Population status, breeding biology and diet of Norwegian Great Cormorants

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Abstract

Two subspecies of the Great Cormorant breed in Norway; the continental *Phalacrocorax carbo sinensis* in the south, along the Skagerrak coast, and the marine *P. c. carbo* from Central Norway and northwards. Here we review the existing information on population status and trends, breeding performance and diet of these two subspecies in Norway. The most recent national population estimates are approximately 2500 (in 2012) and 19,000 (in 2012−2014) breeding pairs of *sinensis* and *carbo*, respectively. The *sinensis* population established itself in 1996 in Rogaland at the southwestern tip of Norway, and in 1997 in Østfold close to the Swedish border, and increased for about ten years. Since then the numbers have stabilised. For *carbo*, the population increased from 21,000 pairs in the early 1980s to 27,000 in 1995, and then decreased to the current number of 19,000 pairs. Significant annual variations in clutch size and reproductive output have been observed, but the drivers of these changes have not been identified. Unidentified gadoids and Atlantic Cod *Gadus morhua* were the most common prey of *carbo,* whereas inshore species such as Corkwing Wrasse *Symphodus melops*, Rockcook *Centrolabrus exoletus*, Goldsinny Wrasse *Ctenolabrus rupestris* and Black Goby *Gobius niger* were the most common caught in the eastern Skagerrak by *sinensis*. *Carbo* take very large numbers of 1-3 yr old gadoids during the year, and we cannot exclude the possibility this can have local effects on fish mortality rates.

Key words: Great Cormorant, Norway, *sinensis*, *carbo*, population changes, breeding performance, diet

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Introduction

Great Cormorants *Phalacrocorax carbo* breed along most of the Norwegian coast, from the Swedish border in the southeast to the Russian border in the northeast, and Norway houses about 40% of the nominate form of the European population of Great Cormorant *Phalacrocorax carbo carbo* (hereafter *carbo*) (Mitchell *et al.* 2004, Anker-Nilssen *et al.* 2015, Fauchald *et al.* 2015). Until 1996, when *P. c. sinensis* (hereafter *sinensis*) became established in the south, *carbo* was the only subspecies breeding in Norway, with all colonies located north of the North Sea. As proposed by Marion & Le Gentil (2006), those breeding in the northernmost areas (from the Lofoten Islands northwards) may belong to a third subspecies, *P. c. norvegicus*, but their genetic status has not yet been clarified. In this paper, we therefore consider all "northern" Great Cormorants to be *carbo*.

A large number of *carbo* colonies have been monitored annually throughout most of the species' distribution range in Norway since the late 1970s, whereas the total breeding population is assessed infrequently. Since most colonies are situated on remote sites, often in the most exposed parts of the coast, very few studies of their breeding performance have been carried out. Parameters of breeding success are monitored in one *sinensis* and one *carbo* colony only, and breeding phenology is studied in one *carbo* colony.

Considering their large body size (ca. 3 kg), numbers and an anecdotal greed for commercially important fish, Great Cormorants have long been a source of concern to fishermen, fisheries biologists and, recently fish farmers and anglers in Norway and elsewhere (Barrett *et al*. 1990, Lorentsen *et al*. 2004 and refs. therein). It is thus surprising that no scientific documentation of Norwegian cormorant diet was attempted before the mid-1980s and that little has been published since. In his definitive monograph of the birds of Norway, Haftorn (1971) simply notes that the cormorant diet consists mainly of fish, including Atlantic Cod *Gadus morhua* (hereafter Cod) and mentions three fish species caught in fresh water (two being trout, presumably *Salmo trutta*, and one European Perch *Perca fluviatilis).*

Here we evaluate recent trends in Norwegian *carbo* and *sinensis* populations and their breeding success and phenology, and describe their diet choice and possible relations with changes in fish stocks.

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METHODS

Population monitoring and breeding numbers

Breeding birds in colonies along the Skagerrak and southwestern coasts (from the Swedish border to Rogaland) were visually identified as belonging to the *sinensis* subspecies mainly due to their extended white colouring of the head and neck, compared to that for the *carbo* subspecies (photos exists from several colonies, including Øra in Østfold county and Rauna in Vest-Agder county, Figure 1). The expansion of *sinensis* into SE Norway has also been reflected by a steep increase in recoveries of Great Cormorants ringed as chicks in Swedish and Danish colonies (Bakken & Anker-Nilssen 2012, Norwegian Bird Ringing Centre unpubl. data).

Apparently occupied nests (AONs, Walsh *et al.* 1995) in *sinensis* and *carbo* colonies were monitored almost annually throughout most of their breeding ranges. Most of the colonies between Central Norway (64°N) and the north shores of the Lofoten Islands (68°N) were monitored using aerial photography, whereas the colonies in western Finnmark (70−71°N) were monitored from boats. The surveys were performed during late incubation, usually in mid-May in southern Norway, first half of June in Central Norway and late June in North Norway. Breeding synchrony may vary between colonies and years (cf. Walsh *et al*. 1995, Bregnballe *et al*. 2012), hence breeding numbers should be considered as a minimum estimate of colony size.

Population indices were calculated using TRIM 3.53 (Pannekoek & van Strien 2005), a software for analysis of time series where missing observations are estimated based on site and year indices. We then used Monte-Carlo simulations to calculate statistics for all trends by comparing the linear regression slope for the *ln*-transformed data set with the corresponding slopes for 10,000 randomised sequences of the same values (see Barrett et al. 2006 for a full description of the procedure).

Reproductive performance and phenology

Reproductive performance of *sinensis* was monitored annually in 2008−2016 in a colony of 7−264 (mean 194) breeding pairs at Rauna (58°34’N 6°40’E), Vest-Agder, close to the southern tip of Norway, where this subspecies started to breed in 2003. Reproductive performance of *carbo* was monitored annually in 2002−2016 for the 31−115 (mean 65) pairs breeding at Røst (67°30’N 12°00’E),

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a small offshore archipelago at the outermost tip of the Lofoten Islands, Nordland county. This population was established in 1997 and has bred on nine different islets, occupying 1-4 of the sites in any given year.

The phenology of *carbo* was also monitored at Røst. Every year, each colony was visited twice; first around hatching in mid-late June to count nests and register clutch sizes, and then in early-mid July to ring chicks. Visits were always kept as short as possible (usually 5−10 min in June and 15−20 min in July) to reduce disturbance and keep predation risk to a minimum. On a few occasions, the first visit was skipped to avoid predation from unusually high numbers of large gulls *Larus* spp. present in the area. Laying date was coarsely assessed by assuming an incubation time of about 30 days (cf. Cramp *et al.* 1977).

Statistical analyses were done in IBM SPSS Statistics ver. 23 (IBM Corp. 2015)

Diet

Here we summarize five studies that have been published since the 1980s, three of *carbo* and two of *sinensis* (Table 1). These were carried out at breeding colonies in five localities (Sør-Varanger, Hovsflesa, Vikna, Sula and Øra) and two at roosting localities (Sørfjord and Munkhomen) (Figure 1, Table 1). Regurgitated pellets or stomach contents (of chicks) and whole fish found regurgitated on the ground were collected during single visits during the chick-rearing period (Barrett *et al*. 1990), or at regular intervals during the respective study periods (Johansen 1998, Skarprud 2003, Lorentsen *et al*. 2004, Sørensen 2012). After collection, all samples were frozen before storage. Thawed pellets were either opened and teased apart to reveal their contents without prior treatment (Barrett *et al*. 1990, Johansen 1998, Lorentsen *et al*. 2004) or after soaking in a weak solution of caustic soda for 3-4 days (Skarprud 2003, Sørensen 2012). Food items were identified from remains found in the pellets, primarily otoliths of fish, but in Barrett *et al*. (1990) shells of molluscs and body parts of invertebrates e.g. crustaceans and polychaetes were also recorded. Sizes of fish were determined mainly from published relationships between otolith size and fish length (Breiby 1985, Härkönen 1986), but sometimes also from measurements of whole, regurgitated fish recorded in the field.

RESULTS

Population monitoring and breeding numbers

Great Cormorant breeding colonies are distributed along most of the Norwegian coast (Figure 1), with *sinensis* along the Skagerrak and southwestern coast, from the Swedish border to Boknafjorden in Rogaland, and *carbo* from Hordaland on the west coast and northeast to the Russian border in Varangerfjorden. Most of the colonies, even those of *sinensi*s, are found on small, barren islands in the outermost parts of the coast (Figure 2). The latest survey (spread in 2005−2016) documented altogether 14 *sinensis* and 117 *carbo* colonies, ranging in size from a few to 968 (mean 184, SE = 64.55) and 1297 (mean 215, SE = 22.38) nests for *sinensi*s and *carbo*, respectively (Figure 3). In Østfold the nests are situated in trees on islands, and in Rogaland the first colony established was in trees by a lake. Otherwise, all nests in the other sinensis colonies are on the ground.

The breeding population of *sinensis* increased from 10 pairs in 1996 to 2500 pairs in 2012, whereas *carbo* increased from 21,000 pairs in the early 1980s to a maximum of 27,000 pairs in 1995, and then decreased to 19,000 pairs around 2012−14 (Table 2). These trends are mirrored in the results from the national monitoring programme for breeding seabirds (Figure 4, Table 3).

Although the breeding population of *sinensis* along the southern coast increased (Figure 4, Table 3), the annual rate of change in 2005−2015 was only half of that during the first ten years after the establishment in 1996. The *carbo* populations along the coast between Central Norway and the Lofoten Islands were more or less stable in 1980−2015 (Table 3), despite a significant decrease in 2006−2015. In Finnmark, the population increased significantly from 1980 to 2015, but was stable in the period 2006−2015 (Figure 4, Table 3).

Reproductive performance and phenology

Mean annual clutch sizes at Rauna (*sinensis*) differed between years (Figure 5, One-way ANOVA $F_{9,2020}$ = 8.15, P < 0.001) with an overall mean of 2.78 and 3.33 when including and excluding empty nests, respectively (Table 4). Clutches (including empty nests) were largest in 2015 and 2016 with a mean number of 3.35 eggs (SE = 0.07, n = 264, and SE = 0.09, n = 254, respectively) and smallest in 2014 (mean 2.01, SE = 0.11, n = 253) (Figure 5).

The mean numbers of chicks produced annually per nest at Rauna (*sinensis*) ranged between 1.25 in 2008 and 2.30 in 2015, with a mean of 1.80 (SE = 0.113, n = 9) (Figure 5).

The clutch size at Røst (*carbo*) at the first visit (mean 22 June) ranged between 0−5 eggs and differed between years (One-way ANOVA $F_{14,957}$ = 9.31, P < 0.001) with an overall mean of 2.40 and 2.77 when

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including and excluding empty nests, respectively. Clutches (including empty nests) were largest in 2013 (mean 3.00, SE = 0.149, n = 36) and smallest in 2014 (mean 0.85, SE = 0.177, n = 41). These years were also the extremes with respect to proportion of empty nests (3% and 61% respectively), which was negatively correlated with mean clutch size in the nests with contents (Pearson $r = -0.605$, $P = 0.017$, n = 15).

At the first visit each year at Røst, hatching had occurred in an average of 46% (SE = 1.7, range 3−88%) of the nests with contents. As expected, the proportion hatched increased significantly with mean visit date ($F_{1,13} = 15.7$, $P = 0.002$), and the coefficient of this relationship (2.7%) indicated the overall midpoint of hatching was on 23 June and that egg-laying thus peaked in the last week of May. The proportion of nests hatched correlated negatively with clutch size (Pearson $r = -0.593$, $P = 0.020$, n = 15). There was also a significant decrease in clutch size with date of visit (Pearson $r = -0.656$, $P = 0.008$, n = 15), indicating that true clutch size was ≥ 3 eggs (Figure 6).

Although the Røst population also decreased significantly (by 9.2% p.a.) in 2005−2015 (ANOVA on log-linear regression $F_{1,13} = 12.12$, $P = 0.007$), we found no effects of population size on clutch size or the proportions of empty nests and clutches hatched at first visit (Pearson correlations, all $p \geq 0.531$, n = 15). Nor were there any apparent temporal trends in these three parameters of reproductive performance (linear regressions, all $p \geq 0.535$, n = 15).

Diet

Great Cormorant diet was collected at seven different sites along the coast of Norway (Figure 1). One site, Øra in the Skagerrak was occupied by *sinensis*, whereas all the others were used by *carbo*. Fish made up the greatest majority of the taxa identified in the pellets and regurgitations with representatives from 25 families and including 44 identified to species (Table 5). Unidentified gadoids and Cod were the most common prey of *carbo* whereas inshore species such as Corkwing Wrasse *Symphodus melops*, Rockcook *Centrolabrus exoletus*, Goldsinny Wrasse *Ctenolabrus rupestris* and Black Goby *Gobius niger* were the most common caught in the Skagerrak by *sinensis*. The four fish species most commonly caught at Øra were all inhabitants of shallow, coastal/littoral waters. Not all the studies presented diet items other than fish, but in those that did, polychaetes, crabs and molluscs were among the commonest items (Table 5).

Most fish species caught had mean or median lengths of ca. 100—150 mm, although several of the Gadidae species were longer (200—250 mm) with maxima approaching 500 mm (Table 6). The gadoids represented age classes up to 5 years (Cod and Saithe *Pollachius virens*), but the majority of

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fish were 1−2 years old (Barrett *et al*. 1990, Johansen *et al*. 1999). At Sula, the majority were, on average, even younger (1-year-old Saithe and 0-year-old Cod) (Lorentsen *et al*. 2004). Longest of all were the European Eels *Anguilla anguilla* caught by *sinensis* breeding at Øra with means of 350—450 mm and a maximum of 657 mm (Sørensen 2012).

DISCUSSION

Distribution, colony sizes, and population trends

Colonies of *sinensis* are currently found along the coast from Østfold near the Swedish border to Rogaland (southwestern Norway). The largest colonies, comprising 80% of the Norwegian breeding population, are located in the eastern part of the Skagerrak where the first colonies were established in the late 1990s. On the northern limit of the range, Rogaland holds 20% of the nests. Most of the nests are situated on the ground on small islands along the coast. Despite the absence of cormorant colonies along the central coast of western Norway, the plumage characteristics of birds in the two small colonies in Hordaland, close to the northernmost *sinensis* colonies, indicate that they are *carbo* (S. Byrkjeland pers. comm.).

In 2015, *sinensis* bred in 14 colonies. The largest colony, founded in 1997, had 968 nests (40% of the national population) and was located at Øra in Østfold, close to the Swedish border. This colony was three times larger than the second largest *sinensis* colony (302 pairs). Six colonies (43%) contained fewer than 100 nests, comprising only 12% of the total population. The *sinensis* population increased steadily during the first 8−10 years following establishment. After that, the population size has more or less stabilised around 2500 pairs.

It is challenging to monitor the population of *carbo* in Norway. The breeding locations are dispersed among 150−200 localities, most of which are isolated islets and cliffs difficult to access. Today, the majority of *carbo* in Norway breed along the shallow shelf seas off central Norway and northwards to the Lofoten islands. Along the coast of Trøndelag and Helgeland in Central Norway, these colonies are located on small islets in the outer archipelago and some of them contain up to a few thousand nests each. Further north, most colonies are smaller and some are on low-lying islands in the fjords whereas others were on cliffs facing the sea, either on the mainland or small islets in the outer archipelago.

In 2015, Norway had an estimated breeding population of 19,000 pairs of *carbo*, slightly fewer than in the previous years. The largest of the 126 extant colonies held 1297 nests, and was situated in Nordland County. Long-term monitoring (from 1980) of the *carbo* population showed a relatively stable population along the coast from central Norway to the Lofoten islands, although there was a decrease over the last ten years (2006−2015). The reason for the recent decrease is unknown, but may have been caused by a number of factors including a growing population of White-tailed Eagles *Haliaeetus albicilla*, disturbance from salmon farming, and disturbance from boat traffic. When the colonies are approached, the adults fly off, leaving the colonies open for predation by large gulls and eagles. In Finnmark, where eagle numbers has been lower, the long-term trends of cormorants have been more positive with an increase in numbers followed by a stabilisation in 2006−2015.

We are not aware of any major shifts in abundance of gadoid fish, their main prey along the Norwegian coast, that can explain these trends. For other coastal species such as European Shags *Phalacrocorax aristotelis* and Eiders *Somateria mollissima* the most recent decadal trends have also been negative in most areas. Similarly, numbers of Herring Gulls *Larus argentatus* and Great Black-backed Gulls *L. marinus* have declined in most of the sites regularly monitored, both over the last 10 years (Anker-Nilssen *et al.* 2016) and in a longer-term perspective (Fauchald *et al.* 2015). In general, both cormorant species have done better that most other coastal seabirds in this area over the last 30 years (Fauchald *et al.* 2015). The reproduction and population dynamics of European Shags seem however largely to be driven by the abundance of young saithe (Bustnes *et al.* 2013, Lorentsen *et al.* 2014), which have their main nursery grounds in the kelp forest along the Norwegian Sea coast. As shown here, the diet of Great Cormorants was much more diverse, but the bell-shaped population trends in Central Norway (Figures 4B and 4D) may reflect some of the parallel trend in the NEA saithe stock, even if the trend in saithe recruitment has been less evident (ICES 2016).

Clutch size and phenology

Clutch sizes and chick production observed at Rauna (*sinensis*) showed considerable variation. The causes of this variation are unknown, partly because food samples collected within the colony still need to be analysed.

Reproductive performance data for the nominate subspecies were also limited to one colony, which, in addition, was relatively small and located in a rather extreme site, the Røst archipelago. Being separated from the rest of the Lofoten Islands by 21 km of open water (to Værøy) and from the mainland by the > 80 km wide Vestfjorden, Røst is by far the most offshore archipelago in mainland Norway and surrounded by waters far too deep for the cormorants to forage. The population was therefore restricted to the archipelago throughout the main breeding period. This is a shallow and exposed, oval-shaped ca. 20 × 10 km area characterised by rich kelp forests, especially in the northwest where the cormorants breed. To what extent this is a representative foraging habitat for *carbo* is unknown, and it is therefore an open question if their clutch size and timing of reproduction is a useful indicator of the species' breeding performance elsewhere in Norway. Ongoing analyses of pellets collected annually at Røst since 2008 will hopefully help assess this in more detail. Nevertheless, as at most other *carbo* colonies along the Norwegian Sea coast, the Røst population also declined significantly in 2005−2015. The apparent lack of a relationship between breeding performance and breeding numbers at Røst suggests, however, that food abundance in the breeding season was not the main driver of the downward population trend, at least not in that population.

The species was seemingly absent at Røst during most of the second half of the 20th century before one colony was discovered in 1997, but it may well have been overlooked given the very rugged waters in which they breed today, where navigating without a detailed GPS map is extremely hazardous. It was reported to breed in Røst in 1897, but was then claimed to nest on inaccessible ledges high up in the bird cliffs (Aarvak 1993), a strikingly different habitat than they use at Røst today but more similar to that presently used by some populations in Finnmark.

Clutch size around hatching was certainly much lower than Løvenskiold's (1947) and Haftorn's (1971) conclusion that Great Cormorants normally lay 4−5 eggs, but they provide no information for that statement. Røv (1984) documented however clutch sizes of 1−6 eggs in colonies of *carbo* at Sklinna in Central Norway in 1983 and 1984 with means of 3.2 and 3.6 eggs, respectively (Table 4). This is close to that documented here for *sinensis* on Rauna, and not far from what we also expect was the actual clutch size for *carbo* in Røst where nest inspections were usually made much closer to hatching than egg laying. Røv estimated peak laying at Sklinna to be in mid-May, slightly earlier than that found for Røst (last week of May)

Diet

Great Cormorants are inshore feeders generally diving to 10 m in search of prey (Cramp *et al.* 1977). The great variety of food items documented along the Norwegian coast reflected the opportunistic feeding habits of the species (Leopold *et al*. 1998, Boström *et al*. 2012). Despite the many biases inherent in the use of pellets and regurgitations in such studies (Barrett *et al*. 2007), it is clear that

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gadoids such as Cod and Saithe were the most commonly recorded prey fishes taken by the Norwegian birds sampled with one or both of these species being recorded at all seven sites. Furthermore, the young age-classes of all gadoids they had eaten reflected the summer near-coast distribution of the youngest fish of both species in shallow water habitats, often among the kelp forests (Bergstad *et al*. 1987, Fosså 1995). Two studies (Skarprud 2003 and Sørensen 2012) on *sinensis* were from the same locality with an 11-year interval, whereas Johansen *et al*. (1999) and Lorentsen *et al.* (2004) were 2−3 year studies of *carbo* at single sites. In all cases, there were small temporal changes in diet composition, possibly explained by local changes in fish availability and reflecting the opportunistic habits of the Great Cormorant (Lehikoinen 2005). There was also an apparent differentiation of diet between the two subspecies, with *carbo* feeding on species typical of the open sea whereas *sinensis* fed on more inshore species including several species in the wrasse family Labridae. The inclusion of European Perch and Black Goby also suggested occasional foraging by the Øra birds in freshwater systems and estuaries, habitats that in other countries are typical for the *sinensis* subspecies (Boström *et al*. 2012). Thus, these differences likely represented fish availability in the feeding areas close to the colonies. Summer feeding near the outlets of rivers and streams has also been observed on the western part of the Skagerrak coast (TAN pers. obs.), even if the breeding colonies there are located at some of the most offshore islets (where the traffic of small boats is minimal).

Great Cormorants are capable of catching and ingesting large fish (e.g. Cod up to 450 mm, Table 3), however, the majority of the prey caught in Norway were in the range of 100−150 mm long, thus representing young stages of many species. The catch of a 657 mm European Eel at Øra (Sørensen 2012) is a new Norwegian record of the longest fish caught by a Great Cormorant. The previous one was an eel of 550 mm (Lorentsen *et al*. 2004).

There is no conclusive evidence that, except perhaps in years of very low fish recruitment, Great Cormorants prey on sufficient numbers of commercially important fish for them to be regarded as a pest in Norway (Barrett *et al*. 1990). However, because very large numbers of 1−3-year old gadoids may be caught over the course of a year, Great Cormorants in Norway may have local effects on fish mortality rates (Barrett *et al*. 1990, Johansen *et al*. 1999). Norwegian studies thus corroborate others that have shown that Great Cormorants may be an important source of mortality of juvenile fish, especially in years with low fish recruitment (Leopold *et al*. 1998). Knowledge of the impact of the fish mortality caused by cormorants, compared to other natural mortality factors (predation by larger fish, disease, food shortage), on the recruitment to the spawning stock is, however, lacking. Furthermore, and in their favour, Great Cormorants may act as good sentinels of fish occurrence in inshore waters where traditional fisheries surveys often fail due to the shallowness of the water and complexities of the biotopes (Lorentsen *et al*. 2004, Lorentsen et al. submitted).

In many parts of the world, attempts have been made over many decades to increase fish stocks through stock enhancement and sea-ranching programmes (Bartley 1999, Svåsand *et al*. 2000). In Norway, small artificially reared Cod have been released in five areas of coastal waters, and finds of tags used to mark the fish in Great Cormorant roosts, plus studies of regurgitated pellets, suggested that cormorants consumed millions of small Cod with consequential negative effects on the result of the experiments (Svåsand *et al*. 2000). For example, in Øygarden in SW Norway, several thousand tags (constituting 4.5% of the released cod) were found on a roosting site for Great Cormorants and European Shags (Otterå *et al*. 1999). Furthermore, during the first years of sea-based salmon farming in Norway there were reports of predation by Great Cormorants, but these problems now seem to have disappeared due to better enclosures to protect the fish.

Final remarks

Great Cormorants of the subspecies *carbo* nested from Sør-Trøndelag (Figure 1) and northwards until 2005 when the breeding range extended southwards with a colony becoming established in Møre og Romsdal and later (2011) in Hordaland. We know very little about the ancient distribution of great Cormorants in Norway. Thus, whether *carbo* have previously bred in current *sinensis* areas is unknown. When *sinensis* became established in Norway, the first colony was found in Rogaland in 1996 and then in Østfold in 1997. These colonies are at the opposite ends of the current distribution range. The Østfold colony has increased, as has all the eastern component of the population, whereas the western component is still quite small. With the current southwards expansion of the *carbo* population, the two subspecies may soon overlap extensively in SW Norway, with a greater potential for interbreeding. This should call for an extended monitoring of population dynamics and feeding niche of Great Cormorants in this area.

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Table 1. Overview of analysed diet samples from Great Cormorants in Norway. The samples collected during June-July were from breeding colonies, whereas those collected at other times of the year were from roosts.

Subspecies	**Locality**	**Date**	**Adult/chick**	**No. of samples**	**No. of food items**	**Source**
P. c. sinensis	Øra, Fredrikstad	June−July 2002	Adult/chick	240 pellets + 273 regurgitated fish	6716 otoliths + 273 fish	Skarprud 2003
	Øra, Fredrikstad	June−July 2011	Adult/chick	211 pellets + 79 regurgitated fish	6612 otoliths	Sørensen 2012
P. c. carbo	Hovsflesa, Lofoten	July 1985 & 1986	Adult/chick	17 & 21 pellets	762 items	Barrett *et al*. 1990
	Munkholmen, Sør-Trøndelag	Sep−Oct 1986	Adult	16 pellets	177 items	Barrett *et al*. 1990
	Vikna, Nord-Trøndelag	July 1987	Adult/chick	13 pellets	142 items	Barrett *et al*. 1990
	Sør-Varanger	July 1989	Adult/chick	Ca 30 pellets	534 items	Barrett *et al*. 1990
	Sørfjord, Troms	Jan−Mar 1996 Oct 1996−Mar 1997	Adult	135 pellets (of 270 collected)	610 items	Johansen 1998, Johansen *et al*. 1999
	Sula, Sør-Trøndelag	June−July 2001−2003	Adult/chick	378 chick regurgitations, 22 whole fish + 208 pellets	1013 items	Lorentsen *et al*. 2004

Table 2. Published total estimates of Norwegian breeding populations of Great Cormorant since the early 1980's.

Subspecies	**Year(s)**	**No. of pairs**	**Source**
P. c. sinensis	1996	10	Lorentsen 2014b
	2012	2500	Lorentsen 2014b
	2013	2653	Fauchald *et al.* 2015
P. c. carbo	1983−1986	21,000	Røv & Strann 1986
	1992	24,000	Debout *et al.* 1995
	1995	27,000	Røv 1997
	2000	25,000	Røv *et al.* 2003
	2012−2014	19,000	Lorentsen 2014a, Anker-Nilssen *et al.* 2015, Fauchald *et al.* 2015

Table 3. Population trends of Great Cormorants in different sections of the Norwegian coast (cf. Figure 4). The *P* values were calculated using Monte Carlo simulations. The trends for the last 10 years (2005–2015) are also indicated.

Area	**Subspecies**	**Time period**	**No. of years with data**	**Annual change (%)**	**Trend**	***P* value**
Skagerrak	*P. c. sinensis*	1997–2015	19	17.6	+	0.0001
		2005–2015	10	6.0	+	0.0175
Central Norway	*P. c. carbo*	1980–2015	36	−0.1	0 (−)	0.7028
		2005–2015	10	−7.7	-	0.0153
Central Norway − Lofoten	*P. c. carbo*	1980–2015	34	0.1	0 (+)	0.2974
		2005–2015	10	−7.3	0 (−)	0.0674
Lofoten−Finnmark	*P. c. carbo*	1980–2015	36	4.3	+	0.0002
		2005–2015	10	−1.4	0 (−)	0.2954

Table 4. Mean annual clutch size of Great Cormorants in three Norwegian colonies.

Colony	Subspecies	Time period	Sample	Mean	SE	n	Source
Rauna	*P. c. sinensis*	2008–2016	All nests	2.78	0.061	2020	This study
			Nest with contents	3.33	0.081	1688	This study
Sklinna	*P. c. carbo*	1983	Nest with contents	3.2	0.054	275	Røv 1984
		1984	Nest with contents	3.6	0.037	555	Røv 1984
Røst	*P. c. carbo*	2002–2016	All nests	2.40	0.039	972	This study
			Nest with contents	2.77	0.029	840	This study

Table 5. List of food items found in pellets and other regurgitates from Great Cormorant adults or chicks in Norway. **Bold type** indicates localities where the frequency of occurrence of a food item was > 50% in samples from in least one season, whereas *italics* indicates a frequency of occurrence of 15−20%. References: 1= Barrett *et al*. 1990, 2 = Lorentsen *et al*. 2004, 3 = Johansen *et al*. 1999, 4 = Skarprud 2003, 5 = Sørensen 2012.

Family/Higher taxon	Species/Genus group	Common name	Locality	Reference
Anguillidae	*Anguilla anguilla*	European Eel	Sula, *Øra*	2,4,5
Clupeidae	*Clupea harengus*	Atlantic Herring	Hovsflesa	1
	Sprattus sprattus	European Sprat	*Øra*	4,5
Cyprinidae	Unid.	cyprinids	Øra	4
	Rutilus rutilus	Roach	Øra	5
Salmonidae	*Salmo* sp.	salmonids	East Finnmark	1
	Salmo trutta	Sea Trout	Øra	4,5
	Coregonus lavaretus	European Whitefish	Øra	4
Osmeridae	*Mallotus villosus*	Capelin	East Finnmark	1
Belonidae	*Belone belone*	Garfish	Øra	5
Gadidae	Unid.	Gadoids	**Hovsflesa, Vikna,** Sula, Øra	1,2,4,5
	Gadus morhua	Atlantic Cod	**East Finnmark, Munkholmen**, **Sula, Sørfjord**, *Øra*	1,2,3,4
	Merlangius merlangus	Whiting	Øra	4,5
	Melanogrammus aeglefinus	Haddock	Hovsflesa, Munkholmen, Sørfjord	1,3
	Pollachius virens	Saithe	East Finnmark, Munkholmen, **Sula**, *Sørfjord*, Øra	1,2,3,4,5
	Pollachius pollachius	Pollock	Øra	5
	Raniceps raninus	Tadpole Fish	Øra	4,5
	Trisopterus sp.		Munkholmen	1
	Trisopterus esmarkii	Norway Pout	Sula	2
	Trisopterus minutus	Poor Cod	Sula	2
	Ciliata mustela	Five-bearded Rockling	Sula	2
Gasterosteidae	*Spinachia spinachia*	Fifteen-spined Stickleback	Sula	2
Ammodytidae	*Ammodytes* sp.	sandeels	East Finnmark	1
	Hyperoplus lanceolatus	Greater Sandeel	Sula	2
	Ammodytes tobianus	Common sandeel	Øra	5
Cottidae	Unid.	sculpins	Sula	2
Sebastidae	*Sebastes* sp.	redfish	Sørfjord	3
Cottidae	*Myoxocephalus scorpius*	Bull-rout	East Finnmark, *Hovsflesa*, Vikna, Sula, Sørfjord, Øra	1,2,4,5
	Taurulus bubalis	Long-spined Sea Scorpion	Øra	4,5
Cyclopteridae	*Cyclopterus lumpus*	Lumpsucker	Sula	2
Pholidae	*Pholis gunnellus*	Butterfish	Sula, Øra	2,4,5

Stichaeidae	*Chirolophis ascanii*	Yarrell's Blenny	Øra	4
Anarhichadidae	*Anarhichas lupus*	Atlantic Wolffish	Sula	2
Bothidae	Unid.		Sula	2
Scophthalmidae	*Zeugopterus punctatus*	Common Topknot	Sula, Øra	2,4,5
	Phrynorhombus norvegicus	Norwegian Topknot	Sula	2
Percidae	*Perca fluvialitis*	European Perch	Øra	4,5
Labridae	Unid.		Munkholmen, Sula, Øra	1,4,5
	Symphodus melops	Corkwing Wrasse	**Øra**	4,5
	Centrolabrus exoletus	Rock Cook	**Øra**	4,5
	Labrus mixtus	Cuckoo Wrasse	Øra	4,5
	Labrus bergylta	Ballan Wrasse	Øra	4,5
	Ctenolabrus rupestris	Goldsinny Wrasse	Sula, **Øra**	2,4,5
Zoarcidae	*Zoarces viviparus*	Eelpout	Sula, Øra	2,4,5
Callionymidae	*Callionymus lyra*	Dragonet	Øra	4,5
Gobidae	Unid.	gobies	Sula	2
	Gobius niger	Black Goby	**Øra**	4,5
Pleuronectidae	Unid.	flatfish	*Hovsflesa*, *Munkholmen*, Vikna, Sula, Øra	1,2,4,5
	Microstomus kitt	Lemon Sole	Sula	2
	Hippoglossoides platessoides	Long-rough Dab	Sula	2,5
	Pleuronectes platessa	Plaice	Øra	4,5
	Glyptocephalus cynoglossus	Witch	Øra	4,5
	Limanda limanda	Dab	Øra	4,5
	Platichtys flesus	Flounder	Øra	4,5
Soleidae	*Solea solea*	Common sole	Øra	4,5
Polychaeta		polychaetes	**Hovsflesa**, *Munkholmen*, Vikna, Sørfjord	1,3
	Lamellibranchia sp.	tubeworms	Hovsflesa, Munkholmen, *Vikna*	1
Isopoda		isopods	Hovsflesa	1
Decapoda	*Hyas* sp.	Hyas crabs	**Hovsflesa**	1
	Pagurus bernhardus	Hermit Crab	*Hovsflesa*	1
		Unid. crab	Hovsflesa, Munkholmen, *Vikna*	1
	Natantia	shrimps and prawns	Hovsflesa	1
	Chitonidae	chitons	Hovsflesa	1
Mollusca	Unid.	molluscs	Sørfjord	3
	Unid. Gastropoda	gastropods	***Hovsflesa*,** *Munkholmen*, Vikna	1
	Helcion pellucidum	Blue-rayed Limpet	*Hovsflesa*	1

Echinoidea	Unid.	sea urchins	*Hovsflesa*, *Vikna*, Sørfjord	1,3

Table 6. Mean size and range (in mm) of fish caught by Great Cormorants in Norwegian studies as determined from otolith lengths when N>20 fish. Where range is not indicated, the value is the median length of fish regurgitated in colony (N>20).

Great Cormorant subspecies	**Fish species**	**Mean/median (mm)**	**Approx. Range (mm)**	**Reference**
P. c. sinensis	*Anguilla anguilla*	335	130–520	Skarprud 2003
P. c. sinensis	*Anguilla anguilla*	449		Skarprud 2003
P. c. sinensis	*Anguilla anguilla*	373	200–650	Sørensen 2012
P. c. sinensis	*Sprattus sprattus*	71	40–90	Skarprud 2003
P. c. carbo	Gadoids	150–180	60–300	Barrett *et al*. 1990
P. c. carbo	Gadoids	69	20–350	Lorentsen *et al*. 2004
P. c. carbo	*Gadus morhua*	200–250	50–400	Johansen *et al*. 1999
P. c. carbo	*Gadus morhua*	134	30–490	Lorentsen *et al*. 2004
P. c. sinensis	*Gadus morhua*	227	20–460	Skarprud 2003
P. c. sinensis	*Gadus morhua*	60	20–450	Sørensen 2012
P. c. carbo	*Pollachius virens*	130–160	50–400	Johansen *et al*. 1999
P. c. carbo	*Pollachius virens*	198	60–500	Lorentsen *et al*. 2004
P. c. carbo	*Zoarces viviparus*	221	110–320	Lorentsen *et al*. 2004
P. c. sinensis	*Zoarces viviparus*	138	50–200	Sørensen 2012
P. c. carbo	*Pholis gunellus*	145	20–180	Lorentsen *et al*. 2004
P. c. sinensis	*Callionymus lyra*	135	50–200	Sørensen 2012
P. c. carbo	Ammodytes sp.	83	60–120	Barrett *et al*. 1990
P. c. carbo	*Myoxocephalus scorpius*	104	80–180	Barrett *et al*. 1990
P. c. carbo	*Myoxocephalus scorpius*	142	20–330	Lorentsen *et al*. 2004
P. c. sinensis	*Myoxocephalus scorpius*	139	40–210	Skarprud 2003
P. c. sinensis	*Myoxocephalus scorpius*	143		Skarprud 2003
P. c. sinensis	*Myoxocephalus scorpius*	116	50–200	Sørensen 2012
P. c. sinensis	*Taurulus bubalis*	100	50–150	Sørensen 2012
P. c. sinensis	*Gobius niger*	79	20–130	Skarprud 2003
P. c. sinensis	*Gobius niger*	109		Skarprud 2003
P. c. sinensis	*Gobius niger*	75	20–100	Sørensen 2012
P. c. sinensis	*Ctenolabrus rupestris*	96	40–130	Skarprud 2003
P. c. sinensis	*Ctenolabrus rupestris*	114		Skarprud 2003

P. c. sinensis	*Ctenolabrus rupestris*	92	50−150	Sørensen 2012
P. c. sinensis	*Centrolabrus exoletus*	107	60−150	Skarprud 2003
P. c. sinensis	*Symphodus melops*	117	60−190	Skarprud 2003
P. c. sinensis	*Symphodus melops*	149		Skarprud 2003
P. c. sinensis	*Symphodus melops*	116	50−200	Sørensen 2012
P. c. sinensis	*Pleuronectes platessa*	115	40−230	Skarprud 2003
P. c. sinensis	*Platychthys flesus*	126	20−210	Skarprud 2003
P. c. sinensis	*Platychthys flesus*	91	20−400	Sørensen 2012

Legends to figures

Figure 1. Map of Norway with colonies of the two subspecies of Great Cormorant, *P. c. sinensis* (open circles, n = 14) and *P. c. carbo* (filled circles, n = 117). The sizes of the circles indicate number of nests in the colonies around 2015. The stars indicate locations (n = 7) were diet samples have been collected and analysed.

Figure 2. Aerial photographs of typical Great Cormorant colonies in Norway. Top *P. c. sinensis* at Rauna (58°34'N 6°40'E), Vest-Agder (Photo: Rune Bergstrøm, 13 May 2012), and bottom *P. c. carbo* at Døssmannsskjæra (63°45'N 8°18'E), Sør-Trøndelag (Photo: Nils Røv, 25 June 2016).

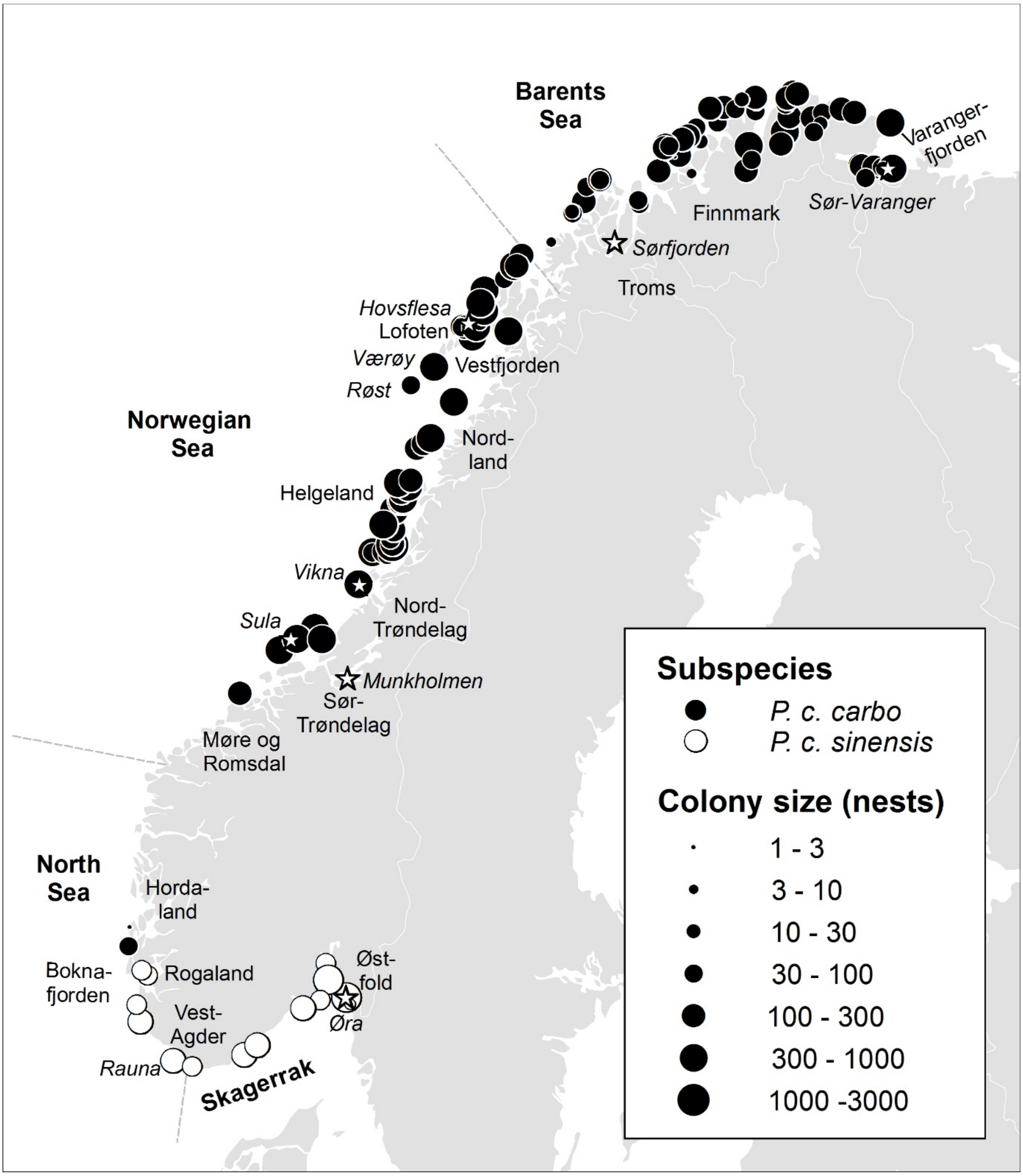
Figure 3. Size distribution of Great Cormorant colonies in Norway in 2005−2016. Left panel *P. c. sinensis*, and right panel *P. c. carbo*.

Figure 4. Population trends of Great Cormorant colonies, presented as population size in % of the overall mean, in different areas along the Norwegian coast since monitoring was initiated; A) Skagerrak coast (*P. c. sinensis*), B) Central Norway (*P. c. carbo*), C) from Central Norway to Lofoten, and D) Lofoten to East Finnmark. Names of the colonies monitored are indicated in each panel. Note the logarithmic scale of the y-axes.

Figure 5. Mean clutch sizes (solid black bars) and numbers of chicks fledged (grey bars) of Great Cormorants *P. c. sinensis* at Rauna in 2008−2016. The estimates also include empty nests.

Figure 6. Clutch size (mean ± 1 SE) of nominate Great Cormorants *P. c. carbo* at Røst at first nest inspection in different years (2002−2016, indicated) in relation to the proportion of nests (± 1 SE) where hatching had already occurred. Empty nests are not included. Sample sizes ranged from 16 (2014) to 107 (2008) with a mean of 56.

Figure 1.



Barents Sea
Varanger-fjorden
Finnmark
Sør-Varanger
Sørfjorden
Troms
Hovsflesa
Lofoten
Værøy
Vestfjorden
Røst
Norwegian Sea
Nord-land
Helgeland
Vikna
Nord-Trøndelag
Sula
Munkholmen
Sør-Trøndelag
Møre og Romsdal
North Sea
Horda-land
Bokna-fjorden
Rogaland
Øst-fold
Vest-Agder
Øra
Rauna
Skagerrak
Subspecies
P. c. carbo
P. c. sinensis
Colony size (nests)
1 - 3
3 - 10
10 - 30
30 - 100
100 - 300
300 - 1000
1000 -3000

Figure 2.

Figure 3.

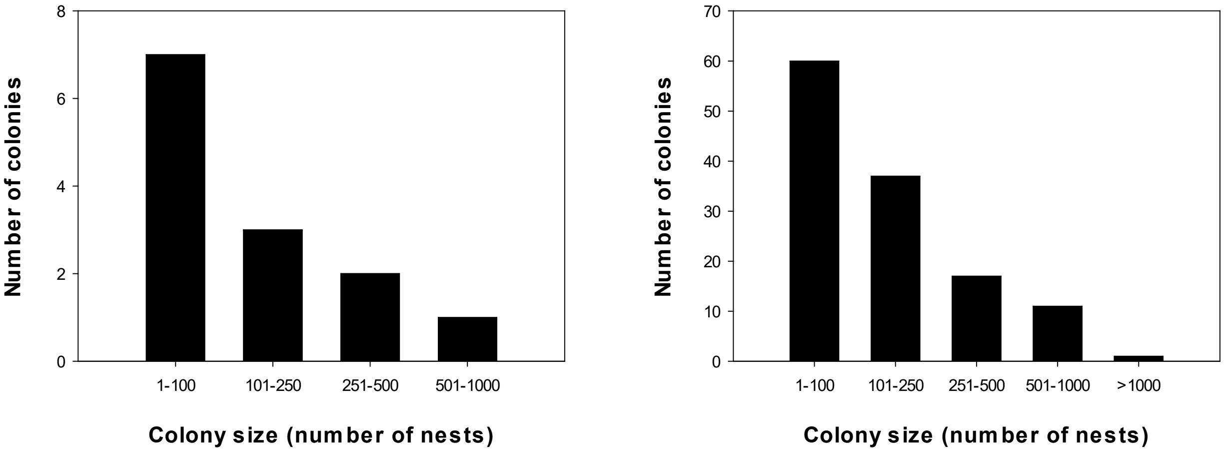

Number of colonies
8
6
4
2
0
1-100
101-250
251-500
501-1000
Colony size (number of nests)
Number of colonies
70
60
50
40
30
20
10
0
1-100
101-250
251-500
501-1000
>1000
Colony size (number of nests)

Figure 4

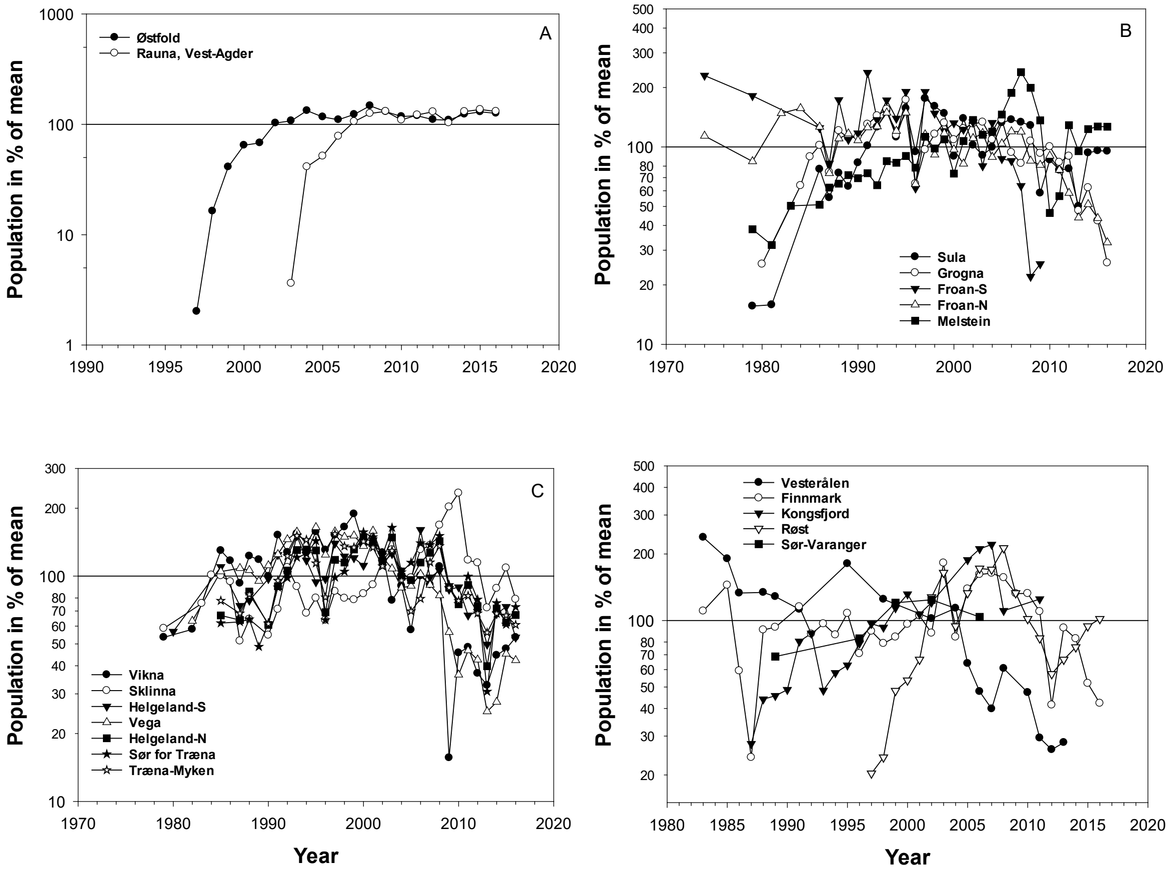
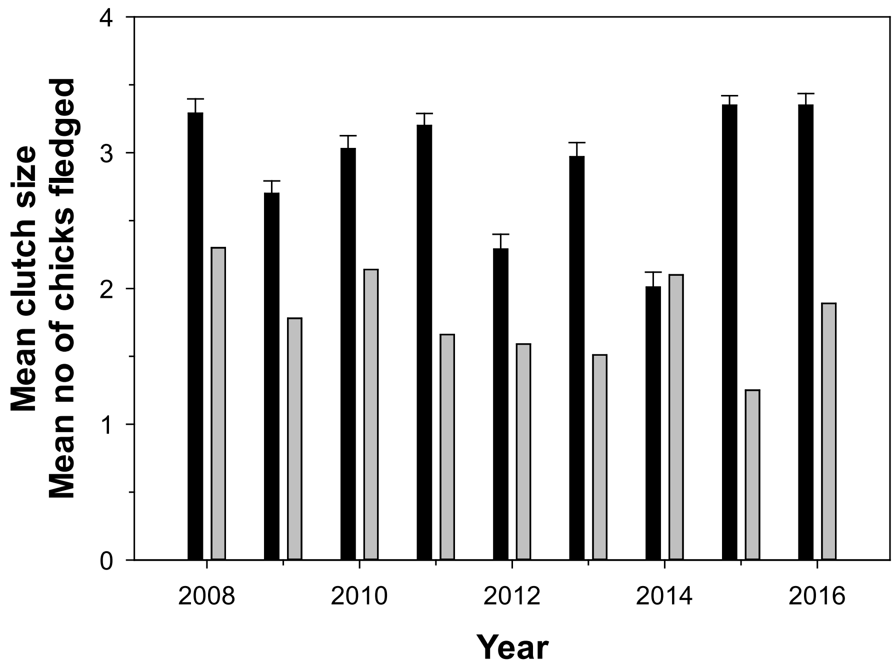
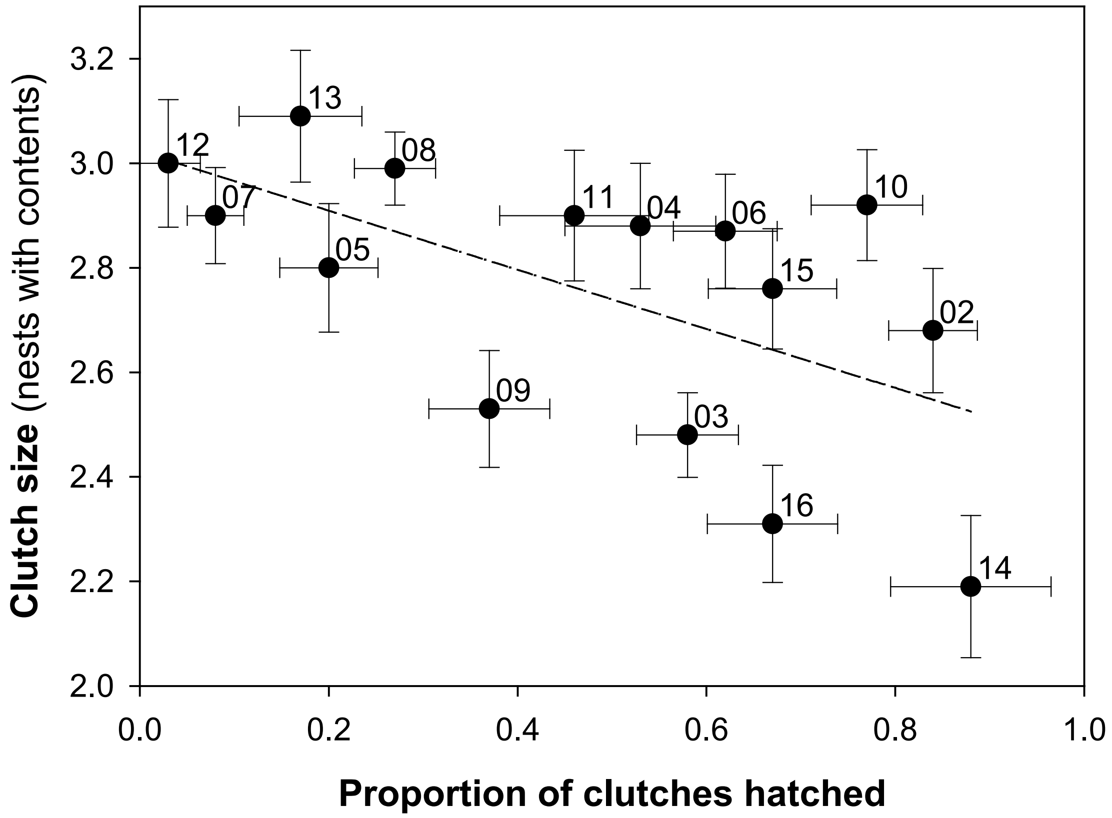

A
Østfold
Rauna, Vest-Agder
Population in % of mean
B
Sula
Grogna
Froan-S
Froan-N
Melstein
C
Vikna
Sklinna
Helgeland-S
Vega
Helgeland-N
Sør for Træna
Træna-Myken
Vesterålen
Finnmark
Kongsfjord
Røst
Sør-Varanger
Year

Figure 5.



Mean clutch size
Mean no of chicks fledged
4
3
2
1
0
2008
2010
2012
2014
2016
Year

Figure 6.



Clutch size (nests with contents)
Proportion of clutches hatched
3.2
3.0
2.8
2.6
2.4
2.2
2.0
0.0
0.2
0.4
0.6
0.8
1.0
12
13
08
07
05
11
04
06
10
15
02
09
03
16
14