





## Fish consumption by great cormorants in Norwegian coastal waters—a human-wildlife conflict for wrasses, but not gadids

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Piscivorous wildlife is often perceived as competitors by humans. Great cormorants of the continental subspecies (*Phalacrocorax carbo sinensis*) in the Baltic and North Sea increase, while local cod (*Gadus morhua*) stocks decline. In contrast, numbers of the Atlantic subspecies (*Phalacrocorax carbo carbo*), breeding along the Norwegian and Barents Seas, have been relatively stable. We investigated the diet of both great cormorant subspecies in breeding colonies along the Norwegian Coast from Lofoten to the Skagerrak and estimated the biomass of fish consumed annually by great cormorants in Norwegian waters. The birds' consumption was compared with estimated fish stock sizes and fishery catches. Cod and saithe (*Pollachius virens*) dominated the diet in the Norwegian Sea and wrasses in the North Sea and Skagerrak. Estimated total fish consumption of cod and saithe by great cormorants was <1.7% of estimated fish stocks and <9% of that of human catches and therefore considered minor. Cormorant consumption of wrasses amounted to 110% of human catches. The practice of using wrasses as cleaner fish in the salmon farming industry leads to a conflict with cormorants, and we urge for a better understanding and management of wrasse populations, taking ecosystem functioning and natural predation into account.

**Keywords:** diet analysis, fish stock size, *Gadus morhua*, Labridae, metabolic rate, North Atlantic, Norway

### Introduction

Generalistic and opportunistic predators are consumers that will feed on a variety of different prey species and adapt their diet depending on availability, nutritional value, and handling costs (MacArthur and Pianka, 1966; Dell'Arte *et al.*, 2007). Flexible foraging behaviour makes generalist predators particularly likely to get involved in human-wildlife conflicts as potential competitors for the same resources. For example, seals and piscivorous bird species compete with humans for fish (Svåsand *et al.*, 2000; Hansson *et al.*, 2018). From a conservation point of view, this competition can be seen from two perspectives since, on the one hand, piscivorous birds and seals may have negative impacts on fish stocks (Cook *et al.*, 2015; Ovegård *et al.*, 2017), whereas

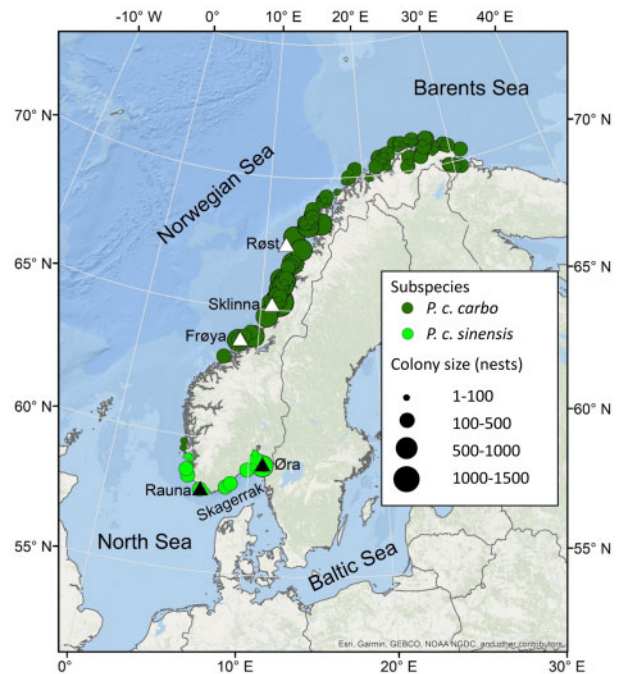
enhanced human fishing efforts and thus competition for resources may put additional pressure on already declining seabird populations (Grémillet *et al.*, 2018). The competition for fish stocks might, in some cases, be more perceived than real (Sørli, 2017), or apply only in those cases where fish stocks are already depleted due to overfishing (Saraux *et al.*, 2020).

The great cormorant (*Phalacrocorax carbo*) is a piscivorous bird species that feeds opportunistically on a range of different fish species (e.g. Cramp and Simmons, 1977). Its predation on fish and competition for commercially harvested species puts the great cormorant into the centre of one of the most prominent and wide-spread human-wildlife conflicts (Russel *et al.*, 2012; Marzano *et al.*, 2013; Rauschmayer and Weiss, 2013). As a result,

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cormorants are being culled in a number of (European) countries, e.g. France (BirdLife International, 2014), Germany (BirdLife International, 2017), Switzerland (Schweizerische Eidgenossenschaft—Bundesamt für Umwelt, 2019), and Denmark (Sterup and Bregnballe, 2019). Within Europe, the great cormorant occurs in two subspecies, the “Atlantic subspecies” (*Phalacrocorax carbo carbo*), which breeds along the north-western European shores, and the “continental subspecies” (*Phalacrocorax carbo sinensis*), which breeds on the continent and the coasts of the Baltic and Greater North Seas including the Kattegat and Skagerrak. Both subspecies target fish species of commercial interest. As such, the Atlantic subspecies has been reported to feed on cod (*Gadus morhua*), saithe (*Pollachius virens*), and plaice (*Pleuronectes platessa*) (Barrett et al., 1990; Lorentsen et al., 2004, in press; Lilliendahl and Solmundsson, 2006), while the continental subspecies—in coastal habitats—commonly targets common roach (*Rutilus rutilus*), perch (*Perca fluviatilis*), plaice, and flounder (*Platichthys flesus*) (Leopold et al., 1998; Lehikoinen et al., 2011; Östman et al., 2013). The perceived conflict with the continental subspecies is worsened by the fact that the European population has increased strongly since the late 1970s due to better protection measures and the ban of DDT and other persistent organic pollutants, and cormorants subsequently recolonized areas where they were previously extinct (Van Eerden and Gregersen, 1995; Herrmann et al., 2019). For example, populations of the continental subspecies breeding in the Baltic Sea region have multiplied from about 2500 breeding pairs in 1970 to about 200 000 in 2018 (Herrmann et al., 2019). In contrast, the population of the Atlantic subspecies has been much more stable over time and occurs at lower numbers, with about 19 000 breeding pairs in Norway in 2014 (Debout et al., 1995; Lorentsen et al., in press) constituting >40% of the European population (Anker-Nilssen et al., 2015). Besides the Atlantic subspecies, which is breeding along the Norwegian and Barents Seas from Central Norway northwards, the continental subspecies colonized the South of Norway in 1996. By now, it has established more than a dozen colonies along the Skagerrak and North Sea coast, numbering about 2700 breeding pairs in 2014 (Fauchald et al., 2015; Lorentsen et al., in press). During the breeding season, the two subspecies overlap spatially only in a very small area in south-western Norway (Figure 1). The overlap is larger in winter, when a part of the Atlantic subspecies population migrates to the North Sea coast and Skagerrak. A recent review of existing literature on Norwegian great cormorants highlighted differences in the summer diet between the two subspecies within Norway (Lorentsen et al., in press). The Atlantic subspecies showed a potential conflict with fishery interests since it was feeding on young cod and saithe (Barrett et al., 1990; Lorentsen et al., 2004, in press). Contrasting the perception as a competitor for fisheries and especially for cod in the nearby Baltic Sea (Hansson et al., 2018), the continental subspecies breeding at Øra on the Norwegian Skagerrak coast was feeding mostly on wrasses (family Labridae) and gobies (Gobiidae), commercially previously not harvested species (Skarprud, 2003; Sørensen, 2012; Lorentsen et al., in press). However, there is growing commercial interest in wrasses for the use as cleaners of salmon lice (*Lepeophtheirus salmonis*) in the aquaculture of salmon (*Salmo salar*), with catches of wrasses reaching 27.75 million individual fish in 2017 (Huse and Bakkeiteig, 2018). This again may result in an increasing conflict of interest between humans and cormorants about a formerly commercially irrelevant fish group. Furthermore, an assessment



**Figure 1.** Study locations of great cormorant (*Phalacrocorax carbo*) diet in Norway (triangles) in relation to existing colonies (circles). The sizes of the circles indicate number of nests in the colonies around 2015. Røst, Sklinna, and Frøya (white triangles) hold populations of the subspecies *carbo*, Rauna, and Øra (black triangles) populations of the subspecies *sinensis*.

of the consumption of especially cod by great cormorants in the Skagerrak is warranted, given the collapse of coastal cod in the Oslofjord and northern Skagerrak area, where both commercial and recreational fishing for cod have been banned for at least three years from June 2019 onwards (<https://www.fiskeridir.no/Fritidsfiske/Vern-av-kysttorsk-i-soer>). The collapse of local stocks in southern Norway is part of a broader trend for cod stocks in the neighbouring region, with cod stocks having declined in the Eastern and Western Baltic Sea, the Kattegat, and the Greater North Sea area (Sguotti et al., 2019).

Based on the need for a better understanding of how cormorants affect local fish resources, the purpose of this study was to investigate the spatial and temporal variation in the diet of great cormorants breeding along the Norwegian Coast and, based on these data, quantify to which extent great cormorants feed on commercially important fish species and how this may impact fish stocks and be in conflict with human fisheries.

## Methods

### Collection of diet samples

Diet samples were collected between 2001 and 2016 from breeding colonies at five different sites spread along the Norwegian coastline (Table 1 and Figure 1): Røst (all colonies, 67.5°N, 12.0°E), Sklinna (65.2°N, 10.9°E), Frøya (63.8°N, 8.5°E), Rauna (58.1°N, 6.7°E), and Øra (59.2°N, 11.0°E). Røst, Sklinna, and Frøya are breeding sites of the Atlantic subspecies, whereas Rauna and Øra hold the continental subspecies. These colonies were chosen based on feasibility to collect pellets without causing too much disturbance to the birds and accessibility to reach colonies

**Table 1.** Number of diet samples of great cormorants (*Phalacrocorax carbo*) per site and year.

Subspecies	Location	Year	Number of pellets	
Atlantic ssp. ( <i>P. c. carbo</i> )	Røst	2008	54	
	Røst	2009	33	
	Røst	2010	13	
	Røst	2011	13	
	Røst	2012	33	
	Røst	2013	31	
	Røst	2014	19	
	Røst	2015	49	
	Røst	2016	36	
	Sklinna	2008	5	
	Sklinna	2009	4	
	Frøya	2001	88	
	Frøya	2002	23	
	Frøya	2003	97	
	Continental ssp. ( <i>P. c. sinensis</i> )	Rauna	2009	46
		Rauna	2010	87
Rauna		2011	85	
Øra		2002	240	
Øra		2010	49	
Øra		2011	207	
Øra		2012	18	

and sample over multiple years and to obtain samples from both subspecies. For repeatability and cost-efficiency, we selected colonies established as long-term monitoring sites by the SEAPOP programme ([www.seapop.no/en](http://www.seapop.no/en)). This dataset represents all available, hitherto unpublished diet data collected from great cormorants in Norway in the past 20 years.

Diet samples consisted of pellets, i.e. indigestible material that is regurgitated daily as a natural part of the digestive process. All samples were collected from the vicinity of nests, thus presumed to originate from breeding adults either directly or via their chicks. After collection, they were stored frozen until being analysed. Samples were collected between 8 May and 24 July, thus spanning from pre-egg laying to chick-rearing and representing the entire breeding season, although most samples were from the late incubation and chick-rearing periods. A visual inspection of histograms did not reveal any temporal patterns in dietary composition, fish length or mass within the summer months. As more elaborate statistics were not advised due to small sample sizes, we therefore pooled all data per site and year, also since the focus of this study was not on intra-annual differences in diet.

### Analyses of diet samples

The treatment of the pellets followed previous work by Hillersøy and Lorentsen (2012). Soft parts were digested in a saturated solution of biological washing powder (Bio-tex<sup>®</sup>) kept at 50°C in an oven for 1–2 days. Fish otoliths were removed and identified to the lowest possible taxonomic level using descriptions in Härkönen (1986), Camphuysen and Henderson (2017) and a reference collection. The length and width of each otolith were measured to the nearest 0.1 mm using a binocular microscope and mm paper.

Fragments of invertebrates were not systematically recorded for all sites and years and therefore not considered for the analyses performed on numerical abundance and proportion of biomass (described below). A complete list of invertebrates and their

frequency of occurrence is given in Supplementary Table S1.1. As with previous diet studies on great cormorants (Barrett *et al.*, 1990; Lorentsen *et al.*, 2004), it remains unclear to which degree invertebrates were primary prey targeted by the cormorants and how much was secondary ingestion of items taken by their fish prey.

### Statistical data analyses

We analysed the frequency of occurrence and numerical abundance of fish species contained in the cormorant diet per location and year following standard methodology (Barrett *et al.*, 2007). Fish mass and fish length were calculated based on otolith length and/or width as given in Härkönen (1986) and Jobling and Breiby (1986; only used for cod fish length). For European whitefish (*Coregonus lavaretus*), we used the formula provided in Lundström *et al.* (2010), and for garfish (*Belone belone*), we used the formula provided by Naturalis Biodiversity Center (2020).

For otoliths of fish where specific formulas were unavailable, or where identification was only made to group level, we proceeded as following: (i) for northern wolffish (*Anarhichas denticulatus*), we used the average formulas of Atlantic wolffish (*A. lupus*) and spotted wolffish (*A. minor*); (ii) for common topknot (*Zeugopterus punctatus*) and Norwegian topknot (*Phrynorhombus norvegicus*), we used the formula for brill (*Scophthalmus rhombus*), which has a similar otolith length/size ratio; and (iii) for black seabream (*Spondyliosoma cantharus*), common roach, and the whole Cyprinidae family, we could not find any formulas to calculate fish mass. Otoliths from these species and all otoliths that could not be identified to family level were therefore disregarded from the analyses involving fish mass. We therefore inevitably overestimated the biomass proportion of the other (identified) fish species to great cormorant's diet. The exact error of this overestimation is difficult to determine—depending on site and year between 1.2 and 20.1% of otoliths could not be used to calculate fish biomass.

For cases where identification to species level was impossible but samples were identified to family/order level, we proceeded as following: (i) for gadids and wrasses, which made up the largest proportion of the cormorant diet, we used the numerical abundance data of the fraction identified to species level to assess the overall proportion of each species and calculated fish length and fish mass for unidentified specimen accordingly; (ii) for Gobiidae, the only species identified was the black goby *Gobius niger*, so we applied the same formula for fish length and fish mass for this species also to the unidentified fraction of Gobiidae otoliths; (iii) for Ammodytidae, we used the average of greater and lesser sandeel (*Hyperoplus lanceolatus* and *Ammodytes tobianus*, respectively); and (iv) for Pleuronectiformes, there was high variation in the numerical occurrence of species, while sample sizes for most years and sites were rather low. The exception was for those from Øra in 2002 and 2011, where we proceeded as described above for gadids and wrasses. For the other Pleuronectiformes samples as well as for Salmonidae, Cottidae, and wolffish, we calculated fish length and fish mass based on the proportion (from the numerical abundance data as above) of all recorded species averaged across all sites and years.

Fish length of cod and saithe was used to assign age classes. Following Lorentsen *et al.* (2004), cod of <150-mm length was defined as 0-group, 150–250-mm-long cod as 1-group and 250–300-mm-long cod as 2-group. Similarly, saithe of < 120 mm was

defined as 0-group, 120–250-mm-long saithe as 1-group and >250-mm-long saithe as 2-group or older, based on Hillersøy and Lorentsen (2012). Fish lengths reported by Lorentsen *et al.* (2004) and Hillersøy and Lorentsen (2012) were all obtained from otolith lengths by applying the same formulas as used in this study.

### Statistical tests

All statistical procedures were conducted in R (version 3.6.3; R Core Team, 2020). We tested for differences in numerical abundance and proportion of biomass of fish species and groups between sites and years using generalized linear models (GLMs) with a quasi-binomial distribution. GLMs were run in the package *lme4* (Bates *et al.*, 2011) and included the site  $\times$  year interaction terms. These models were run for the proportion of gadids and wrasses, i.e. the two fish families that dominated the diet both numerically and by biomass, as well as for cod and saithe, i.e. the two fish species consumed most frequently by the Atlantic subspecies and which are also of commercial interest. We present deviation and *p*-values as obtained from likelihood ratio tests. For subsequent multiple comparisons following GLMs (for site and year differences), we show *z*-values and *p*-values based on Tukey *post hoc* tests performed with the *multcomp* package (Hothorn *et al.*, 2008). Where multiple tests were conducted on the same set of dependent variables (i.e. GLMs to test for differences in numerical and biomass proportions of fish groups among years within the same sites), we applied the Bonferroni correction to avoid type-I errors.

### Estimation of fish consumption by great cormorants in Norwegian waters per year

Using the dietary composition by biomass evaluated in this study for cormorants in the Norwegian Sea and the greater North Sea area in combination with literature data on daily metabolic rate, population numbers, and migratory patterns, we estimated for the Norwegian part of the greater North Sea area and the Norwegian and Barents Sea area, respectively, (i) the total amount of fish consumed by great cormorants and (ii) the amount of commercially exploited fish species.

The data used for this estimation are given in Table 2. Inevitably, this estimate is based on many assumptions and generalisations. In the absence of detailed dietary information from other colonies than those included in this study, we assumed our dataset to be representative of the diet of great cormorants in Norway. This is corroborated by previous studies on great cormorant diet which found similar prey biomass proportions, especially of gadids (Barrett *et al.*, 1990; Barrett *et al.*, 2002; Lorentsen *et al.*, 2004).

The dietary composition by biomass was averaged for the Atlantic subspecies and the continental subspecies and we assumed that great cormorants in the Barents Sea were feeding on the same species as those along the Norwegian Sea. There is only one published study on diet of great cormorants from the Barents Sea, which found cod to be the dominant prey item, besides capelin and sandeel (Barrett *et al.*, 1990). We further assumed that dietary composition would not differ between the breeding and non-breeding season. Great cormorants are migratory birds and based on ring recoveries we estimated that on average 25% of birds of the Atlantic subspecies would migrate from the Barents Sea and Norwegian Sea into the Norwegian part of the North Sea

and Skagerrak, while 50% of the Norwegian populations of the continental subspecies would leave Norwegian waters during the non-breeding season (Bakken *et al.*, 2003). For those individuals of the Atlantic subspecies that overwinter in the North Sea and Skagerrak area we assumed a diet shift, with diet from September to April resembling that of the continental subspecies in the same area.

We calculated variances for the total amount of fish consumed by great cormorants with parametric bootstrap sampling with functions of the R-base package (R Core Team, 2020). We assumed a normal error distribution for all underlying data for which a mean and SD were available (see Table 2). If only the range was available, bootstrapping was done based on a uniform (flat) error distribution. Bootstrap sampling was run for 100 000 iterations. We calculated the variance of the input parameters stepwise and took a random draw for each input parameter, which were combined to the estimates to calculate fish consumption.

### Estimation of the cormorant consumption of cod and saithe stocks of different age classes

In the final step, we estimated the cormorant consumption of the different age classes of cod and saithe stocks. For this purpose, we estimated the stock sizes of cod for age classes 0, 1, 2, and 3+ and saithe for 0, 1, and 2+, as follows.

For cod and saithe in the Norwegian Sea (north of 62°N to the Russian border), we based stock estimates on an age-dependent mortality rate, i.e. assuming reduced mortality with increasing fish size and age as described by Lorenzen (1996). For cold-temperate climate, the applied mortality was calculated according to:

$$M_i = 1.69 \times W_i^{-2.92},$$

with  $M_i$  being the mortality at age  $i$  and  $W_i$  being the average individual body mass at age  $i$ . The estimated average annual coastal cod recruitment (at age 2) over the years 2001–2016 was 34 million [varying between 27 million (in 2016) and 43 million (in 2011)] (ICES, 2019a). Stock numbers at ages 0, 1, and 3+ were estimated based on the formula above.

The estimated average annual saithe recruitment (at age 3) over the years 2001–2016 was 191 million (varying between 73 million and 421 million). Stock numbers at ages 0 and 1 were estimated based on the formula above. For age 2+, the stock size of 1117 million was adopted from ICES (2019a).

Stock size assessments for cod and saithe in the Greater North Sea area were based on stock size estimates by ICES of the North Sea cod and saithe in ICES sub-areas 20 (including the Skagerrak) and 4 (the main North Sea) over the period 2002–2012 (ICES, 2019b). Stock sizes of cod in Norwegian waters were estimated by applying the proportion of cod biomass landings harvested by Norway (15.7% of international catches) in ICES sub-areas 20 plus 4 relative to the total international landings in the same areas. This assumption seems reasonable since the quota shares reflect the historical national fishing zones. Similarly, stock sizes of saithe in the Norwegian part of the Greater North Sea were calculated by applying the corresponding fraction of saithe biomass fished by Norway (53.5% of international catches) in ICES sub-areas 20 plus 4.

**Table 2.** Data used to estimate food consumptions of great cormorants in Norwegian waters.

Parameter	<i>N</i> ± error	Unit	Source	Explanation
Breeding success per pair	1.2 ± 0.37	Chicks/year	T. Anker-Nilssen (unpubl. Data)	Data from Røst 2002–2018
Chick age at fledging	50	Days of age	Cramp and Simmons (1977)	
First year survival	58 (40–70)	% per year	Frederiksen and Bregnballe (2000a)	Intermediate survival
Second year survival	87.9 (70–92)	% per year	Frederiksen and Bregnballe (2000b)	
Start of breeding	3 (2–4)	Years of age	Schjørring <i>et al.</i> (1999)	
Atlantic ssp. ( <i>P. c. carbo</i> )				
Number of breeding adults	38 000 (34 200–41 800)	Birds	Fauchald <i>et al.</i> (2015)	Range assumed to be ±10% of breeding pairs ×2
Number of chicks during summer	22 800 ± 7 199	Birds	Own calculation	Based on population size and breeding success
Number of 1- and 2-year-old birds	24 848 ± 8 116	Birds	Own calculation	Based on number of chicks and survival probabilities
% remaining in Norwegian and Barents Seas during winter	75 (65–85)	%	Bakken <i>et al.</i> (2003)	Estimation based on ring recoveries, error assumed
% migrating to North Sea in winter	25 (15–35)	%	Bakken <i>et al.</i> (2003)	Estimation based on ring recoveries, error assumed
Adult body mass: male	3 200 ± 183	g	Grémillet (1997)	
Adult body mass: female	2 325 ± 117	g	Grémillet 1997	
Continental ssp. ( <i>P. c. sinensis</i> )				
Number of adults	5 400 (4 860–5 940)	Birds	Fauchald <i>et al.</i> (2015)	Range assumed to be ±10% of breeding pairs ×2
Number of chicks during summer	3 240 ± 1 013	Birds	Own calculation	Based on population size and breeding success
Number of 1- and 2-year-old birds	3 531 ± 1 150	Birds	Own calculation	Based on number of chicks and survival probabilities
% remaining in North Sea in winter	50 (40–60)	%	Bakken <i>et al.</i> (2003)	Estimation based on ring recoveries
% leaving Norway in winter	50 (40–60)	%	Bakken <i>et al.</i> (2003)	Estimation based on ring recoveries
Adult body mass: male	2 423 (2 020–2 810)	g	Cramp and Simmons (1977)	
Adult body mass: female	2 085 (1 810–2 555)	g	Cramp and Simmons (1977)	
Field metabolic rate of breeding birds	16.69 × mass <sup>0.651</sup>	kJ/day	Ellis and Gabrielsen (2002)	As recommended by Ridgway (2010)
Field metabolic rate of non-breeding birds	2.5 × 3.201 × mass <sup>0.719</sup>	kJ/day	Ellis and Gabrielsen (2002)	As recommended by Ridgway (2010)
Daily food intake of chicks	332.5 (327–338)	g/day	Ridgway (2010)	Average value of suggested range; taken into account for 50 days (= age at fledging) during summer
Prey assimilation efficiency	0.8 (0.77–0.85)		Ridgway (2010)	
Duration of the breeding season	123	Days	Bakken <i>et al.</i> (2003)	May–August based on timing of migration
Duration of the non-breeding season	242	Days	Bakken <i>et al.</i> (2003)	September–April based on timing of migration
Energy content of prey species				
Cod	4.00	kJ/g	Barrett <i>et al.</i> (2002)	
Saithe	4.00	kJ/g	Barrett <i>et al.</i> (2002)	
Wolffish	4.00	kJ/g	Barrett <i>et al.</i> (2002)	
Wrasses	5.40	kJ/g	Spitz <i>et al.</i> (2010)	
Other fish	5.42	kJ/g	Ridgway (2010)	
Invertebrates <sup>a</sup>	4.50	kJ/g	Barrett <i>et al.</i> (2002)	

Errors are presented as ± SD or as range (in brackets), based on availability in the literature.

<sup>a</sup>See Supplementary material S4 for estimates on cormorant consumption when assuming a diet consisting of 15% invertebrate prey (by biomass).

### Estimation of the cormorant consumption of Labridae in comparison to commercial catches

In 2017, a total of 27.8 million individual wrasses were caught in Norwegian waters (Halvorsen *et al.*, 2020). According to the quota advice, 78% of wrasses should be taken in the Greater North Sea area and 22% in the Norwegian Sea (Huse and Bakkeiteig, 2018). We therefore assigned 22% of catches to the Norwegian Sea and 78% to the Greater North Sea area. Catches of wrasses are commonly reported as number of individual fish and not in tonnes. We used data on average body mass collected in the framework of the study by Halvorsen *et al.* (2020) to calculate catches of wrasses in tonnes (separately for each species). We also—as an alternative—present the wrasse catches by cormorants in numbers (see [Supplementary material S2](#)). For doing so, we divided the estimated total mass of each wrasse species consumed by cormorants on an annual basis, by the average body mass of the respective wrasse species in the cormorant diet. Since the body masses of wrasses consumed by great cormorants were highly variable, the estimated numbers of such fish taken by cormorants are of course associated with a large confidence interval.

### Potential effects of corrosion of otoliths and of invertebrate prey

Our study was based on analyses of undigestible diet remains in pellets collected during the breeding season. The pros and cons of using pellets as well as other regurgitates for this purpose have been reviewed in detail (Carss *et al.*, 1997; Barrett *et al.*, 2007). In the context of our study, it is important to note the issues arising from the wear and tear of otoliths. This can first lead to an underestimation of diet contributions from fish species with small or hyaline otoliths (i.e. sprat, herring, and sandeels; Jobling and Breiby, 1986; Johnstone *et al.*, 1990) and second to an underestimation of fish length and mass from otoliths that are strongly worn (Suter and Morel, 1996). Across years and sites, both of these effects should be comparable. Regarding the first issue, an underestimation of sandeels, sprat, and herring may have caused an overestimation of other fish groups in the diet. In a similar way, any otoliths that could not be identified to fish group level and also those (very few) fish species or groups for which no formulas to assess fish mass from otoliths were available, inevitably caused an overestimate of all other (identified) fish groups in the diet.

For our study, the overestimation of all identified fish groups would imply that the consumption of particularly the commercially important species (cod, saithe, wolffish, and wrasses) were possibly lower, but certainly not higher than assessed here. For the issue of otolith erosion, we would to some degree have underestimated fish length, fish mass, and thus age class. This source of bias would have no strong effect on the estimated total fish mass consumed by cormorants per species and year but overestimated the proportions of younger cohorts, which we only assessed for cod and saithe. However, otoliths of gadids in general are more resistant against erosion than those of most other fish species (Jobling and Breiby, 1986; Johnstone *et al.*, 1990). To nevertheless assess an effect of otolith corrosion, we re-calculated otolith length by adding 10% to the measured otolith length and re-run the calculations of biomass proportions, age-class distribution as well as the cormorants' total consumption per year and its magnitude compared to the commercial harvest. These results are presented in [Supplementary material S3](#).

Finally, we did not take invertebrates into account when estimating dietary composition by biomass since we assume that invertebrates mainly represent secondary ingestion rather than primary prey. In support of this, all pellets analysed in this study that contained fragments of invertebrates also contained otoliths or other fish remains. When estimating food consumption by seabirds in Norwegian waters, Barrett *et al.* (2002) considered 10 and 20% of prey biomass of great cormorants in the Barents and Norwegian Seas, respectively, to originate from invertebrates, which seems high compared with other diet studies of the species (Leopold *et al.*, 1998; Boström *et al.*, 2012). If realistic, then the amount of fish consumed by great cormorants would be correspondingly lower. To also assess this possibility, we re-calculated the estimated consumption by cormorants, assuming a 15% contribution of invertebrates to their diet biomass. The results of this scenario are presented in [Supplementary material S4](#).

## Results

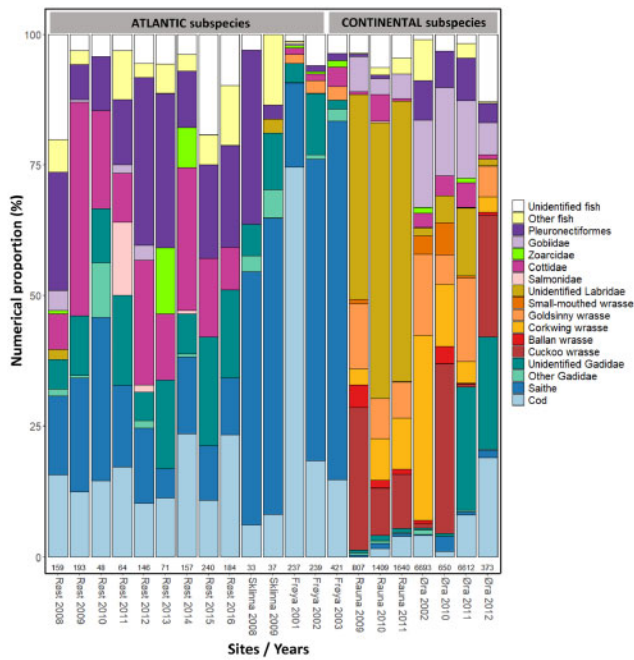
### Frequency of occurrence of fish taxa per pellet

A total of 44 different fish species from 21 different fish families were identified from 1230 samples of pellets of great cormorants ([Supplementary Table S1.2](#)). Pellets from the Atlantic subspecies from Røst, Sklinna, and Frøya contained 25 different fish species, and those from the continental subspecies from Rauna and Øra contained 38 different fish species. In the Atlantic subspecies, cod was the most frequently recorded species, and was present in 35.6% of samples, followed by saithe (24.5%) and shorthorn sculpin *Myoxocephalus scorpius* (12.3%; [Supplementary Table S1.2](#)). In the continental subspecies, diet by frequency was dominated by the goldsinny wrasse *Ctenolabrus rupestris*, which was present in 57.2% of all samples, followed by corkwing wrasse *Symphodus melops* (49.6%), black goby (32.5%), and cod (30.3%; [Supplementary Table S1.2](#)).

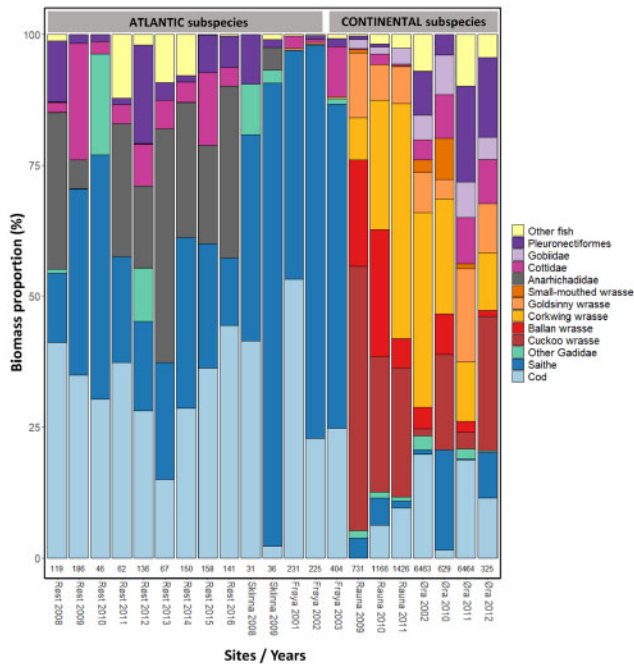
### Differences in numerical and biomass proportions of fish taxa between the cormorant subspecies

The fish diet of the Atlantic subspecies was dominated by gadids both numerically (53.9%) and by biomass (82.5%). Cod made up 27.5% of fish prey by number and 29.5% of fish prey biomass, and saithe correspondingly 17.6% by numbers and 49.8% by biomass ([Figures 2 and 3](#)). Pleuronectiformes (14.0%) and Cottidae (10.5%) were the second and third most frequently caught fish groups, but in terms of biomass, wolffish were more important ([Figures 2 and 3](#)). The diet of the continental subspecies was dominated by wrasses both by number (59.9%) and biomass (64.5%). The species composition of wrasses in the cormorant diet varied strongly between years and sites, both numerically and for biomass ([Figures 2 and 3](#)). Overall, cuckoo wrasse (*Labrus mixtus*) and corkwing wrasse were the two most important wrasse species both numerically and by biomass, followed by Ballan wrasse (*Labrus bergylta*) and goldsinny wrasse, and finally the small-mouthed wrasse ([Figures 2 and 3](#), [Supplementary material S2](#)). Gadids were the second most important fish group in the diet of the continental subspecies (11.6% numerically and 15.5% by biomass) with proportions of 5.5% numerically and 9.1% by biomass for cod and 0.9% numerically and 5% by biomass for saithe. Numerically, Gobiidae ranked third (8.6%) ([Figure 2](#)), but by biomass, Pleuronectiformes were more important ([Figure 3](#)).

Numerically, the majority of cod and saithe taken by great cormorants across years and sites were young fish of age groups 0–2



**Figure 2.** Proportions by frequency of fish taxa in the diet of great cormorants at different sites and years. Numbers below the bars indicate the total number of otoliths examined per site and year. Prey items other than fish were not considered.



**Figure 3.** Proportions by biomass of fish taxa in the diet of great cormorants at different sites and years. Numbers below the x-axis indicate the number of otoliths per site and year for which biomass could be calculated. Prey items other than fish were not considered.

for cod and 0–1 for saithe, respectively (Figures 4 and 5). By biomass, however, cod and saithe of age groups 3+ and 2+, respectively, were more important (Figures 4 and 5).

### Differences in numerical and biomass proportions of fish taxa between sites and years

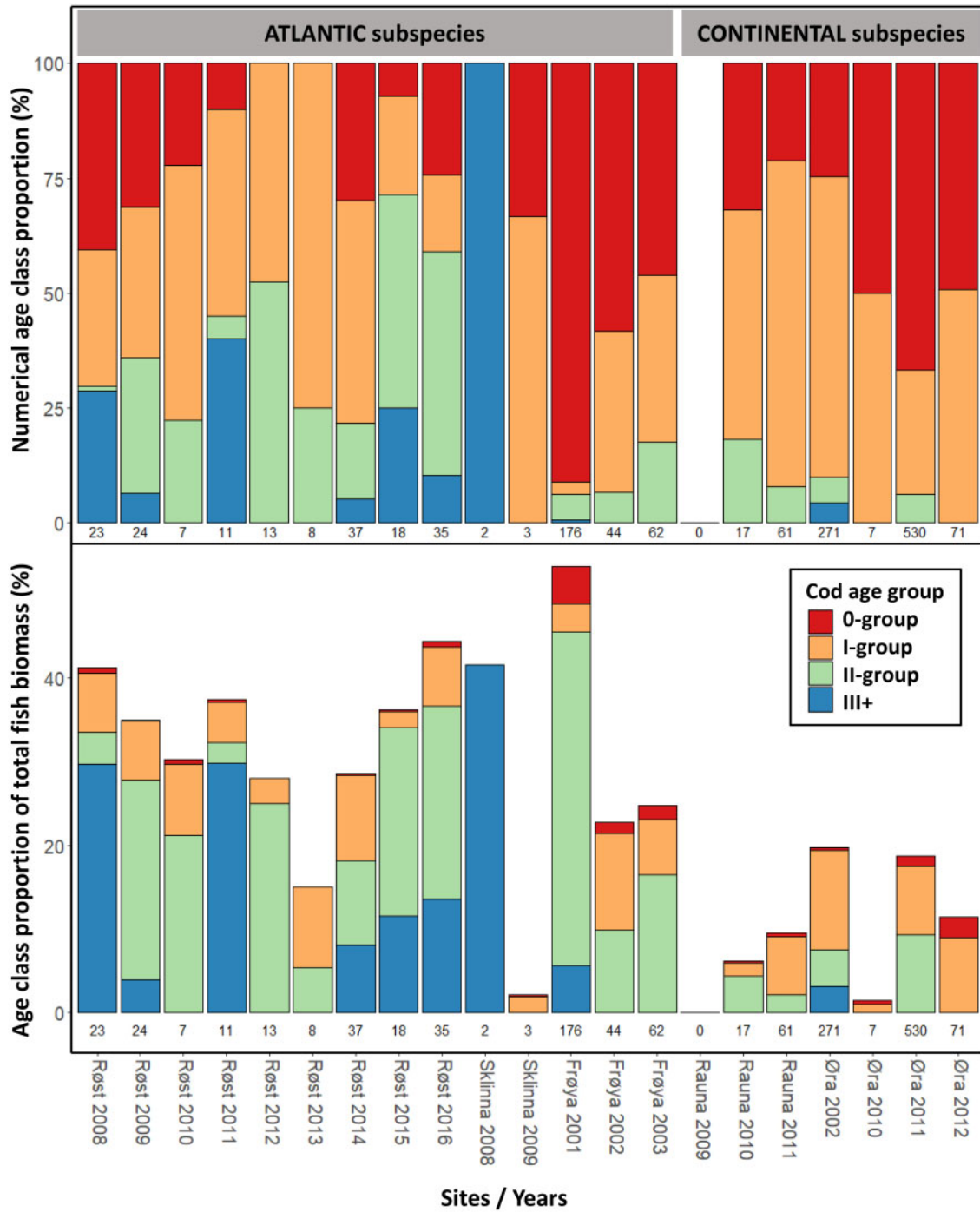
We found significant interactions between sites and years for numerical proportions of gadids and wrasses (GLMs: all  $Dev \geq 7.31$ ,  $p \leq 0.013$ ) and therefore tested for differences among sites and years separately. We followed the same procedure for models based on biomass proportion, where the interaction between sites and years was only significant for wrasses (GLM:  $Dev_1 = 3.27$ ,  $p = 0.020$ ) but not gadids, cod, or saithe (GLMs: all  $Dev_5 \leq 4.72$ ,  $p \geq 0.166$ ). Pooled over years, both the numerical and biomass proportion of gadids in the great cormorant diet were highest at Sklinna and Frøya, followed by Røst, Øra, and Rauna with the lowest proportion (see Table 3 for statistical outcomes). Among gadids, the numerical and biomass proportion of cod in the diet was highest at Frøya, followed by Sklinna and Røst, and lowest at Rauna (Table 3). Saithe had the highest proportion (both numerically and by biomass) in diet at Sklinna, followed by Frøya, Røst, and finally Rauna and Øra. Finally, the numerical proportion of wrasses in the diet was higher at Rauna than at Øra ( $z = 9.35$ ,  $p < 0.001$ ), but there were no differences in proportion of biomass between these two sites ( $z = 0.917$ ,  $p = 0.225$ ).

Inter-annual diet variation in either numerical or biomass proportion was present at Frøya and Øra for all main prey items. At Rauna, only the proportion of cod (both numerically and by biomass) but no other prey items differed significantly between years, whereas at Sklinna and Røst we found no such temporal variation in either numerical or biomass proportion of main prey items (Table 4 and Figures 2 and 3).

### Estimated consumption of fish by great cormorants across the year and impact on fish stocks

Estimated annual consumption of cod and saithe by great cormorants in relation to stock sizes in Norwegian waters both in the Norwegian and Barents Sea area (north of 62° N) and in the greater North Sea area was small (<1.7% of total fish stocks; Table 5). Great cormorants had the highest effect on cod and saithe of age group 1 both in the Norwegian and Barents Sea area (15.8 and 8.3% of cod and saithe stocks of this age group consumed by cormorants, respectively) and in the Greater North Sea area (correspondingly 7.0 and 0.7% for cod and saithe, respectively; Table 5). The impact of great cormorants on the age groups that are targeted by commercial fisheries (cod of age 3+ and saithe of age 2+) was effectively negligible (<0.8%; Table 5).

Compared to commercial landings, great cormorants were estimated to take <8.8% of total cod catches and <4.5% of total saithe catches in both the Norwegian and Barents Sea area and the Greater North Sea area (Table 5). For the three species of wolffish, cormorant consumption was estimated to be on average 18.4% of commercial catches (Table 5). For wrasses in the Greater North Sea area, there was a significant overlap between fishery interests and great cormorants, with great cormorants taking an estimated equivalent of 110% as compared to the commercial harvest in tonnes. This overlap was considerably higher when estimating the consumption in absolute fish numbers (see Supplementary material S2). Furthermore, a significant proportion of the wrasses were above the minimum size limits applied by the commercial wrasse fishery (Figure 6),



**Figure 4.** Numerical age-class distribution of cod consumed by great cormorants (top) and contribution of cod age classes to total fish biomass consumed by great cormorants along the Norwegian coast. Numbers below the x-axis indicate the number of otoliths examined per site and year.

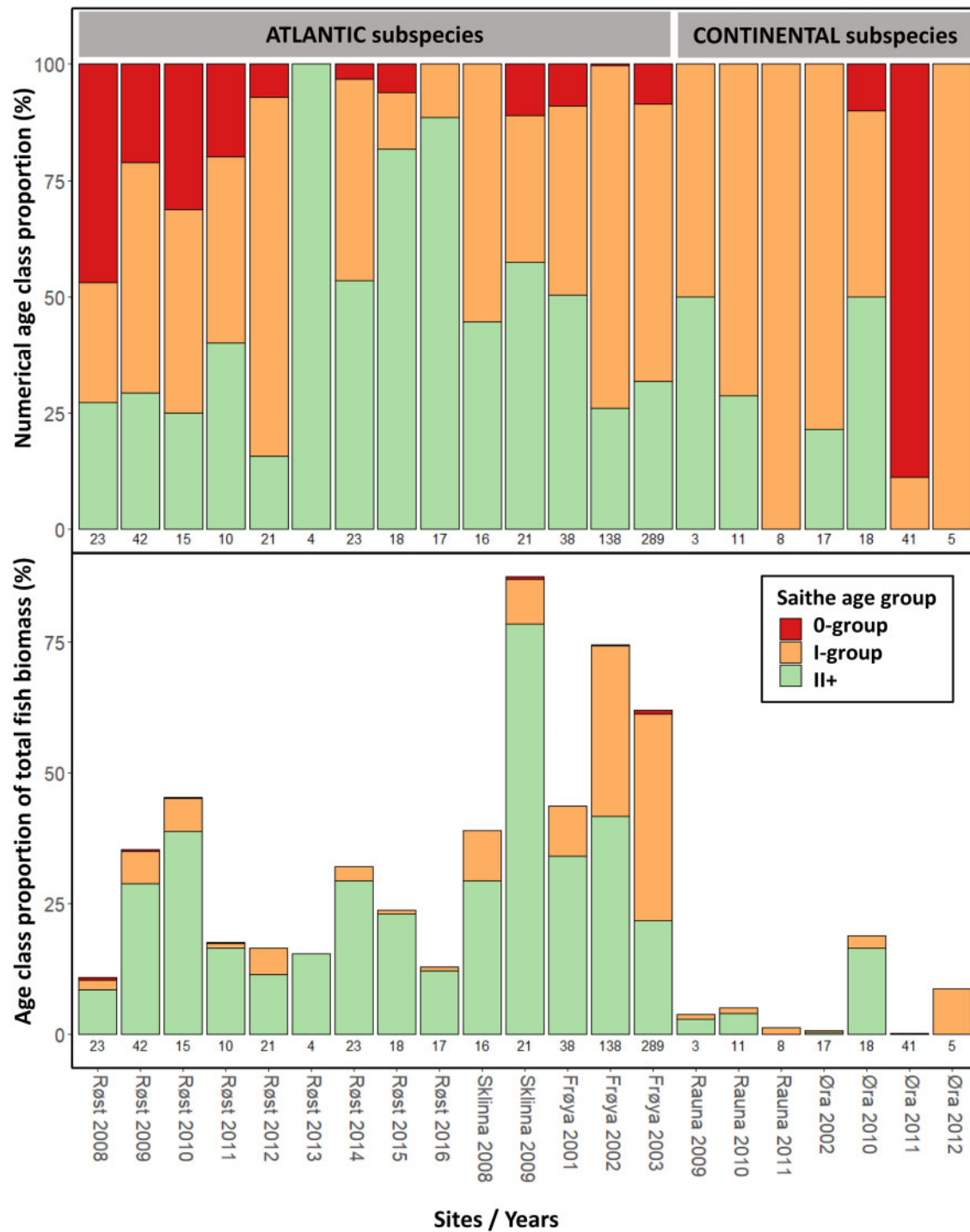
thus reflecting a direct overlap in the size range targeted by both cormorants and humans. However, the wrasse species with the highest commercial landings, the Ballan wrasse, was less targeted by great cormorants, with an estimated consumption proportion of 21% by biomass and 26% by absolute numbers, respectively, when compared to the commercial harvest (Supplementary material S2).

## Discussion

### Assessment of alternative scenarios, assuming corrosion of otoliths, and invertebrate diet

As explained in the Methods, the results of our study may have been affected by corrosion of otoliths and the assumption that invertebrates in the diet reflected secondary consumption of food items eaten by their prey.





**Figure 5.** Numerical age-class distribution of saithe consumed by great cormorants (top) and contribution of saithe age classes to total fish biomass consumed by great cormorants along the Norwegian coast. Numbers below the x-axis indicate the number of otoliths examined per site and year.

The scenario that assumed all measured otoliths in this study were in fact 10% longer than measured led to a very similar contribution of fish taxa by biomass as the original dataset (Supplementary Figure S3.1). Accordingly, the main results changed little, and cormorant consumption amounted to <1.7% of cod and saithe fish stock sizes and <9% of commercial catches for cod, <5% of saithe, 20% for wolffish, and 108% for wrasses

(Supplementary Table S3.1). As expected, under this scenario cormorants fed on a higher proportion of older age groups of cod and saithe (Supplementary Figures S3.2 and S3.3). Nevertheless, the estimated cormorant consumption of fish stocks of age 3+ cod and age 2+ saithe remained small and was only slightly higher (<2.5%) than when ignoring the potential effect of otolith corrosion. Furthermore, cormorants would have targeted a

**Table 3.** Model outcomes for differences in numerical and biomass proportions of gadids, wrasses, cod, and saithe in the diet of great cormorants between sites.

	Gadidae			Cod			Saithe			Labridae		
	Numerical prop.	Biomass prop.	Numerical prop.	Biomass prop.	Numerical prop.	Biomass prop.	Numerical prop.	Biomass prop.	Numerical prop.	Biomass prop.	Numerical prop.	Biomass prop.
Differences between sites												
Røst—Sklinna	$z = -2.00, p = 0.0234$	$z = -1.98, p = 0.246$	$z = 1.17, p = 0.733$	$z = 0.81, p = 0.915$	$z = -3.89, p < 0.001$	$z = -2.898, p = 0.027$	$na$	$na$	$na$	$na$	$na$	$na$
Røst—Frøya	$z = -7.23, p < 0.001$	$z = -6.21, p < 0.001$	$z = -6.62, p < 0.001$	$z = -5.01, p < 0.001$	$z = -3.00, p = 0.019$	$z = -1.79, p = 0.350$	$na$	$na$	$na$	$na$	$na$	$na$
Røst—Rauna	$z = 10.24, p < 0.001$	$z = 9.31, p < 0.001$	$z = 6.46, p < 0.001$	$z = 5.78, p < 0.001$	$z = 5.25, p < 0.001$	$z = 5.52, p < 0.001$	$na$	$na$	$na$	$na$	$na$	$na$
Røst—Øra	$z = 10.23, p < 0.001$	$z = 9.33, p < 0.001$	$z = 6.14, p < 0.001$	$z = 3.90, p < 0.001$	$z = 8.11, p < 0.001$	$z = 8.05, p < 0.001$	$na$	$na$	$na$	$na$	$na$	$na$
Sklinna—Frøya	$z = 0.07, p = 1.000$	$z = 0.38, p = 0.995$	$z = -2.21, p = 0.145$	$z = -1.84, p = 0.310$	$z = 2.83, p = 0.031$	$z = 2.29, p = 0.130$	$na$	$na$	$na$	$na$	$na$	$na$
Sklinna—Rauna	$z = 6.27, p < 0.001$	$z = 5.01, p < 0.001$	$z = 0.93, p = 0.864$	$z = -0.04, p = 1.000$	$z = 6.75, p < 0.001$	$z = 5.76, p < 0.001$	$na$	$na$	$na$	$na$	$na$	$na$
Sklinna—Øra	$z = 4.56, p < 0.001$	$z = 4.04, p < 0.001$	$z = -0.12, p = 1.000$	$z = -0.04, p = 1.000$	$z = 8.23, p < 0.001$	$z = 6.71, p < 0.001$	$na$	$na$	$na$	$na$	$na$	$na$
Frøya—Rauna	$z = 14.39, p < 0.001$	$z = 13.58, p < 0.001$	$z = 9.86, p < 0.001$	$z = 9.11, p < 0.001$	$z = 6.24, p < 0.001$	$z = 6.48, p < 0.001$	$na$	$na$	$na$	$na$	$na$	$na$
Frøya—Øra	$z = 17.75, p < 0.001$	$z = 15.55, p < 0.001$	$z = 13.76, p < 0.001$	$z = 10.01, p < 0.001$	$z = 10.00, p < 0.001$	$z = 9.36, p < 0.001$	$na$	$na$	$na$	$na$	$na$	$na$
Rauna—Øra	$z = -4.79, p < 0.001$	$z = -3.45, p = 0.004$	$z = -3.32, p = 0.006$	$z = -3.63, p = 0.002$	$z = -0.51, p = 0.984$	$z = 0.70, p = 0.950$	$z = 9.23,$	$z = 1.21,$	$z = 9.23,$	$z = 1.21,$	$z = 9.23,$	$z = 1.21,$
							$p < 0.001$	$p = 0.225$	$p < 0.001$	$p = 0.225$	$p < 0.001$	$p = 0.225$

Model results are the outcomes of Tukey *post hoc* tests based on GLMs. Significant results are highlighted in bold. Wrasses occurred in very low abundances in the diet of the Atlantic subspecies and were therefore omitted from most models, indicated by *na*.

**Table 4.** Model outcomes of GLMs for differences in numerical and biomass proportion of gadids, wrasses, cod, and saithe in the diet of great cormorants at sampling sites between years.

	Gadidae			Cod			Saithe			Labridae		
	Numerical prop.	Biomass prop.	Numerical prop.	Biomass prop.	Numerical prop.	Biomass prop.	Numerical prop.	Biomass prop.	Numerical prop.	Biomass prop.	Numerical prop.	Biomass prop.
Røst	$Dev = 5.74, p = 0.336$	$Dev = 9.22, p = 0.236$	$Dev = 8.27, p = 0.116$	$Dev = 8.40, p = 0.274$	$Dev = 8.12, p = 0.044$	$Dev = 7.38, p = 0.368$	$na$	$na$	$na$	$na$	$na$	$na$
Sklinna	$Dev = 0.11, p = 0.680$	$Dev = 0.55, p = 0.366$	$Dev = < 0.01, p = 0.955$	$Dev = 0.47, p = 0.364$	$Dev = 0.19, p = 0.565$	$Dev = 0.01, p = 0.913$	$na$	$na$	$na$	$na$	$na$	$na$
Frøya	<b><math>Dev = 35.53, p &lt; 0.001</math></b>	<b><math>Dev = 34.07, p &lt; 0.001</math></b>	<b><math>Dev = 88.02, p &lt; 0.001</math></b>	<b><math>Dev = 90.45, p &lt; 0.001</math></b>	<b><math>Dev = 9.90, p = 0.003</math></b>	<b><math>Dev = 12.49, p &lt; 0.001</math></b>	$na$	$na$	$na$	$na$	$na$	$na$
Rauna	$Dev = 1.09, p = 0.074$	$Dev = 1.90, p = 0.146$	<b><math>Dev = 2.93, p = 0.002</math></b>	<b><math>Dev = 6.05, p &lt; 0.001</math></b>	$Dev = 0.52, p = 0.145$	$Dev = 2.02, p = 0.131$	$Dev = 1.27,$	$Dev = 5.99,$	$Dev = 1.27,$	$Dev = 5.99,$	$Dev = 1.27,$	$Dev = 5.99,$
Øra	<b><math>Dev = 20.34, p &lt; 0.001</math></b>	$Dev = 1.57, p = 0.428$	<b><math>Dev = 5.10, p = 0.001</math></b>	<b><math>Dev = 8.62, p = 0.001</math></b>	$Dev = 1.79, p = 0.252$	<b><math>Dev = 10.93, p &lt; 0.001</math></b>	$Dev = 22.50,$	$Dev = 25.67,$	$Dev = 22.50,$	$Dev = 25.67,$	$Dev = 22.50,$	$Dev = 25.67,$
							$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$

Significant results are highlighted in bold. Wrasses occurred in very low abundances in the diet of the Atlantic subspecies and were therefore omitted from most models, indicated by *na*. Level of significance after Bonferroni correction:  $p = 0.010$ .

**Table 5.** Estimated annual consumption of fish species by great cormorants in Norwegian waters (middle) in relation to fish stock sizes and landings (bottom) of commercial fisheries in the same areas; the calculations were based on the birds' energy expenditure (see Table 2) and dietary composition (top); values represent mean  $\pm$  SD (and mean only for fish stock sizes and fish commercial harvest); note that cod and saithe values are differentiated by age classes, whereas all age classes were pooled for other species.

Fish age class	Norwegian and Barents Sea area (north of 62° N)					Greater North Sea area				
	Age 0	Age 1	Age 2(+)	Age 3+	Total	Age 0	Age 1	Age 2(+)	Age 3+	Total
Dietary composition by biomass in % <sup>a</sup>										
Cod	0.84 $\pm$ 0.95	4.62 $\pm$ 2.79	10.90 $\pm$ 2.83	13.08 $\pm$ 11.76	29.45 $\pm$ 5.38	0.35 $\pm$ 0.15	5.03 $\pm$ 2.12	3.19 $\pm$ 1.41	0.48 $\pm$ 0.55	9.06 $\pm$ 3.80
Saithe	0.24 $\pm$ 0.10	12.35 $\pm$ 10.01	37.16 $\pm$ 15.90		49.76 $\pm$ 17.60	0.06 $\pm$ 0.07	1.71 $\pm$ 0.68	3.54 $\pm$ 1.28		5.32 $\pm$ 1.88
Wolffish					8.09 $\pm$ 9.93					0.00 $\pm$ 0.00
Wrasses					0.14 $\pm$ 0.20					67.07 $\pm$ 18.29
Other fish					12.57 $\pm$ 5.91					18.56 $\pm$ 12.61
Estimated consumption in tonnes/year <sup>b</sup>										
Cod	124.8 $\pm$ 140.9	681.7 $\pm$ 420.8	1 607 $\pm$ 1 255	1 930 $\pm$ 1 764	4 345 $\pm$ 956	11.78 $\pm$ 5.70	170.8 $\pm$ 82.7	108.2 $\pm$ 54.4	16.16 $\pm$ 16.08	306.9 $\pm$ 148.6
Saithe	36.25 $\pm$ 15.37	1 822 $\pm$ 1 497	5 482 $\pm$ 2 451		7 340 $\pm$ 2 757	2.14 $\pm$ 2.50	58.03 $\pm$ 26.63	120.1 $\pm$ 51.3		180.24 $\pm$ 76.27
Wolffish					1 193 $\pm$ 1 483					0.00 $\pm$ 0.00
Wrasses					20.75 $\pm$ 29.82					2 273 $\pm$ 810
Other fish					1 854 $\pm$ 1 891					628.9 $\pm$ 459.9
Total					<b>14 751 <math>\pm</math> 1 774</b>					<b>3 389 <math>\pm</math> 749</b>
Fish stock sizes in Norwegian waters in tonnes <sup>c</sup>										
Cod	1 291	4 318	13 718	237 334	256 661	379	2 457	9 392	10 541	22 768
Saithe	10 412	21 969	909 494		941 875	2 497	8 354	295 940		306 791
Cormorant consumption in % of fish stocks in Norwegian waters <sup>d</sup>										
Cod	9.67 $\pm$ 11.22	15.79 $\pm$ 10.11	11.72 $\pm$ 9.43	0.81 $\pm$ 0.76	1.69 $\pm$ 0.43	3.11 $\pm$ 1.58	6.95 $\pm$ 3.53	1.15 $\pm$ 0.61	0.15 $\pm$ 0.16	1.35 $\pm$ 0.68
Saithe	0.35 $\pm$ 0.16	8.29 $\pm$ 7.00	0.60 $\pm$ 0.28		0.78 $\pm$ 0.31	0.09 $\pm$ 0.10	0.70 $\pm$ 0.34	0.04 $\pm$ 0.02		0.06 $\pm$ 0.03
Fish commercial harvest in Norwegian waters in tonnes/year										
Cod <sup>e</sup>	0	0	142	49 006	49 148	0	348.8	1 229	3 326	4 904
Saithe <sup>e</sup>	0	0	162 830		162 830	0	0	162 830		162 830
Wolffish <sup>f</sup>					6 485					0
Wrasses <sup>g</sup>					581					2 062
Cormorant consumption in % of commercial harvest <sup>h</sup>										
Cod	na	na	1 132 $\pm$ 911	3.94 $\pm$ 3.70	8.84 $\pm$ 2.25	na	48.96 $\pm$ 24.84	8.80 $\pm$ 4.63	0.49 $\pm$ 0.50	6.26 $\pm$ 3.19
Saithe	na	na	3.37 $\pm$ 1.60		4.51 $\pm$ 1.81	na	na	0.07 $\pm$ 0.03		0.11 $\pm$ 0.05
Wolffish					18.40 $\pm$ 23.00					0
Wrasses					3.57 $\pm$ 5.25					110.2 $\pm$ 42.2

<sup>a</sup>Own data from diet analyses.

<sup>b</sup>Calculated based on dietary composition and energy expenditure.

<sup>c</sup>Fish stocks in Norwegian waters were estimated based on ICES data as explained in Methods. Estimates for coastal cod and saithe in the Norwegian and Barents Seas were based on ICES data from 2001 to 2016, and estimates for coastal cod and saithe in the North Sea area on ICES data from 2002 to 2012.

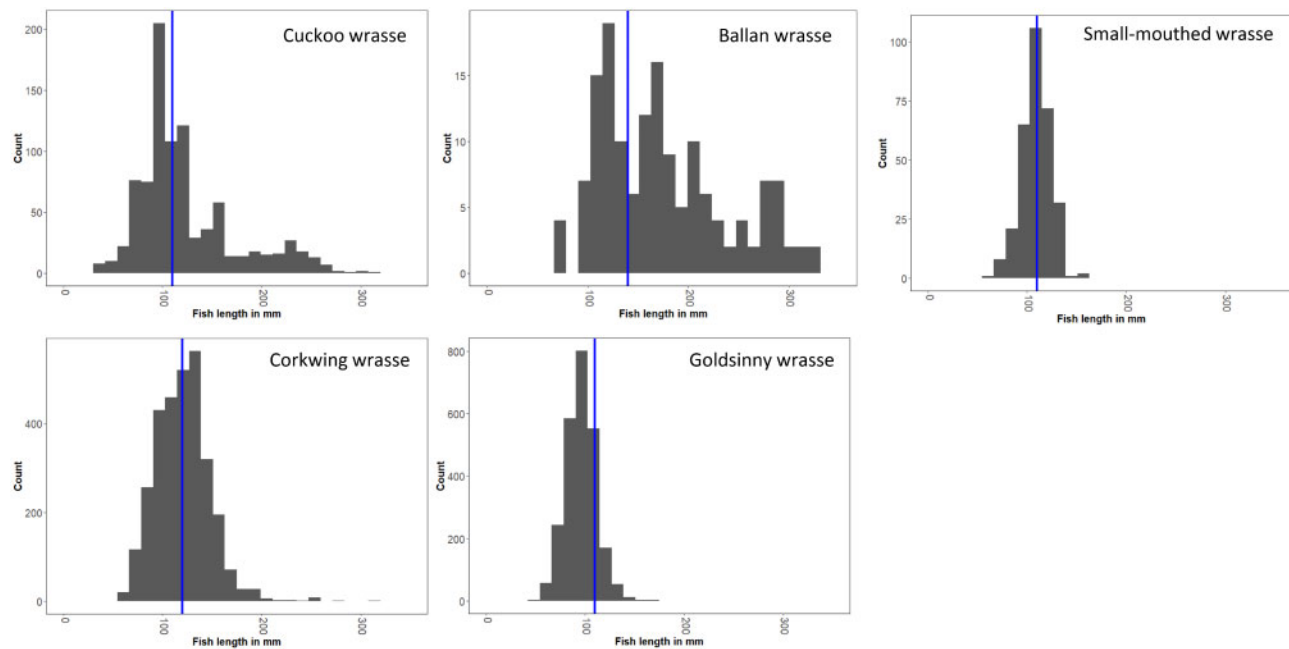
<sup>d</sup>Own calculations based on fish stock sizes in Norwegian waters and estimated consumption by great cormorants. SD estimates were based on a bootstrap procedure assuming a 20% error range of fish stock sizes.

<sup>e</sup>Commercial harvest of cod and saithe stocks in Norwegian waters were estimated based on landings—see Methods for details.

<sup>f</sup>Catch statistics from 2017 as published in Huse and Bakkevig (2018), pooled for all three wolffish species.

<sup>g</sup>Mass estimates were based on the number of catches in 2017 and average weight and length—see Methods for details.

<sup>h</sup>Own calculations based on commercial harvest and estimated consumptions by great cormorants. SD estimates were based on a bootstrap procedure assuming a 20% error range of fish harvest numbers.



**Figure 6.** Estimated fish length of Labridae species in the diet of great cormorants in Norway (histograms) in relation to the minimum size limits applied by the commercial wrasse fishery (vertical blue lines; Skiftesvik et al., 2014).

slightly larger proportion of wrasses above the minimum size limit applied by the commercial fisheries (Supplementary Figure S3.4). A reduction in otolith length by 10% due to corrosion is quite extreme, especially for otoliths of gadids, which are more resistant against erosion than those of most other fish species (Jobling and Breiby, 1986; Johnstone et al., 1990). Since we did not systematically record otolith corrosion, it is difficult to assess which of the two scenarios (the one presented in Supplementary material S3, or the one in the main manuscript) is the most accurate. The reality is probably somewhere in between, but we still conclude that an effect of otolith corrosion on the results of this study would be very small.

The other factor of uncertainty in this study was the proportion of invertebrates in the diet of great cormorants. Based on the assumptions made by Barrett et al. (2002), we also re-calculated the consumption by great cormorants under the scenario that their diet consists of 85% fish and 15% invertebrates. The consumption of commercially important fish species would then have been somewhat lower, with  $\leq 1.4\%$  of cod and saithe fish stock sizes and  $\leq 7\%$  of commercial catches for cod,  $< 5\%$  of saithe, 16% for wolffish, and 84% for wrasses (Supplementary material S4).

### Differences in diet between subspecies and among sites and years

We found significant differences in the diet of great cormorants breeding along the Norwegian Sea (i.e. Atlantic subspecies) compared with those breeding along the North Sea and Skagerrak coasts of Norway (i.e. continental subspecies). In agreement with the review by Lorentsen et al. (in press), the Atlantic subspecies was shown to take a higher proportion of gadids, especially cod and saithe, than the continental subspecies whose diet was dominated by wrasses. Fish species associated with freshwater and brackish water were only found in the diet of the continental

subspecies, matching previous findings that this subspecies is more associated with inshore or limnic foraging habitats (Cramp and Simmons, 1977). However, we also found significant differences in the diet composition (both numerically and by biomass) among sites holding the same subspecies (e.g. between Røst and Frøya, both holding the Atlantic subspecies as well as between Rauna and Øra, both holding the continental subspecies). Temporal variation in diet between years was only present at some of the sites, but apparently insignificant for example at Røst, for which we had the longest data series spanning 9 years. Great cormorants are opportunistic foragers with a well-documented, wide range of forage fish species (e.g. Lehikoinen, 2005; Boström et al., 2012; Lorentsen et al., in press). This high variation is also reflected in our data, with 44 different fish species from 21 families identified, although only a few species of three fish families (gadids, wolffish, and wrasses) dominated the diet both numerically and by biomass. It is thus likely that the spatio-temporal variation in diet of great cormorants that we found was driven mostly by spatial and temporal differences in the availability of different fish species, a typical pattern in great cormorants (Liordos and Goutner, 2008; Lehikoinen et al., 2011; Dias et al., 2012) and other opportunistic seabird species (e.g. Montevecchi and Myers, 1995; Montevecchi et al., 2009; Waluda et al., 2017). Similarly, the variation in cod and saithe age-class composition that we found in the cormorants' diet was likely the result of spatio-temporal variation in the recruitment of these species, as has previously been found in great cormorants and closely related European shags (*Phalacrocorax aristotelis*; Barrett, 1991; Lorentsen et al., 2004, 2018). It is thus likely that the differences in diet between the Atlantic and continental subspecies are mainly a result of prey availability in their respective marine environments, not necessarily because the two subspecies have different dietary preferences *per se*. This is also why we assumed in our model that Atlantic cormorants that winter in the North Sea and

Skagerrak area would switch to a wrasse-dominated diet, equivalent to that of the continental subspecies.

### Potential impact of great cormorants on fish stocks

Compared to estimates of fish stock size and human catches, the estimated total consumption of both cod and saithe by great cormorants in the Norwegian and Barents Sea area as well as in the Greater North Sea area was minor. The impacts on fish stocks were estimated to be low even though cod and saithe dominated the diet of the Atlantic subspecies. It is worth noting that for our calculations, we took fish stocks and fish harvest into account for larger spatial areas (including offshore areas within Norwegian territory) than cormorants will utilize, both during summer and winter. This was done due to a lack of data on fish stocks and human catches in the coastal zone only. Although foraging ranges of great cormorants in summer are up to 70 km from their colonies (Potier *et al.*, 2015), they exclusively forage in shallow coastal waters where sea depth is typically <11 m (Grémillet *et al.*, 1999). Due to their need to dry their feathers (Ribak *et al.*, 2005), they remain in coastal areas throughout the year; thus, direct overlap with human activities will naturally be highest in coastal areas, even when a large part of the fish stocks and the fisheries are situated further offshore. More important in this context is, however, that great cormorants feed primarily on younger age groups of cod and saithe that are not commercially targeted. These age groups have their nursery grounds in nearshore waters where they are exposed to high natural mortality (see declining stock sizes with age in Table 5). The take by great cormorants is part of the natural mortality for these cohorts. Other causes of natural mortality are predation by other fish species (Strand *et al.*, 2020) or by conspecifics, since cannibalism is common in gadids (Bogstad *et al.*, 1994; Bromley *et al.*, 1997). Cannibalism is in fact estimated to be one of the most important factors determining natural mortality of age groups 0–3 in cod (Yaragina *et al.*, 2009). The overall competition between great cormorants and humans for fish of the same age group was therefore limited, and the impact of great cormorants on cod and saithe fish stocks is likely to be very low. This was particularly the case in the greater North Sea area including the Oslofjord, where cod stocks recently have collapsed. Based on the data from this study that were collected between 2002 and 2012 and therefore before the recent collapse, it is unlikely that great cormorants are responsible for the collapse of the cod stocks in the area. It therefore appears that for the North Sea area—as previously seen with other piscivorous predators (Sørli, 2017), the competition between humans and cormorants at least for cod and saithe is a perceived conflict rather than a real one.

Among those fish species that are of direct interest for human consumption, great cormorants only had a significant overlap (18.4%) with human interests for wolffish. The reconstructed fish length based on otolith length (4–65 cm) suggested that great cormorants not only feed on immature, but also on mature wolffish of a similar size as targeted by commercial fisheries. Notably, in our study, we found wolffish only in the diet of great cormorants at Røst. All three species of wolffish that occur in the Norwegian and Barents Seas were present in the diet (see Supplementary Table S1.2) and all are of commercial interest (Huse and Bakkevig, 2018). Numerically, wolffish was not a very common prey at Røst, and even absent in the samples from the year with lowest sample size. Barrett *et al.* (1990) found low numbers of

wolffish in the diet of great cormorants at another Lofoten colony, 130 km north of Røst, but not at two colonies in Central Norway. Overall, wolffish appear to be a rather uncommon prey for great cormorants in general, but given their opportunistic foraging behaviour, great cormorants prove capable of supplementing their diet with wolffish at those places where they are accessible. In this case, we would expect a rather limited conflict for wolffish between cormorants and commercial fisheries. Stock size estimates of wolffish in Norwegian waters are lacking, and estimates on the impact of great cormorants on wolffish stocks are therefore difficult. Recent evidence suggests that stocks of wolffish and other predatory fish species may be depleted due to overfishing, resulting in the loss of kelp forests due to sea urchin blooms (Norderhaug *et al.*, 2021). The depletion of fish stocks could also be the reason for the comparatively large overlap in cormorant consumption with human catches—as has been recently postulated for forage fish (Saraux *et al.*, 2020).

Finally, we noticed the largest overlap between great cormorant diet and human interests for wrasses. There are currently no estimates of stock sizes available for any wrasse species (Halvorsen *et al.*, 2017a). Fish mortality due to commercial harvesting (using traps) may reduce wrasse populations by 31–41% over a period of only 4 months (Halvorsen *et al.*, 2017b). The impact from great cormorants may be in the same range, but better data on fish stocks are needed to assess the impacts of both cormorants and the commercial fishery. Both cormorants and the fishery overlap in the size range of wrasses taken (Figure 6), and the same five species that are taken by cormorants are also caught for the aquaculture industry (Supplementary material S2; Halvorsen *et al.*, 2020). However, for the most valuable and most targeted cleaner-fish species, the Ballan wrasse, the overlap between fishery and cormorants appeared to be least, with cormorants taking 21–26% compared to human catches (Supplementary material S2).

Commercial harvesting of wrasses in Norwegian waters and particularly the greater North Sea area has increased markedly since 2010 (Halvorsen *et al.*, 2017a). Since two of the targeted wrasse species (cuckoo wrasse and Ballan wrasse) are protogynous, and in addition, corkwing wrasses also show sexual size dimorphism, the size range of targeted fish can have profound effects on the population structure and size (Halvorsen *et al.*, 2016). Concerns that the wrasse fishery could have severe impacts on fish stock populations of these generally slow growing species have also been brought forward by the scientific community (Skiftesvik *et al.*, 2014; Halvorsen *et al.*, 2016, 2017a). To prevent potential overfishing, Norwegian fisheries authorities set a maximum quota for commercial catches of wrasses to 18–19 million fish per year for both 2019 and 2020 (<https://www.fiskeridir.no/Yrkesfiske/Tall-og-analyse/Fangst-og-kvoter/Fangst-av-leppefisk>). If wrasse stocks are declining, changes in community structure may have profound consequences for the marine ecosystem (Halvorsen *et al.*, 2017a). Furthermore, under this scenario we would expect great cormorants to adapt their diet to other prey, shifting to potentially already declining cod or alternatively other fish species of human interest. We therefore fear that the ongoing high demand for wrasses might lead to an increasing conflict between cormorants and human interests—for both wrasses and in the long term also for other fish stocks. However, it is unclear if wrasse stocks are really in decline and some recent papers suggest that the decline of larger piscivorous fish species such as cod even led to an increase of meso-predators, including wrasses (Östman *et al.*, 2016). Climate change is further contributing to a northwards range shift of some wrasse species (Knutzen *et al.*, 2013). A high

abundance of meso-predators can also negatively affect seagrass *Zostera marina* and seaweed *Fucus* spp. beds (Östman et al., 2016), as well as the abundance of blue mussels (Christie et al., 2020). Taking all information together, there appears to be an urgent need for a better monitoring of wrasse populations and factors affecting them.

## Conclusions

Our study presents the most up-to-date information on the diet of both subspecies of great cormorants breeding along the Norwegian coast. Based on this solid data set and the best estimates of fish stock sizes and catch quotas available, we were able to quantify the impact of great cormorant predation on commercial fish stocks and the corresponding conflict with human interests. Under any of the scenarios assessed in this study, we found the existing conflict between great cormorants and fishery for human consumption to be small or negligible, in particularly for cod and saithe. This limited conflict is in agreement with previous studies in the nearby Baltic Sea investigating cormorant-human interactions (Östman et al., 2012, 2013). Importantly, our data indicate that the increasing population of great cormorants of the continental subspecies along the Skagerrak coast is not responsible for the decline of cod stocks in this particular area.

The main potential for conflict between great cormorants and human fisheries is linked to the large proportion of wrasses taken by great cormorants in the Greater North Sea area since this fish group is now also targeted commercially for use as cleaner fish in the salmon farming industry. This may lead to a direct competition for wrasses between humans and cormorants, with a longer-term potential to also cause a diet shift in cormorants to other fish species, including cod and saithe, if wrasse stocks decline. Given the manifold concerns around the catch of wrasses while stock size information is lacking, we here highlight once more the urgent need for an assessment of wrasse stock sizes to further quantify the impact of the salmon farming fishery as well as the take of great cormorants.

## Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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## Data availability statement

The complete diet dataset is available in Dryad ([doi:10.5061/dryad.b5mkkwhcd](https://doi.org/10.5061/dryad.b5mkkwhcd)). All other data used to derive our results are presented in tables in this manuscript or in the supplements.

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