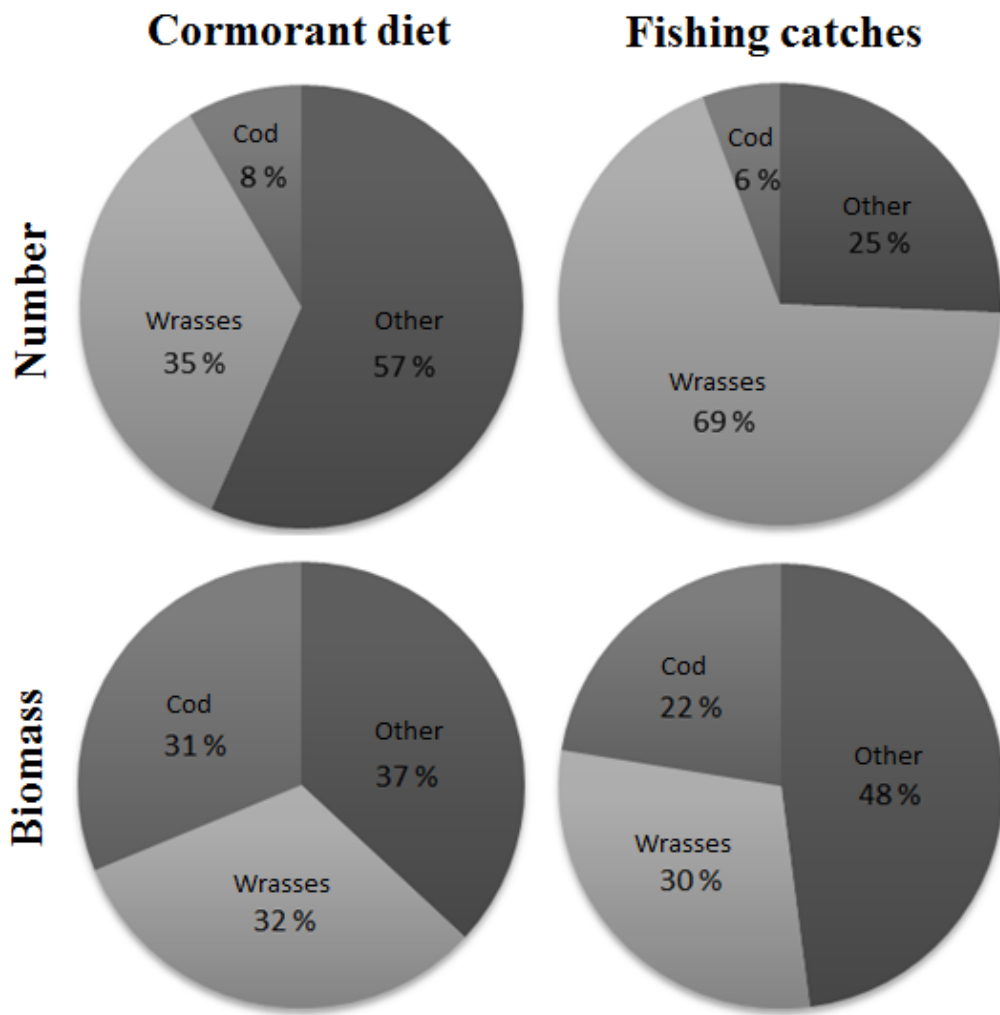
Fig. 5: The percentages of cod, wrasses and other prey fish species of total number and total biomass in the cormorant diet and the test fishing catches, respectively. The scope of data is restricted to include fish species found in both the cormorant diet (stomachs and regurgitation pellets) and the test fishing catches, in the weight interval of 10–1000 grams. Subsequently, these restrictions leaves 321 fish individuals in the cormorant diet and 2475 fish individuals in the test fishing catches, thus the basis of the percentages represented in the charts.
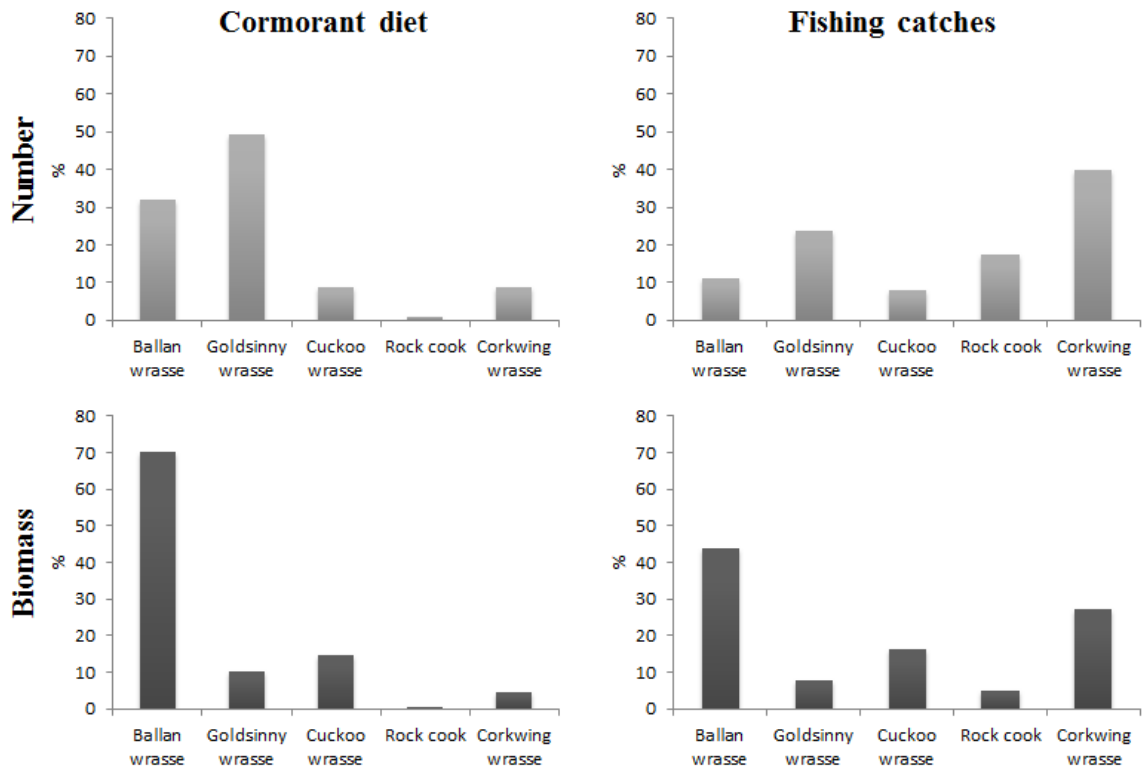
Fig. 6: The proportions in number individuals (grey bars) and biomass (black bars) of wrasses in cormorant diet and test fishing catches. In both groups, the ballan wrasse dominated by 70% and 44% of total wrasse biomass, respectively. Considering the most numerous species, the goldsinny wrasse in cormorant diet and the corkwing wrasse in test fishing catches represented 49% and 40% of total wrasse individuals, respectively.
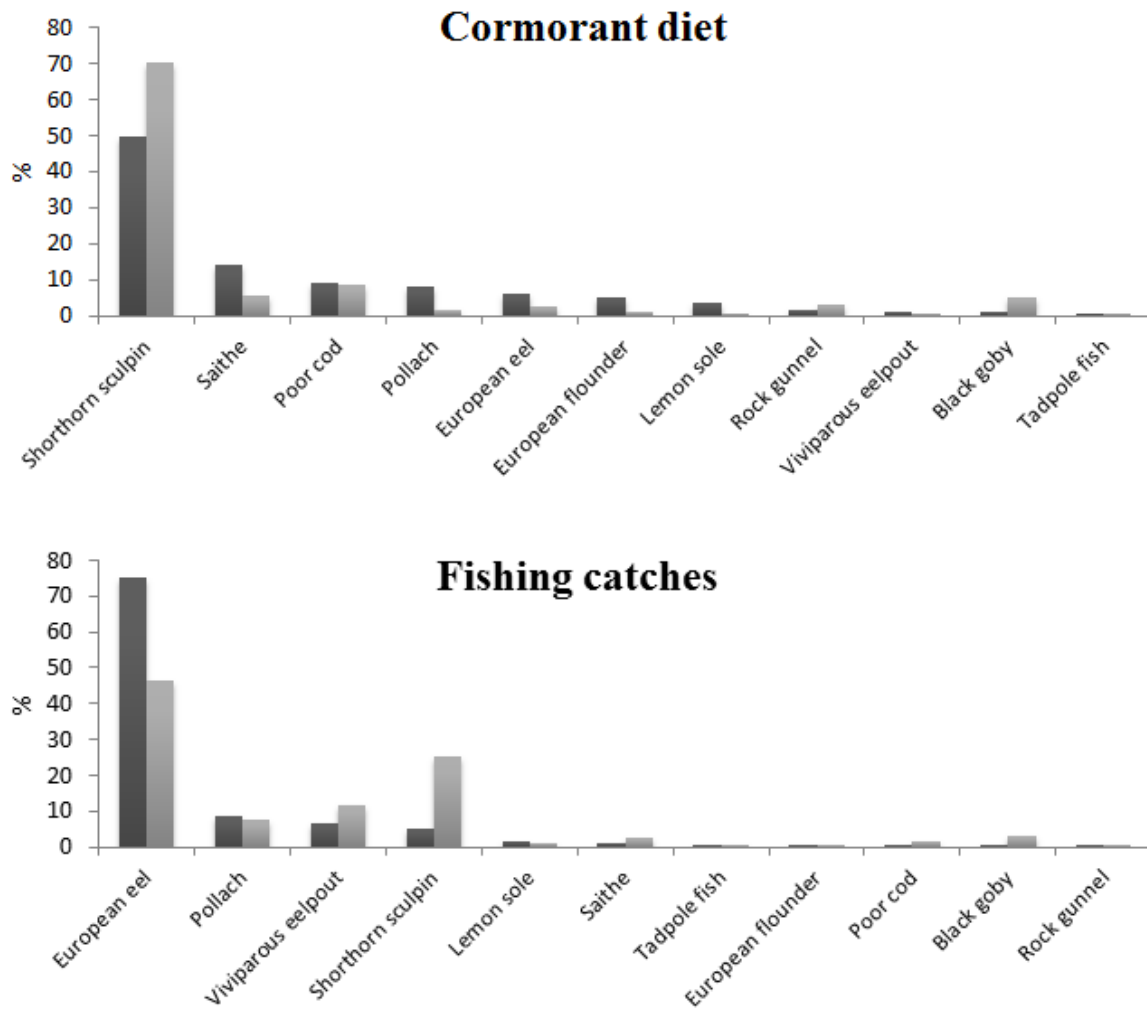
20

Fig. 7: The distribution of biomass (black bars) and number (grey bars), in percentages on the species represented in both cormorant diet and the test fishing catches, when excluding cod and wrasses. Consequently, this bar graph presentation specifies the group of fish species named "other" in Fig. 5, constituting 37% and 48% of total fish biomass, and 57% and 25% of total number fish individuals in cormorant diet and test fishing catches, respectively .

Overall, both fish prey individuals in cormorant diet and the fish individuals caught in the test fishing catches covered a wide range of different weights within in the restricted interval of 10–1000 grams. Hence, dividing all fish individuals into five weight classes (Table 7) was considered expedient when visualizing the results. Uniformly, the biomass of fish prey individuals found in cormorant stomachs covered all five weight classes. However, fish individuals within weight class 2 (50–150 grams) dominated in cormorant diet by 32% of total prey biomass (Fig. 8). Considering the weight class of prey individuals preyed most frequent, more than 60% were represented in weight class 1 (10–50 grams). Mean weight of fish prey individuals (n=321) was calculated to 80 grams (Table 7), including all weight classes. Overall, maximum fish individual biomass found in cormorant stomachs was 915 grams. In the test fishing catches, the percentages of total fish biomass within weight class 4 (300–500 g) and 5 (500–1000 g) dominated by 27% and 42%, respectively (Fig. 8). Nevertheless, similar to cormorant diet, fish individuals caught most frequent were represented in weight class 1, constituting 58% of total number individuals caught (Fig. 8). Including all weight classes, mean weight of each fish individual caught was calculated to 155 grams (Table 7).

Table 7: Number of fish individuals (N), total weight (W_t) and mean weight (W_m) within each weight class 1–5, representing cormorant diet (both stomachs and regurgitation pellets) and the test fishing catches.

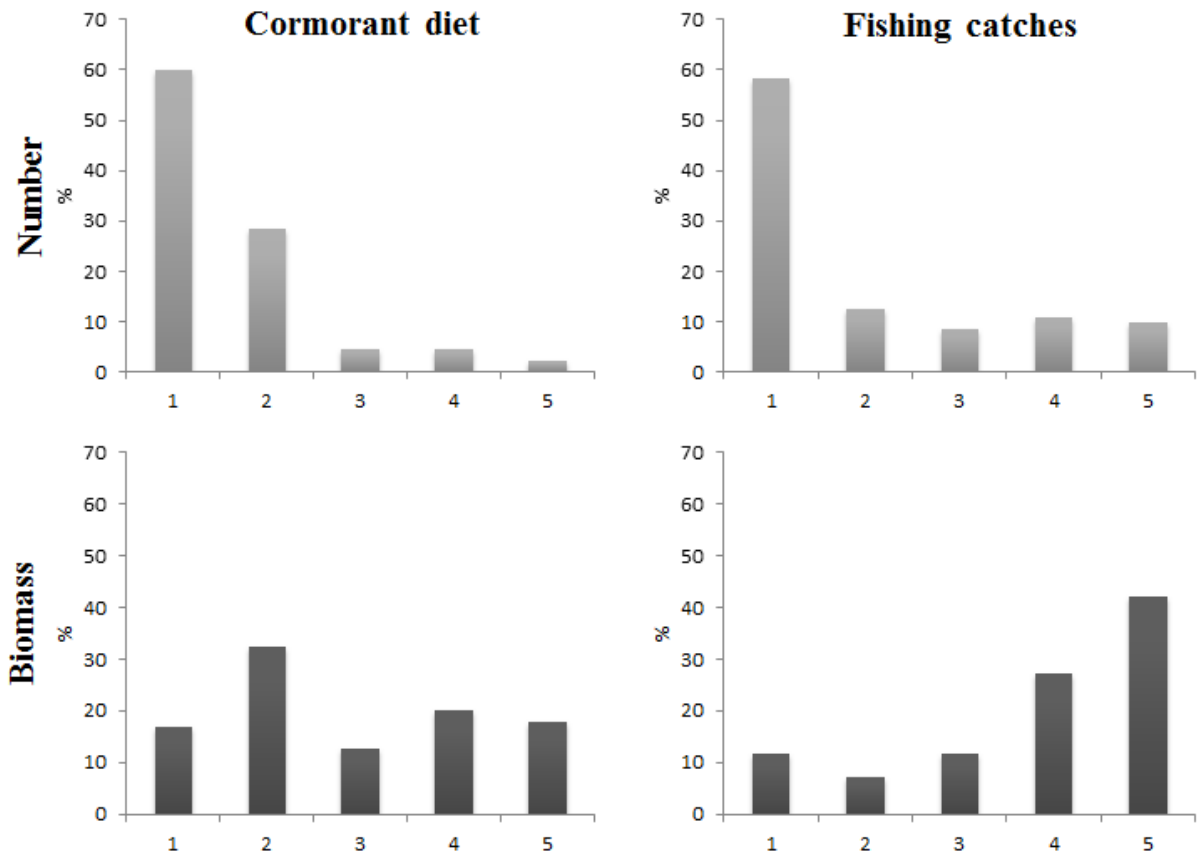| Weight class (grams)	N	W_t	W_m
Cormorant diet			
(1) 10–50	193	4357	23
(2) 50–150	91	8288	91
(3) 150–300	15	3240	216
(4) 300–500	15	5168	345
(5) 500–1000	7	4590	656
Sum	**321**	**25643**	**80**
Test fishing catches			
(1) 10–50	1443	45088	31
(2) 50–150	306	27521	90
(3) 150–300	210	44394	211
(4) 300–500	271	105133	388
(5) 500–1000	245	162116	662
Sum	**2475**	**384252**	**155**

Fig. 8: The distribution of number fish individuals (grey bars) and biomass (black bars) on weight classes (1–5), in percentage of total number and biomass, among the fish species present in both cormorant diet and test fishing catches. The weight classes 1–5, in grams: (1) 10–50, (2) 50–150, (3) 150–300, (4) 300–500, (5) 500–1000.

4 Discussion

4.1 Opportunistic or selective foraging?

Despite some significant differences between great cormorant diet and the test fishing in my study, the very broad diet, including a total of 24 fish species, representing 74% of those registered by test fishing, suggests opportunistic foraging in cormorants preying on benthic fish species in this coastal marine ecosystem. My analyses mainly revealed the diet between October and March, since only a small proportion of the overall diet was collected in summer, i.e. in the period of test fishing. But although one single collection of regurgitation pellets from the nesting colony Rivingen may not be sufficient to reveal a credible picture of cormorant diet composition through the nesting season, this single collection represents a good basis to illustrate the diversity of species in cormorant diet.

The lack of comprehensive data considering summer diet composition in my study might be complemented by previous summer dietary surveys in Øra nature reserve, located approximately 140 km further east into the Oslo fiord, and representing the same spectrum of prey species diversity and marine habitats (Skarprud 2003; Sørensen 2012). Based on analyses of regurgitated fish and otoliths in pellets, 26 different fish prey species were represented in the summer diet of 766 breeding pairs of the P. c. sinensis subspecies (Skarprud 2003). Superiorly, the occurrence of wrasses and cod dominated, constituting 53% and 21% of total biomass consumed based on otolith estimates. In comparison, the equivalent values in my study were 32% and 31%. Subsequently, these differences might reflect seasonal variations in prey size preferences, suggesting that cormorants hunt larger fish individuals in the winter months (Čech et al. 2008), or spatiotemporal variations in fish stock densities as argued in Skarprud (2003) and Sørensen (2012).

In 2011, a sequel study was conducted in Øra nature reserve, examining prey species diversity and proportions in the diet, prey species size and, finally, arguing whether changes in the great cormorant diet are related to fluctuations in prey species populations compared to the 2002 findings (Sørensen 2012). Overall, corresponding percentages of wrasses and cod in the 2011 diet were 31% and 21% of total biomass, highly related to the equivalent percentages of wrasses (30%) and cod (22%) biomass in the test fishing catches of my study (Fig. 5). The proportions of wrasses in cormorant diet found in both Sørensen (2012) and my thesis were considerably smaller compared to those found in Skarprud (2003), may be explained by the intensive harvesting of wrasses for the growing industry of salmon farming in recent years

(Espeland et al. 2010), as argued in Sørensen (2012). Nevertheless, when excluding the disproportionate biomass of eel in my test fishing catches, the percentages of wrasses and cod were 46% and 36% of total biomass caught, respectively, leaving another 19% on remaining species ("other" species). In my thesis, higher proportions of cod in both cormorant diet and test fishing catches might reveal significant west-east differences in densities of coastal cod populations, as previously documented (Nedreaas et al. 2008; Aglen et al. 2016).

Furthermore, some observations regarding seasonal varieties in species diversity in the diet composition were made when I compared stomach contents from late fall to early spring with contents from pellets collected in summer. Most considerable, no eels were found in cormorant stomachs representing winter diet, in contrast to the presence of five eel regurgitations on Rivingen nature reserve in the nesting season. However, as eel hibernates in the mud during winter and resumes activity in shallow waters from late spring to early fall (Pedersen 2010), the time window of availability to cormorant predation is defined. Nevertheless, eel proportions in the cormorant diet revealed by Skarprud (2003) and Sørensen (2012) were low compared to other fish species, indicating no specific eel preference by breeding cormorants in this marine ecosystem. However, although great cormorant impact on eel populations is likely to be moderate considering the ecology of this fish species (Engström 2001; Carpentier et al. 2009), nesting great cormorants might feed significant on eel populations exposed at shallow grounds during high water temperatures in summer within the study area of my thesis, considering the great proportion of eel in the test fishing catches.

Further indications of opportunistic foraging in breeding great cormorant populations have been illustrated by the considerable occurrence of Capelin (*Mallotus villosus*) in the diet of cormorants feeding in the summer distribution area of this fish species (Barrett et al. 1990). Moreover, significant changes in the diet of great cormorants feeding on fish populations in the Baltic Sea were disclosed when comparing 1992 and 2009 diets, partly explained by temporal shifts in the fish community (Boström et al. 2012). Overall, most dietary studies of great cormorants tend to support the hypothesis of highly opportunistic foraging in this top-predator seabird species, also supported by the results of my thesis.

4.2 Cormorant prey preferences

When comparing the great cormorant diet revealed by stomachs and regurgitation pellets with the relative supply of fishery resources (Engström 2001), my study should reach a great value considering prey preferences as well as the issue of possible impacts on certain fish populations. Although some active fish species might be overestimated by the use of passive fishing gear, the use of classical eel traps, which catches fish swimming in an interval of 50 cm above the seabed, must be considered as a favorable and realistic method of test fishing in my study, considering challenges related to seasonal fluctuations in fish depth distributions (Neilson & Perry 1990; Clark & Green 1991; Neat et al. 2006; Heino et al. 2012). Furthermore, the use of eel traps in shallow depths is likely to reveal the relative prey species supply for nesting cormorants, considering frequent foraging close to the seabed (Barrett et al. 1990; Goutner et al. 1997; Grémillet et al. 1998) in depth sites down to 10 meters below the sea surface (Carss & Ekins 2002). Moreover, based on radio-tracking data from cormorants at the Chausey Islands in France, nearly 60% of the dives were benthic during the nesting season (Grémillet et al. 1998). Eel traps will certainly underestimate the number of fish species in the pelagic zone, like brown trout, mackerel, herring, saithe and pollack, but most of these species also constituted a minor part of cormorants' diet.

The ratio of cod/wrasses in cormorant diet was greater than the respective ratio in the test fishing catches. In the diet, cod constituted 20.6% of the total number of cod and wrasses found, whereas the respective percentage of cod in the test fishing catches was 10.3%. Moreover, in the regurgitation pellets, cod constituted 5.6% of total number cod and wrasses, whereas the respective percentage of cod found in stomachs was 31.2%. These observations might indicate higher cod availability to cormorant predation compared to wrasses in winter months.

My study indicated that cormorants prey most frequent on fish individuals less than 100 grams. Equivalent patterns in size selectiveness of foraging great cormorants are well documented (Lorentsen et al. 2004; Čech et al. 2008; Gagliardi et al. 2015), indicating favorable prey handling of fish individuals representing such small weight classes. Surveys from the Archipelago Sea outside the coast of Finland suggest that pikeperch (*Sander lucioperca*) in the age classes 2–4 years are most exposed to cormorant predation (Heikinheimo et al. 2015).

Furthermore, in my study, the weight proportions of cods in cormorant diet differed significantly between seasons, indicating larger cod size preference in the winter months. Significant seasonal variations in cormorant foraging behavior and prey size selectiveness have previously been revealed (Johansen et al. 2001), indicating reduced diving frequency but large fish preferences during cold winter months (Čech et al. 2008). Most likely, such response in cormorant foraging efficiency during cold water temperatures reflects metabolism economics due to limitations in bird physiology (Gremillet et al. 2001), forcing cormorants to prey on larger fish individuals. Reduced activity rates of larger fish individuals during cold water temperatures compared to conditions of high water temperatures during summer (Randall & Brauner 1991) might also constitute an explanation to such cormorant foraging behavior. As documented in Johansen et al. (2001), the number of dives and prey fish individuals were halved in wintering great cormorants, whereas the biomass of each fish individual consumed doubled.

4.3 Cormorant impact on fish populations

In Norway, the importance of cormorant predation on cod mortality has been widely debated and is thus a highly relevant question in dietary studies of cormorants. In my thesis, the relative proportions of cod in both number and biomass were slightly larger than the respective proportions in the estimated fishery supply, indicating a cod preference in the cormorant diet. However, the percentage of total mortality in cod recruits caused by cormorant predation has previously been estimated to be insignificant compared to the mortality caused by fish cannibalism (Nielsen et al. 1999). Moreover, the survival of North Sea cod larvae has been highly related to changes in plankton communities (Beaugrand et al. 2003), adding support to the bottom-up perspective of predator-prey interactions.

Hypothetically, the presence of feeding cormorants in coastal ecosystems might counteract reduced growth rates and age at spawning caused by evolutionary changes in some fish populations, probably stimulated by size-selective fishing on large individuals over decades (Conover & Munch 2002; Kuparinen & Merilä 2007; Swain et al. 2007; Fenberg & Roy 2008; Uusi-Heikkilä et al. 2008). Considering the limitation on maximum great cormorant fish prey biomass in the order of 1000 grams, and most frequent foraging in fish sizes below 100 grams (Skarprud 2003; Lorentsen et al. 2004; Čech et al. 2008), evolutionary responses caused by cormorants feeding on depleted fish populations in terms of increased growth rates and age at spawning might be detected in some species, although prior freshwater studies on this issue revealed no interconnections (Suter 1995).

Engstrøm (2001) concluded that cormorant predation is likely to represent compensatory mortality in fish populations. For instance, in Finland, where the mortality on pikeperch of age groups 2–4 years caused by great cormorants varied between 5–34% of the total annual mortality. Other sources of mortality were absolutely essential when estimating the isolated mortality caused by cormorants (Heikinheimo et al. 2015). This bottom-up perspective will most likely apply to most mobile fish species with great reproductive capacity and fluctuations in population densities, e. g. pelagic species like saithe (Barrett et al. 1990; Lorentsen et al. 2004) and herring (Røttingen 1990), performing coastal spawning migrations in winter/spring. In contrast, stationary fish species populations might show great vulnerability to cormorant predation, as previously suggested for scorpaeniformes, eelpouts, gobies and some flounder species, living close to large cormorant nesting colonies (Hoffmann 2000). For the European plaice population living on shallow grounds in the Wadden Sea of Netherlands, the mortality of small plaice recruits caused by cormorants was estimated to 30–50% of the total mortality (Greenstreet et al. 1999). Reduced populations of such fish species may affect cods or other species of economic value indirectly, as they constitute considerable preferences in the diet of gadoids (Salvanes & Nordeide 1993).

Freshwater lakes and marine ecosystems representing great variations in macrophyte covers and depth distributions provide wide ranges of fish refuges, likely to reduce the mortality caused by top-predators like cormorants. Most likely, fish species living in shallow habitats of scattered macrophyte distribution would be most vulnerable in terms of reduced fish recruitment caused by cormorant predation. In central Norway, multi-trophic level effects of experimental harvesting in kelp (*Laminaria hyperborean*) forests were evaluated in terms of fish population densities and great cormorant foraging efficiency, disclosing the importance of habitat viability (Lorentsen et al. 2010). Overall, the density of gadoids (<15 cm) was 92% lower in areas newly exposed to kelp harvesting, continuous for at least 1 year. Furthermore, cormorant foraging frequency in kelp-forested areas differed significantly from harvested areas, thus indicating higher prey densities on kelp forested sea beds (Lorentsen et al. 2010).

4.4 Conclusions
Logically, the expansion and sustaining of predator populations depends on the supply of prey species. Moreover, a marine ecosystem experiencing high seabird populations should be considered as healthy in terms of satisfying prey biomass. In light of this, populations of cormorants are likely to fluctuate in relation to changes in total fish biomass caused by bottom-up mechanisms in the marine ecosystem studied in my thesis. However, high densities

of cormorants foraging in more isolated marine habitats, e.g. threshold fiords and basins of shallow water, might stabilize local populations of some fish species at lower levels compared to conditions of cormorant absence (Hoffmann et al. 2002). This is most likely applicable to species that are vulnerable to predation but constitute a minor proportion of cormorants' diet.

My study corresponds to prior dietary studies of great cormorants in terms of disclosing this bird species as highly opportunistic in foraging strategies (Steven 1933; Skarprud 2003 Lilliendahl & Solmundsson 2006; Sørensen 2012). Cormorant diet tends to reflect the composition of fish species densities in both freshwater and marine ecosystems, and is thus likely to constitute an indicator of fish species densities and spatiotemporal fluctuations in fish populations. Considering the amount of fish biomass needed to sustain a large and growing great cormorant population, the environmental authorities should implement further actions to prevent escalations in conflicts of interest. A large scale model study was conducted on the population of great cormorants in northwestern Europe, concluding that 13% removal of the population annually would be a critical level of population decline (Frederiksen et al. 2001). Especially, more intensive management actions of the expanding *P. c. sinensis* subspecies populations would be favorable to improve coastal, small scale fishing in fiords and inner archipelago, where fish populations are more isolated and consequently may be less tolerant to exploitation (Musick 1999; Dulvy et al. 2003; Berkeley et al. 2004), likely to apply for parts of the study area in my thesis.

5 References

Aglen, A., Nedreaas, K., Moland, E., Knutsen, H., Kleiven, A. R., Johannessen, T., Wehde, H., Jørgensen, T., Espeland, S. H. & Olsen, E. M. (2016). Oppdatert kunnskapsstatus om kystnær torsk i Sør Norge, 0071-5638.

Barrett, R. T., Rov, N., Loen, J. & Montevecchi, W. A. (1990). Diets of shags phalacrocorax-aristotelis and cormorants phalacrocorax-carbo in norway and possible implications for gadoid stock recruitment. *Marine Ecology Progress Series*, 66 (3): 205-218.

Barrett, R. T. & Krasnov, Y. V. (1996). Recent responses to changes in stocks of prey species by seabirds breeding in the southern Barents Sea. *ICES Journal of Marine Science: Journal du Conseil*, 53 (4): 713-722.

Beaugrand, G., Brander, K. M., Souissi, J. A. L. S. & Reid, P. C. (2003). Plankton effect on cod recruitment in the North Sea. *Nature*, 426 (6967): 661.

Berkeley, S. A., Hixon, M. A., Larson, R. J. & Love, M. S. (2004). Fisheries sustainability via protection of age structure and spatial distribution of fish populations. *Fisheries*, 29 (8): 23-32.

Boström, M. K., Östman, Ö., Bergenius, M. A. & Lunneryd, S.-G. (2012). Cormorant diet in relation to temporal changes in fish communities. *ICES Journal of Marine Science: Journal du Conseil*, 69 (2): 175-183.

Botsford, L. W., Castilla, J. C. & Peterson, C. H. (1997). The management of fisheries and marine ecosystems. *Science*, 277 (5325): 509-515.

Bregnballe, T., Hansen, R. & Therkildsen, O. R. (2013). Status of the breeding population of Great Cormorants in Denmark in 2012. *National Reports From the 2012 Breeding Census of Great Cormorants Phalacrocorax Carbo in Parts of the Western Palearctic*, 8771560181: DCE-Danish Centre for Environment and Energy, Aarhus University. 34-37 pp.

Bustnes, J., Christie, H. & Lorentsen, S. (1997). Seabirds, kelp beds and kelp trawling: a summary of knowledge. *Nina Oppdragsmelding*, 472: 1-43.

Carpentier, A., Marion, L., Paillisson, J. M., Acou, A. & Feunteun, E. (2009). Effects of commercial fishing and predation by cormorants on the Anguilla anguilla stock of a shallow eutrophic lake. *Journal of Fish Biology*, 74 (9): 2132-2138.

Carss, D. N. & Ekins, G. R. (2002). Further European integration: Mixed sub-species colonies of Great Cormorants Phalacrocorax carbo in Britain: Colony establishment, diet, and implications for fisheries management. *Ardea*, 90 (1): 23-41.

Čech, M., Čech, P., Kubečka, J., Prchalová, M. & Draštík, V. (2008). Size selectivity in summer and winter diets of great cormorant (Phalacrocorax carbo): does it reflect season-dependent difference in foraging efficiency? *Waterbirds*, 31 (3): 438-447.

Clark, D. S. & Green, J. M. (1991). Seasonal variation in temperature preference of juvenile Atlantic cod (Gadus morhua), with evidence supporting an energetic basis for their diel vertical migration. *Canadian Journal of Zoology*, 69 (5): 1302-1307.

Clark, R. A., Fox, C. J., Viner, D. & Livermore, M. (2003). North Sea cod and climate change–modelling the effects of temperature on population dynamics. *Global Change Biology*, 9 (11): 1669-1680.

Conover, D. O. & Munch, S. B. (2002). Sustaining fisheries yields over evolutionary time scales. *Science*, 297 (5578): 94-96.

Cowx, I. G. (2003). Interactions between fish and birds: implications for management. In: Wiley Online Library.

Cury, P., Shannon, L. & Shin, Y.-J. (2003). The functioning of marine ecosystems: a fisheries perspective. *Responsible fisheries in the marine ecosystem*: 103-123.

Cury, P. M., Boyd, I. L., Bonhommeau, S., Anker-Nilssen, T., Crawford, R. J., Furness, R. W., Mills, J. A., Murphy, E. J., Österblom, H. & Paleczny, M. (2011). Global seabird response to forage fish depletion—one-third for the birds. *Science*, 334 (6063): 1703-1706.

Dulvy, N. K., Sadovy, Y. & Reynolds, J. D. (2003). Extinction vulnerability in marine populations. *Fish and fisheries*, 4 (1): 25-64.

Engström, H. (2001). *Effects of Great Cormorant predation on fish populations and fishery*. PhD. Uppsala: Acta Universitatis Upsaliensis, Department of Population Biology. 39 pp.

Espeland, S. H., Nedreaas, K. H., Mortensen, S. H., Skiftesvik, A. B., Agnalt, A.-L., Durif, C. M., Harkestad, L. S., Karlsbakk, E., Knutsen, H. & Thangstad, T. (2010). Kunnskapsstatus leppefisk: Utfordringer i et økende fiskeri.

Fenberg, P. B. & Roy, K. (2008). Ecological and evolutionary consequences of size-selective harvesting: how much do we know? *Molecular ecology*, 17 (1): 209-220.

Frederiksen, M., Lebreton, J. D. & Bregnballe, T. (2001). The interplay between culling and density-dependence in the great cormorant: a modelling approach. *Journal of Applied Ecology*, 38 (3): 617-627.

Fromentin, J.-M., Stenseth, N. C., Gjøsæter, J., Johannessen, T. & Planque, B. (1998). Long-term fluctuations in cod and pollack along the Norwegian Skagerrak coast.

Gagliardi, A., Preatoni, D., Wauters, L. & Martinoli, A. (2015). Selective predators or choosy fishermen? Relation between fish harvest, prey availability and great cormorant (Phalacrocorax carbo sinensis) diet. *Italian Journal of Zoology*, 82 (4): 544-555.

Goutner, V., Papakostas, G. & Economidis, P. S. (1997). Diet and growth of great cormorant (Phalacrocorax carbo) nestlings in a Mediterranean estuarine environment (Axios Delta, Greece). *Israel journal of zoology*, 43 (2): 133-148.

Greenstreet, S., Becker, P., Barrett, R., Fossum, P. & Leopold, M. (1999). Consumption of pre-recruit fish by seabirds and the possible use of this as an indicator of fish stock recruitment. *Diets of seabirds and consequences of changes in food supply. ICES cooperative Research Report*, 232: 6-17.

Gremillet, D., Storch, S. & Peters, G. (2000). Determining food requirements in marine top predators: a comparison of three independent techniques in Great Cormorants, Phalacrocorax carbo carbo. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 78 (9): 1567-1579.

Gremillet, D., Wanless, S., Carss, D. N., Linton, D., Harris, M. P., Speakman, J. R. & Le Maho, Y. (2001). Foraging energetics of arctic cormorants and the evolution of diving birds. *Ecology Letters*, 4 (3): 180-184.

Grémillet, D., Argentin, G., Schulte, B. & Culik, B. (1998). Flexible foraging techniques in breeding Cormorants Phalacrocorax carbo and Shags Phalacrocorax aristotelis: benthic or pelagic feeding? *Ibis*, 140 (1): 113-119.

Heikinheimo, O., Rusanen, P., Korhonen, K. & Rochet, M.-J. (2015). Estimating the mortality caused by great cormorant predation on fish stocks: pikeperch in the Archipelago Sea, northern Baltic Sea, as an example. *Canadian Journal of Fisheries and Aquatic Sciences*, 73 (1): 84-93.

Heino, M., Svåsand, T., Nordeide, J. T. & Otterå, H. (2012). Seasonal dynamics of growth and mortality suggest contrasting population structure and ecology for cod, pollack, and saithe in a Norwegian fjord. *ICES Journal of Marine Science: Journal du Conseil*: fss043.

Heithaus, M. R., Frid, A., Wirsing, A. J. & Worm, B. (2008). Predicting ecological consequences of marine top predator declines. *Trends in Ecology & Evolution*, 23 (4): 202-210.

Hoffmann, E. (2000). *Fisk og fiskebestande i Limfjorden 1984-1999*: Danmarks Fiskeriundersøgelser.

Hoffmann, E., Lockyer, C., Larsen, F., Jepsen, P., Bregnballe, T., Teilmann, J., Scheel-Bech, L., Kongsted, E. & Thøgersen, H. (2002). Udvalget om Miljøpåvirkninger og fiskeriressourcer: Delrapport vedr. topprædatorer, 8790968352: Danmarks Fiskeriundersøgelser.

Hutchings, J. A. & Myers, R. A. (1993). Effect of age on the seasonality of maturation and spawning of Atlantic cod, Gadus morhua, in the Northwest Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences*, 50 (11): 2468-2474.

Johansen, R., Barrett, R. T. & Pedersen, T. (2001). Foraging strategies of Great Cormorants Phalacrocorax carbo carbo wintering north of the Arctic Circle. *Bird Study*, 48 (1): 59-67.

Kuparinen, A. & Merilä, J. (2007). Detecting and managing fisheries-induced evolution. *Trends in Ecology & Evolution*, 22 (12): 652-659.

Lekve, K., Stenseth, N. C., Gjøsæter, J., Fromentin, J.-M. & Gray, J. S. (1999). Spatio-temporal patterns in diversity of a fish assemblage along the Norwegian Skagerrak coast. *Marine Ecology progress series*, 178: 17-27.

Leopold, M. F., van Damme, C. J. G. & van der Veer, H. W. (1998). Diet of cormorants and the impact of cormorant predation on juvenile flatfish in the Dutch Wadden Sea. *Journal of Sea Research*, 40 (1-2): 93-107.

Lilliendahl, K. & Solmundsson, J. (2006). Feeding ecology of sympatric European shags Phalacrocorax aristotelis and great cormorants P. carbo in Iceland. *Marine Biology*, 149 (4): 979-990.

Lorentsen, S.-H., Sjøtun, K. & Grémillet, D. (2010). Multi-trophic consequences of kelp harvest. *Biological Conservation*, 143 (9): 2054-2062.

Lorentsen, S. H., Gremillet, D. & Nymoen, G. H. (2004). Annual variation in diet of breeding great cormorants: Does it reflect varying recruitment of gadoids? *Waterbirds*, 27 (2): 161-169.

Lorentsen, S. H. (2013). Status of the breeding population of Great Cormorants in Norway in 2012. *National Reports From the 2012 Breeding Census of Great Cormorants Phalacrocorax Carbo in Parts of the Western Palearctic*: Danish Centre for Environment and Energy, Aarhus University. 75-78 pp.

Michalsen, R. K. (2003). Havforskningsinstituttet, februar 2003. *Fisken og havet, særnummer*, 0802 0620. 30-32 pp.

Musick, J. A. (1999). Criteria to define extinction risk in marine fishes: the American Fisheries Society initiative. *Fisheries*, 24 (12): 6-14.

Neat, F. C., Wright, P. J., Zuur, A. F., Gibb, I. M., Gibb, F. M., Tulett, D., Righton, D. A. & Turner, R. J. (2006). Residency and depth movements of a coastal group of Atlantic cod (Gadus morhua L.). *Marine Biology*, 148 (3): 643-654.

Nedreaas, K. H., Aglen, A., Gjøsæter, H., Jørstad, K. E., Knutsen, H., Smedstad, O. M., Svåsand, T. & Ågotnes, P. (2008). Kysttorskforvaltning på Vestlandet og langs Skagerrakkysten: Vurdering av status for kysttorsk på strekningen svenskegrensen–Stad med forslag om forvaltningstiltak.

Neilson, J. & Perry, R. (1990). Diel vertical migrations of marine fishes: an obligate or facultative process? *Advances in marine biology*, 26: 115-168.

Nielsen, E., Neuenfeldt, S. & Vinther, M. (1999). Betydning af skarvens prædation på torsk vurderet ved hjælp af flerartsmodellen (MSVPA), 8788047598: Danmarks Fiskeriundersøgelser.

Ostman, O., Bergenius, M., Bostrom, M. K. & Lunneryd, S.-G. (2012). Do cormorant colonies affect local fish communities in the Baltic Sea? *Canadian Journal of Fisheries and Aquatic Sciences*, 69 (6): 1047-1055.

Pedersen, M. I. (2010). Effektvurdering af åleudsætninger i Roskilde Fjord, 8774811282: DTU Aqua. Institut for Akvatiske Ressourcer.

Randall, D. & Brauner, C. (1991). Effects of environmental factors on exercise in fish. *Journal of Experimental Biology*, 160 (1): 113-126.

Røttingen, I. (1990). A review of variability in the distribution and abundance of Norwegian spring spawning herring and Barents Sea capelin. *Polar Research*, 8 (1): 33-42.

Salvanes, A. G. V. & Nordeide, J. T. (1993). Dominating sublittoral fish species in a west Norwegian fjord and their trophic links to cod (Gadus morhua L.). *Sarsia*, 78 (3-4): 221-234.

Sjøtun, K. & Lorentsen, S. (2003). *Kelp forest (Laminaria hyperborea) as habitat for juvenile gadoids*. Poster presented at the 3 rd European Phycological Congress, Belfast, North-Ireland. 21-26 pp.

Skarprud, M. (2003). *Sommerføden til storskarven Phalacrocorax carbo i Øra naturreservat, Fredrikstad*. Ås: Norges Landbrukshøgskole, Institutt for biologi og naturforvaltning. 43 pp.

Steffens, W. (2010). Great Cormorant–substantial danger to fish populations and fishery in Europe. *Bulgarian journal of agricultural Science*, 16 (3): 322-331.

Steven, G. (1933). The food consumed by shags and cormorants around the shores of Cornwall (England). *Journal of the Marine Biological Association of the United Kingdom (New Series)*, 19 (01): 277-292.

Suter, W. (1995). The effect of predation by wintering cormorants Phalacrocorax carbo on grayling Thymallus thymallus and trout (Salmonidae) populations: two case studies from Swiss rivers. *Journal of Applied Ecology*: 29-46.

Suter, W. (1997). Roach rules: Shoaling fish are a constant factor in the diet of cormorants Phalacrocorax carbo in Switzerland. *Ardea*, 85 (1): 9-27.

Swain, D. P., Sinclair, A. F. & Hanson, J. M. (2007). Evolutionary response to size-selective mortality in an exploited fish population. *Proceedings of the Royal Society of London B: Biological Sciences*, 274 (1613): 1015-1022.

Sørensen, A. (2012). *Sommerdiett hos storskarv (Phalacrocorax carbo sinensis) i Øra naturreservat, 15 år etter kolonietablering*: Norwegian University of Life Sciences, Ås.

Uusi-Heikkilä, S., Wolter, C., Klefoth, T. & Arlinghaus, R. (2008). A behavioral perspective on fishing-induced evolution. *Trends in Ecology & Evolution*, 23 (8): 419-421.