

NORWEGIAN UNIVERSITY OF LIFE SCIENCES



Preface

This master thesis was undertaken at the Department of Ecology and Natural Resource Management at the Norwegian University of Life Sciences, in cooperation with the Norwegian Institute of Nature Research. This thesis made up the final 30 credits of my Masters of Science in Natural Resource Management.

I would firstly like to thank my supervisors, Svein-Håkon Lorentsen and Vidar Selås, for invaluable help, advice and encouragement in the process of collecting and analysing data, and while writing the thesis! Also, I would like to thank Torstein Pedersen for great help and advice on methodological issues, and for providing me with fish for otolith analyses. Thank you to Ronny Steen for supporting me on statistical analyses and writing, and to Rob Barrett for helping me with otolith identification. Thank you also to the Norwegian Directorate for Nature Management for financial support to the project. I would also like to thank my dear Tony for being so patient and for supporting me during this very intense year!

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Grethe Hillersøy

Abstract

Monitoring of seabirds is an important task due to large current environmental and ecosystem changes which have affected many species of seabirds severely through affecting their food supplies. Declines in food supplies for seabirds are often closely reflected in their reproductive effort and success. The diet of the European shag *Phalacrocorax aristotelis* has been extensively studied throughout its range. Sandeels *Ammodytidae* spp. and herring *Clupea harengus* comprise the main prey species during the breeding period in most areas. In Norway, however, fish from the Gadoid family are the main prey species together with sandeels. The colony of shags at Sklinna, central Norway, is the second largest colony in Norway. This colony has experienced large inter-annual changes in the size of breeding population (pairs) and other reproductive parameters, and it was hypothesized that this was reflected in the diet of the shags in this colony. Previous studies have suggested that saithe *Pollachius virens*, and particularly year class 1-saithe, may be of importance to the reproductive success of shags at Sklinna. Regurgitated pellets were collected from the colony during the main breeding period from 2007 to 2010. Any hard parts, such as otoliths and pharyngeal plates from fish, were separated out, and were used to identify prey items to the lowest possible taxonomic level. The length and width of otoliths were measured and used to estimate fish body length and mass. The diet of the shags at Sklinna was varied and was based on a minimum of seventeen different species of fish. Sandeels contributed little to the diet of the shags at Sklinna. Gadoid species including saithe, cod *Gadus morhua* and Poor cod *Trisopterus minutus* were the main prey species. Saithe dominated the diet by numerical frequency, biomass and frequency of occurrence in all study years. No apparent relationship was found between breeding parameters of the shags and the total amount of saithe in the diet. The breeding variables of the shags appeared to correlate positively with the abundance of year class 1-saithe in the diet. It was speculated that this year class may represent a more profitable prey size due to catchability, energy content, digestability, or a combination of these. However, a continued effort in surveying of both the breeding success and diet of the shags at Sklinna are vital to understand more about the dynamics between these parameters.

Key words: Shag • *Phalacrocorax aristotelis* • Diet • Saithe • *Pollachius virens* • Norway

Samandrag

Overvaking av sjøfugl er ei viktig oppgåve på grunn av store endringar i miljø og økosystem. Desse endringane har påverka mange artar av sjøfugl gjennom å redusere tilgangen på mat. Nedgang i mengda mat tilgjengeleg for sjøfugl er tett knytt til deira innsats og suksess i reproduksjon. Dietten for toppskarv *Phalacrocorax aristotelis* har vore studert utfyllande i store delar av sitt utbreiingsområde. Sil Ammodytidae spp. og sild *Clupea harengus* utgjer hovudføda i størstedelen av området. I Noreg derimot, er fisk frå torskefamilien Gadidae spp. hovudføda, saman med sil. Kolonien av skarv på Sklinna i midt-Noreg er den nest største kolonien i Noreg. Denne kolonien har gjennomgått store årlege variasjonar i storleik på hekkebestand (par) og andre reproduktive variablar, noko som kunne forventast å vera reflektert i dietten hos skarven. Tidlegare studiar indikerer at sei *Pollachius virens*, og spesielt årsklasse 1-sei, kan ha betyding for reproduksjonen til skarv på Sklinna. Oppgulpa pellets frå toppskarven vart samla inn frå denne kolonien i løpet av hovuddelen av hekkesesongen frå 2007 til 2010. Harde bestandsdelar, som øyrebein og svelgplater frå fisk, vart sortert ut og brukt til å identifisere byttedyr til lågast mogleg taksonomisk nivå. Lengde og breidde på øyrebeina vart målt og brukt til å estimere lengde og vekt for fisk i dietten. Toppskarvens diett var variert og bestod av minst sytten ulike artar av fisk. Sil bidrog lite til dietten for skarven på Sklinna. Torskefisk inkludert sei, torsk *Gadus morhua* og sypike *Trisopterus minutus*, utgjorde størstedelen av dietten for skarven på Sklinna. Sei dominerte dietten både i antal, biomasse og førekomst i prøvar gjennom heile studieperioden. Det vart ikkje funne nokon tydleg samanheng mellom ulike variablar for reproduksjon for skarv og total mengde sei i dietten. Reproduksjonen verka meir å korrelere positivt med mengda årsklasse 1-sei i dietten. Det vart foreslått at denne årsklassen kan vera av ein meir profitabel størrelse på grunn av fangst rate, energiinnhald, fordøyingsrate, eller ein kombinasjon av desse. Vidare studiar på både skarvens reproduksjon og diett er likevel nødvendige for å sikkert kunne fastslå ein samanhengen mellom reproduksjon og diett.

Nøkkelord: Toppskarv • *Phalacrocorax aristotelis* • Diett • Sei • *Pollachius virens* • Noreg

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Introduction

The marine environment is currently changing in a multitude of ways due to over-harvesting, pollution, habitat modifications and global climate change (e.g. Halpern *et al.* 2008). Many seabird species in the North and Norwegian Seas have, for instance, experienced large reductions in population size and breeding success during the last decades. This is probably due to the effects of reduced prey abundance caused by overfishing, but factors such as kelp harvesting, habitat alterations, and pollution might also be important (e.g. Tema Nord 2010). In this context, long-term monitoring of seabirds is important to survey population trends and, ultimately, to determine the possible causes of decline. Monitoring the diet of seabirds over extended periods of time is especially important as it may give indications of changes in the whole ecosystem, dietary needs for successful survival and breeding, and effects on seabirds of for example fisheries (Montevecchi & Myers 1996; Litzow *et al.* 2000; Barrett *et al.* 2007). Seabirds have also been suggested as natural samplers of the younger year classes of many commercially important fish species, which are often inaccessible to fisheries researchers for abundance estimates until the age of two to three years (Barrett 1991; Litzow *et al.* 2000; Anker-Nilssen 2005).

Seabirds are long-lived species adapted to feed on prey of highly variable abundances. Only large reductions in prey abundances may affect the population size of these birds. Small changes in prey abundance may be counteracted behaviorally by for example increased time spend feeding, while medium changes in prey abundances often result in reduced breeding efforts. (Furness 1996 and references therein). Food abundance during the breeding period is therefore normally closely reflected in seabird reproductive success (Barrett 2002). Variation in the numbers of adults breeding, laying date, clutch size, brood size, fledgling success, and subsequent recruitment of juveniles into the breeding population have been correlated to the abundance and availability of prey (Baird 1990; Pierotti & Annett 1990; Barrett 2002; Anker-Nilssen 2005; Velando *et al.* 2005; Kitayski *et al.* 2006). Understanding the relationship between seabird diet and their reproductive success is therefore important in order to identify the direct and indirect effects of environmental changes on different marine species.

The diet of many seabird species is studied by analyzing the content of regurgitated pellets from the birds. The pellets contain indigestible components of prey such as fish otoliths and bones, and their utilization for dietary studies have two benefits; it allows for the collection of

a large number of samples and is non-invasive to the birds. Many studies use otoliths to study the diet composition and to estimate the length and body mass of the fish eaten by the bird based on the length or width of the otoliths. A problem with this method is the partial digestion of hard parts in the intestine of the bird prior to regurgitation. This causes the otoliths, especially from small specimens, to be partially or fully digested before a pellet is produced (Jobling & Breiby 1986; Johnstone *et al.* 1990; Harris & Wanless 1993; Skarprud 2003; Mariano-Jelicich & Favero 2006). This may cause biased results concerning the abundance of prey species, and also cause underestimation of the size and body mass of the prey species. Nevertheless, the utilization of pellets to study diet does give a good minimum estimate of the main prey species, and is a useful method to compare dietary differences on a temporal, spatial or interspecific scale (Jobling & Breiby 1986; Barrett *et al.* 1990; Johnstone *et al.* 1990; Mariano-Jelicich & Favero 2006; Barrett *et al.* 2007).

A seabird that has been extensively studied with regard to diet is the European shag *Phalacrocorax aristotelis* (hereafter referred to as shag). The species exhibits a relatively narrow diet on a local scale with a few species dominating the diet, but does also show high plasticity in both feeding habitat and choice of prey species throughout its range (Barrett & Furness 1990; Barrett *et al.* 1990; Barrett 1991; Wanless *et al.* 1991a; Aebischer & Wanless 1992; Álvarez 1998; Grémillet *et al.* 1998; Velando & Freire 1999; Velando *et al.* 2005; Lilliendahl & Solmundsson 2006; Watanuki *et al.* 2008). The prey species composition may differ between closely situated colonies (<15 km) (Velando & Freire 1999) or change during the chick-rearing period depending on the abundance or availability of different prey species (Velando & Freire 1999; Wanless *et al.* 1998; Lilliendahl & Solmundsson 2006).

For shags, the diet consists of different fish species associated with kelp, sandy-bottom, and pelagic habitats (e.g. Cramp & Simmons 1977; Anker-Nilssen 2005; Watanuki *et al.* 2008). Sandeel Ammodytidae spp. and herring *Clupea harengus* are the main prey species during the breeding period in most areas studied (Harris & Wanless 1991; Aebischer & Wanless 1992; Álvarez 1998; Velando & Freire 1999; Velando *et al.* 2005; Lilliendahl & Solmundsson 2006). These species are of relatively high calorific value which is important to the breeding success of seabirds (Barrett *et al.* 1987; Kitaysky *et al.* 2006). Along the Norwegian coast, however, Gadoid species such as saithe *Pollachius virens* and cod *Gadus morhua* are important prey species during the breeding period, along with sandeels (Barrett & Furness 1990; Barrett *et al.* 1990; Barrett 1991).

The shag has been assumed to be less sensitive to small or moderate declines in prey abundance, due to factors such as large body size, ability to dive deep and to switch to alternative prey (Furness & Tasker 2000). However, several studies have demonstrated that the reproductive effort and success of shags correlate with the abundance or availability of its main prey (Aebischer 1986; Aebischer & Wanless 1992; Furness & Tasker 2000; Rindorf *et al.* 2000; Velando *et al.* 2005).

In two of the largest shag colonies in Norway, including Sklinna, some of the variation in laying date and clutch size could be explained by the occurrence of the two youngest year classes, particularly year class 1, of saithe, and the NAO-index (North Atlantic Oscillation) (Anker-Nilssen 2005). The NAO-index reflects climatic conditions and may thus have ecological effects. The link between the NAO-index and climate appears to be particularly strong along the Norwegian coast (Ottersen *et al.* 2001). The climatic parameters associated with varying NAO-indices affects for example the recruitment and growth of fish (Ottersen *et al.* 2001), and as such probably the fish populations upon which the shag feeds (Anker-Nilssen 2005). Anker-Nilsen (2005) demonstrated that the correlation between the abundance saithe and reproduction for shags was not as strong for the colony at Sklinna as the Røst colony (Anker-Nilssen 2005). However, the correlation was of an indirect nature where the abundance of year classes 0- and 1-saithe were back-calculated from the abundance of year class 2-saithe two years later on a regional scale. Another study on shags in Great Britain found that laying dates correlated with the abundance of herring in February, around the time when the birds decided whether to breed or not (Aebischer & Wanless 1992). Further, breeding parameters were not related to the estimated abundance of sandeels in the North Sea (Aebischer & Wanless 1992). A parallel dietary study found no herring in the diet of the shags from the same colony, neither during the winter, pre-breeding period or the breeding period (Harris & Wanless 1991). The main prey of the shags was sandeel, which possibly correlated with the abundance of herring through environmental factors (Harris & Wanless 1991). One should therefore be careful about linking breeding parameters with indirect estimates of putative prey species as environmental conditions may affect prey species similarly (Harris & Wanless 1991). Further, care should be taken when using abundance estimates on a regional scale as species abundances may differ on a local scale. Determining the diet composition of the shag at Sklinna is therefore an important step towards linking diet and breeding success directly.

The aims of this study were threefold. Firstly, to document the diet of the shags at Sklinna by analysing pellet content. Secondly, compare the dietary composition between years. And thirdly, to examine whether the changes in reproductive effort and success during the study years may be reflected in the diet. If saithe is indeed the main prey item in the diet, does there appear to be any correlation between the total amount of saithe, and specifically in the composition of year classes, and the reproduction of the shags.

Methods

Study site and species

Sklinna is a small, isolated archipelago in Nord-Trøndelag, central Norway (65°13'N 10°58'E) (Fig. 1). The topography of the archipelago consists of islands and shallow water areas of 10–20 m of depth, interspersed with deeper water. Sklinna is a seabird reserve and is also suggested as a Ramsar site.

Sklinna is one of the most important breeding colonies in Norway for the European shag (Røv 1994). This has also been one of the main sites for seabird population monitoring in Norway since the early 1980s (e.g. Lorentsen & Eriksen 2009). In 2007 the site also became a SEAPOP key-site (national monitoring) and the population monitoring of this species was extended to also cover adult survival, diet, clutch size, hatching success and chick survival. Pellets from the European shag have been collected at Sklinna since 2007. The population of European shag at Sklinna has increased since the onset of population surveys in the early 1980s to a current level of around 3000 breeding pairs (Røv & Nygård 2005). The main hatching period for the shags in this area is from the 10th to the 15th of June (Lorentsen, pers. comm.). The population has experienced large inter-annual differences in size of breeding population and breeding success during the years of survey (S.-H. Lorentsen unpubl. data). For example, the number of breeding pairs at Sklinna was reduced by 40% between 2008 and 2009, while 2007 and 2010 were of intermediate levels.



Fig. 1. Sklinna Archipelago, central Norway (•) (Modified from www.suzuki.no).

The species occurs throughout Europe and northern Africa. The birds breed in loosely associated colonies from 15 to a few thousand breeding pairs (Røv 1994). A clutch of 2-5 eggs is normally laid in May. Laying dates vary greatly between pairs (Potts *et al.* 1980; Røv 1994). Chicks are fledged at an age of about 50 days (Røv 1994; Velando & Freire 2003; Velando *et al.* 2005). During the breeding season the birds' feeding activities are restricted to the area surrounding the colony. The feeding radius during the period of chick rearing may reach a maximum of 25 km from the colony (S.-H. Lorentsen, pers. comm.), although feeding locations are normally closer to the colony (Wanless *et al.* 1991a; Velando & Freire 1999; Anker-Nilssen 2005).

Data collection

Approximately 20 fresh pellets were collected every 5-day period, throughout the main breeding seasons of 2007–2010 (5th June–19th July). Pellets were stored in a freezer prior to analysis. The pellets were then thawed, dissolved in a strong detergent solution and kept at 50°C in an oven for 1-2 days. Hard parts, mainly otoliths from fish, but also other fish bones, pharyngeal teeth from Labridae spp., mouth parts from polychaetes, squid beaks or hard parts from crustaceans, were then separated out by using a sieve and tweezers. The hard parts from each pellet were dried and stored in glass jars until further analysis.

Otoliths were sorted in pairs based on matching sides (left/right), length and/or width ($\pm 0,2$ mm), and wear class (degree of erosion). These were identified to the lowest possible taxonomic level using Härkönen (1986), Leopold *et al.* (version 1.0) and a reference collection. The length and width of each otolith was measured to the nearest 0.1 millimeter by using a stereomicroscope and millimeter paper. The minimum length required to distinguish different species from the Gadidae family was set to 3 mm. This lower limit was based upon comparisons of otoliths of decreasing size from cod and saithe, the two dominant species from the Gadidae family present in the samples, to determine at which size the otoliths from the two species started to differentiate in shape. All otoliths with a length below this limit from this family were automatically recorded as Gadidae species. A sub-sample was taken of the otoliths in pellets with more than 40 otoliths from the Gadidae or year class 0-saithe groups. The subsample constituted 10–50% of the total number of otoliths of that specific size group, with a minimum of 20 otoliths. The otoliths in the subsample were paired and measured, and the relationship between the total number of otoliths and individuals (based upon the pairing of otoliths) and the mean length and width was extrapolated to the total number of otoliths of

that specific size group in that specific pellet. The length of broken otoliths were estimated from its paired counterpart or, where not paired, from the mean width:length ratio from complete otoliths in all samples. Dietary differences between years were examined by comparing the numerical frequency, frequency of occurrence, or biomass (Table 1).

Table 1. The dietary composition of the European shag may be expressed in several parameters (Modified from Duffy & Jackson 1986).

Measurement	Explanation	Purpose
Numerical frequency	Relative numerical abundance of the total number of prey items	“Frequency of prey encounter”
Estimated biomass	Length and mass of the prey item estimated by measuring the length and width of otoliths	“Approximate nutritional contribution of similar prey to diet”
Frequency of occurrence	Proportion of pellets in which a prey taxon occurs	“Variability of prey abundance”

Estimating fish length and body mass

For the majority of the fish species the equations from Härkönen (1986) were used to calculate length and body mass from otolith length or width (Appendix 1). For saithe and cod, two different sets of equations for estimation of fish length exists (Härkönen 1986; Jobling & Breiby 1986). These two studies are based on fish from different geographical areas and cover different ranges of fish lengths, and have therefore concluded with somewhat different equations for estimating fish length. Data on otolith to fish length relationships for saithe and cod had been collected at Sklinna during the study period in 2010 using fish traps or angling equipment, and this was supplemented with similar data for fish from Finnmark, northern Norway (T. Pedersen 2010). Known otolith to fish length relationships from this material were compared with estimates made by use of the two sets of equations to find which of them were the most appropriate to use for the Sklinna-material. The equation from Jobling and Breiby (1986) estimated the fish length best for year class 0-saithe, and was therefore used for this year class (Fig. 2A). However, the equation from Härkönen (1986) estimated fish lengths for year class 1-saithe better, and was used for this age group and above. The fish length estimates using Jobling & Breiby (1986) corresponded well with the measured fish lengths for the total length range of cod and was therefore used for this species (Fig. 2B).

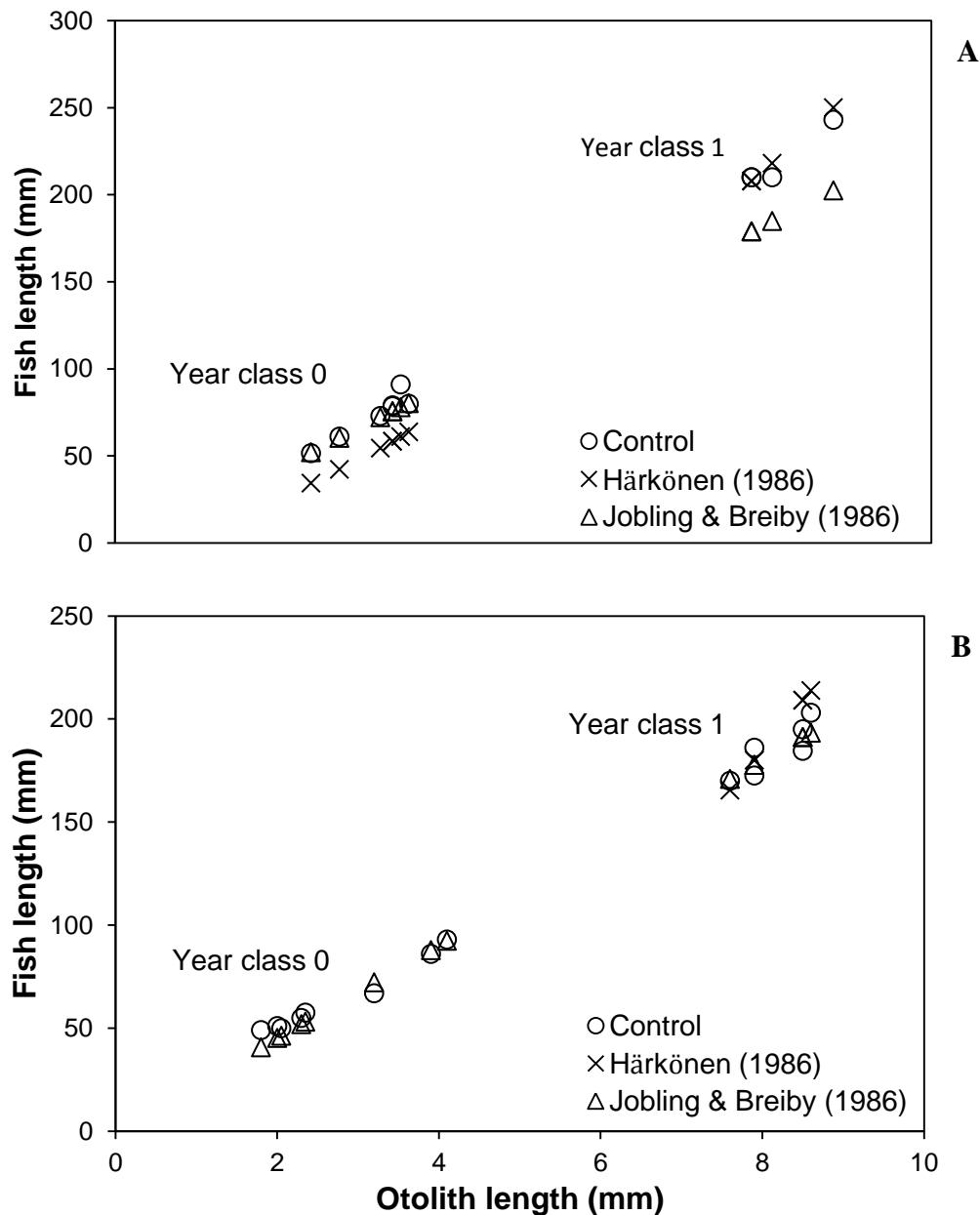


Fig. 2. Relationship between otolith length (mm) and fish length (mm) for (A) saithe from 2010, and (B) cod from 2005, 2006, 2008 and 2010, from Sklinna, central Norway, and Finnmark, northern Norway (Controls), and the relationships estimated using equations from Härkönen (1986) and Jobling & Breiby (1986). Note that estimates for year class 0 based on Härkönen (1986) is not shown as this resulted in estimated fish lengths of negative value.

In cases where taxonomic identification was possible only to family level, the fish lengths were estimated by combining the formulae from different putative species based on otolith similarity, occurrence in the study area, and occurrence within the diving range of shags (maximum depth of 40 meters - Wanless *et al.* 1991b) (Appendix 1).

Year classes

To assess the relative contribution of different year classes of saithe to the shag's diet, individual fish had to be assigned to distinct year classes. For several reasons, it is difficult to determine exact limits for fish body lengths between year classes (Johansen *et al.* 1999):

1. Variability in body lengths within a year class
2. Variability in body lengths between years due to environmental conditions
3. Overlap of body lengths between year classes

Using external sources to segregate the year classes, such as recorded fish body lengths by research trawls, also present several difficulties where estimated fish lengths may not correspond well with the measured fish length from these sources:

1. Erosion of otoliths in the digestive system of the bird causes a subsequent underestimation of original fish lengths and distributions (Jobling & Breiby 1986; Johnstone *et al.* 1990).
2. Available data on lengths at age-distributions often stem from fish caught in autumn or winter, and usually from areas other than the present study area (Bergstad *et al.* 1987; Barrett 1991; Johansen *et al.* 1999; Mehl *et al.* 2009).
3. Fish caught by piscivorous birds may cover the lower range of body length of the fish in year classes present in a particular area (Johansen *et al.* 1999).

One solution to these problems is to determine the age of individuals by counting the growth zones in the otoliths from the pellets (Johansen *et al.* 1999), but this is a very time consuming method. Therefore, the estimation of year classes for saithe in the present study was based on the size distribution of individual fish estimated from otoliths. The distribution showed marked peaks in body lengths of the fish, and these were assumed to represent different year classes, as was also done in previous studies (Barrett *et al.* 1990; Barrett 1991; Johansen *et al.* 1999; Mehl *et al.* 2009). As in these studies, the segregation line between the year classes were set at the approximate mid-point between peaks.

Statistical analysis

The data from pellets collected throughout the breeding season were pooled for each year prior to analysis. As saithe, and the different year classes of saithe, did not occur in each

pellet, there were two components of the total numbers or biomass; the number of fish or biomass per pellet where the object of analysis was indeed present, and the frequency of occurrence in pellets. Both categories were tested statistically to get an overall impression of the total number of fish or biomass of total saithe and for the specific year classes.

One-way ANOVA (Zar 2001) was used to test for differences in the number of fish per pellet between years for year classes 0 and 1. The data for year class 0-saithe was square root transformed to obtain homogeneity of variance (Levene statistics_{3,432}=2.3, p=0.08). The data for year class 1-saithe was transformed with log₁₀ to obtain homogeneity of variance (Levene statistics_{3,331}=1.3, p=0.3). The data on total saithe and year class 2-saithe could not be transformed to obtain homogeneity of variance (Levene statistics, p < 0.05), and Kruskal-Wallis statistics was used to analyse for overall differences in the number of fish per pellet, while pairwise Mann-Whitney U-tests were used to test for specific differences in the number of fish per pellet between years. A Bonferroni-correction (Dunn 1961) was performed to correct the p-level to multiple pairwise comparisons for the number of tests done (6) which reduced the significance-level of p to 0.0083 for the Mann-Whitney U-tests. All data analysed with parametric tests were normally distributed, or approximately so (Appendix 2).

The biomass per pellet may be affected by inter-annual in fish body mass for year classes (for example affected by the NAO). Differences in this was tested between years to see if any discrepancies in the results in number of fish and biomass per pellet were related to the differences in fish mass between years. Kruskal-Wallis and Mann-Whitney U-tests (Bonferroni corrected) were performed to test for overall and pairwise differences in fish body mass for the different year classes between years as these could not be transformed to obtain normal distributions (Levene statistics, p < 0.05).

One-way ANOVA was used to test for differences in biomass per pellet between years for total saithe and year class 1. The data for total saithe was square root transformed to obtain homogeneity of variance (Levene statistics_{3,489}=2.1, p=0.1), and year class 1 was transformed with log₁₀ (Levene statistics_{3,331}=2.3, p=0.08). Kruskal-Wallis tests were performed to test for overall differences in biomass per pellet for year classes 0 and 2, as these could not be transformed to obtain homogeneity of variance (Levene statistics, p < 0.05). Pairwise Mann-Whitney U-tests were used to test for specific differences in biomass per pellet between years (Bonferroni corrected).

Chi-square tests (Zar 2001) were used to analyse for overall differences in the frequency of occurrence of the different year classes between years. If significant result were detected ($p < 0.05$), pairwise Chi-square tests were performed between years to analyse for specific differences (Bonferroni-corrected). Chi-square tests were performed in Minitab 3.1 (2010). Other tests were performed using SPSS (PASW) Statistics 18.

Two different significance levels were used; 0.05, and 0.0083 when Bonferroni corrections were used. Where a critical p-value of 0.05 applied this was marked with † in the results, and where a critical p-value of 0.0083 applied this was marked with ††.

The number of fish and biomass per pellet were depicted using the mean \pm SE to be able to visually compare the different years and age classes. Non-parametric tests, however, are based on the median of the data as this data is not normally distributed. Results from non-parametric tests reported in the result section can therefore not be compared to the figures depicting the mean for same data. The median and range (range shown in parenthesis) are therefore reported for the test results in question.

Results

Dietary composition

A total of 19,041 individual prey items were identified from 28,199 otoliths, fish bones, pharyngeal teeth and polychaete mouth parts in 528 regurgitated pellets from the European shag colony at Sklinna, 2007–2010. Number of collected pellets was 79, 120, 140, and 189 in 2007, 2008, 2009, and 2010, respectively. At least seventeen different fish species and an unidentified species of polychaete were identified (Appendices 4–6; species-specific length measurements reported in Appendix 7).

The group ‘unidentified Gadidae’ mainly comprised otoliths with lengths less than 3 mm (fish body lengths < 40.4 mm) due to the uncertainty with identifying such small otoliths to species level. Saithe and cod were the only two Gadidae species identified to species level within range of body lengths for the year class 0-group (fish body lengths 40.4–120 mm.), comprising 99.8 and 0.2% of the total number of individual otoliths in this size group, respectively. Assuming that this distribution is similar for the unidentified Gadidae-group, this group would mostly be made up by year class 0-saithe. This assumption is strengthened by

the changes in distribution of unidentified Gadidae and year class 0-saithe throughout the breeding season of the shags, where the number of correctly identified saithe increased during the season (Appendix 3). This is probably due to the fact that year class 0-saithe grows above the identification limit (3 mm otolith length, 40.4 mm body length) during the study season. Thus, the otoliths from unidentified Gadidae (otolith length < 3 mm) were included in the year class 0-saithe group in the analyses.

Saithe dominated the diet in numerical frequency, biomass and frequency of occurrence in all four study years. Saithe contributed 69.7–91.7% of the total number of individuals (Fig. 3A, Appendix 4), and 61.6–88.2% of the total biomass (Fig. 3B, Appendix 5). Saithe was present in 92.5–94.2 % of the pellets (Table 2).

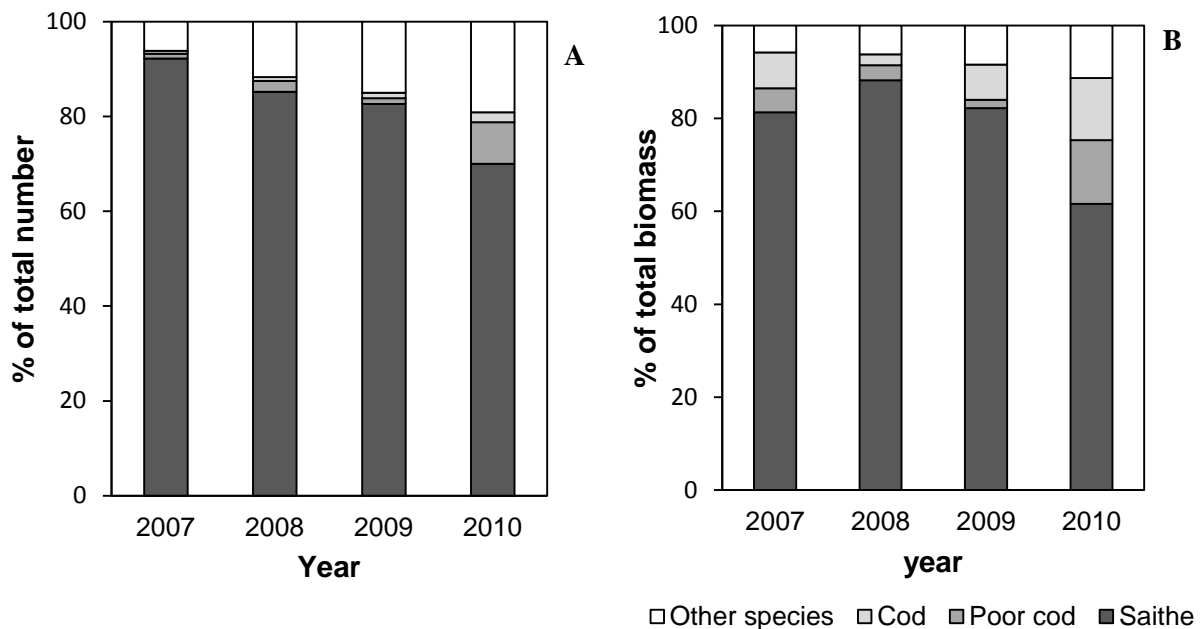


Fig. 3. Percentage contribution to (A) total number of individual prey items and (B) total biomass, for some prey species in pellets from the European shag at Sklinna, central Norway, 2007–2010. Exact values are given in Appendices 4–5.

Table 2. Frequency of occurrence for some prey species in pellets from European shag at Sklinna, central Norway, 2007–2010. Complete information for all identified species is shown in Appendix 6.

Species/Family	2007		2008		2009		2010	
	N	%	N	%	N	%	N	%
Saithe <i>Pollachius virens</i>	74	93.7	111	92.5	130	92.9	178	94.2
Poor cod <i>Trisopterus minutus</i>	8	10.1	15	12.5	17	12.1	63	33.3
Cod <i>Gadus morhua</i>	12	15.2	20	16.7	36	25.7	93	49.2
Ammodytidae spp.	6	7.6	11	9.2	17	12.1	23	12.2
Total number of pellets	79		120		140		189	

Poor cod *Trisopterus minutus* and cod contributed little to the overall diet of the shag in 2007–2009, but more in 2010, with 8.8 and 2.1% of the numerical frequency, respectively (Fig. 3A, Appendix 4) The contribution of these two species to the total biomass also increased in 2010, as compared to previous years, with 13.7 and 13.4%, respectively (Fig. 3B, Appendix 5). Both poor cod and cod showed a marked increase in frequency of occurrence from 2007–2009 to 2010, to a frequency of occurrence of 33.3 and 49.2%, respectively (Table 2).

Sandeels (greater sandeel and unidentified Ammodytidae) contributed little to both numerical frequency and biomass with a total of 1 % or less in both categories in all years (Figure 3A–B, Appendix 4–5). Sandeels were present in about 10% of the pellets during the study period (Table 2).

Saithe in the diet of the shags

The size-frequency distribution of saithe in pellets from the shag at Sklinna showed a bimodal distribution which represented year classes 0 and 1 (Fig. 4). From this I assumed that fish smaller than 120 mm belonged to year class 0, fish between 120 and 250 mm belonged to year class 1, and fish longer than 250 mm belonged to year class 2+, and these groupings were used in the further analyses.

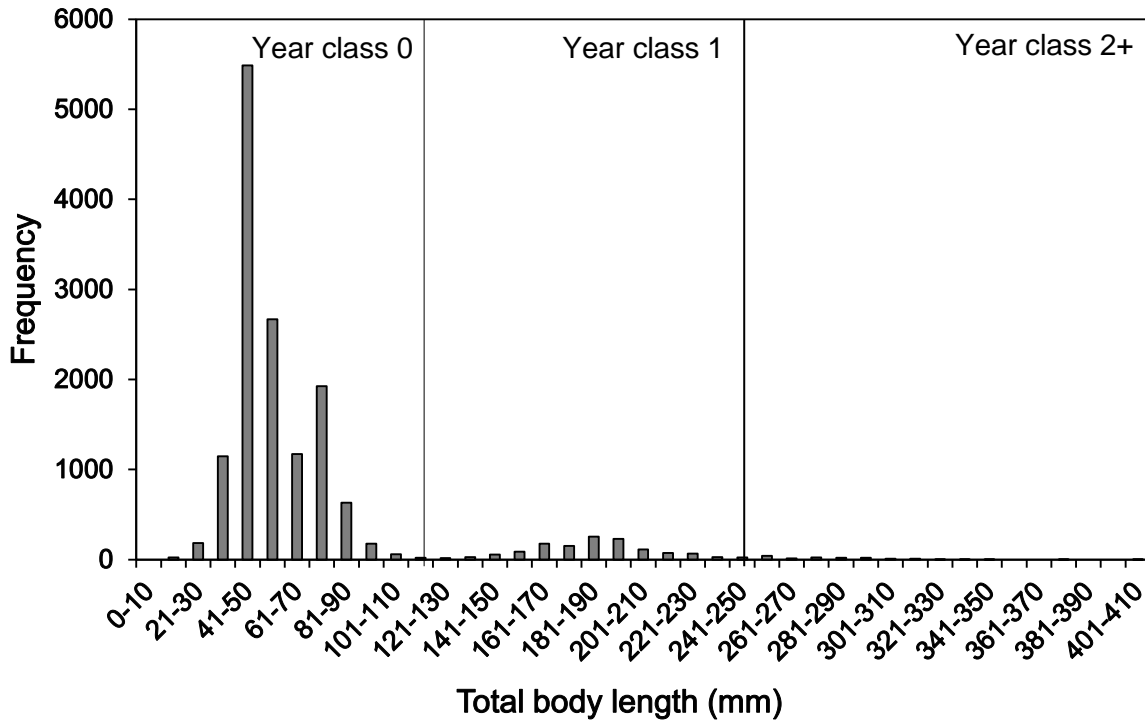


Fig. 4. Size-frequency distribution (total body length, mm) of saithe in pellets from European shag at Sklinna, central Norway, 2007–2010. Separations into year classes are shown.

Total saithe

Total number of saithe per pellet did not differ significantly between years (Kruskal-Wallis=3.2, df=3, $p=0.4\ddagger$). Biomass per pellet of total saithe was significantly different between years ($F_{3,489}=9$, $p < 0.001\ddagger$, Fig. 5). Specifically, biomass per pellet was significantly higher in 2008 as compared to 2007 and 2010 (Tukeys test for differences between groups; 2007-2008: $p < 0.001\ddagger$; 2008-2010: $p=0.002\ddagger$), and biomass per pellet was significantly higher in 2009 than in 2007 (Tukeys test for differences between groups; 2007-2009: $p=0.007\ddagger$). No significant differences were found between the other comparisons of years (Tukeys test for differences between groups; 2007-2010: $p=0.1\ddagger$; 2008-2009: $p=0.2\ddagger$; 2009-2010: $p=0.4\ddagger$). Also, the frequency of occurrence of saithe did not differ significantly between years ($\chi^2_3=0.4$, $p=0.9\ddagger$).

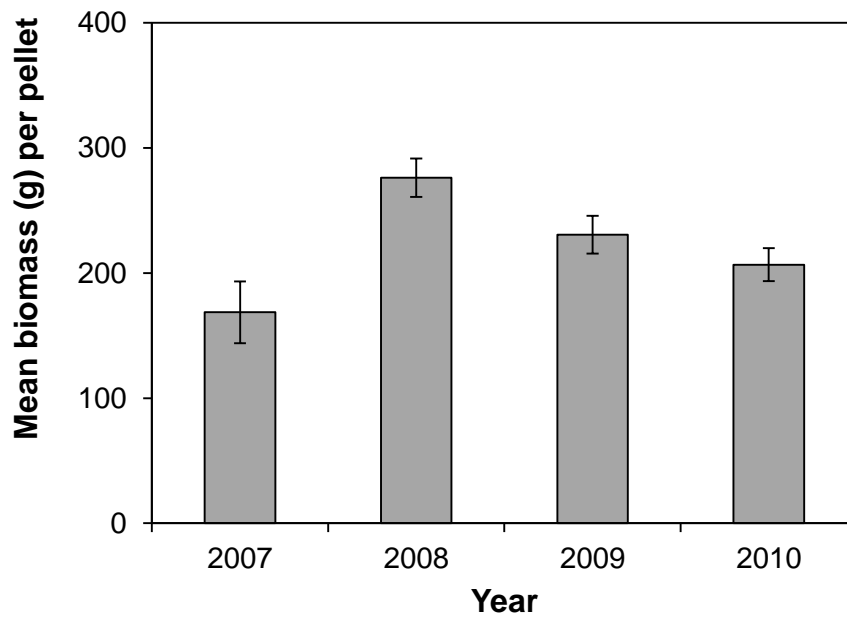


Fig. 5. Mean biomass \pm SE per pellet (g) for total saithe in pellets from European shag at Sklinna, central Norway, 2007–2010. Error bars represent SE.

Contribution of the different year classes

In all years, year class 0 dominated in percentage of total number of saithe, although the number of year class 1-saithe was more prominent in 2008 as compared to other years (Fig. 6A, Appendix 8).

In all years, year class 1 dominated in percentage of total biomass, except in 2009 when year class 2+ dominated (Fig. 6B, Appendix 8). Year class 1 contributed most to the biomass of saithe in 2008. Year class 0 contributed little to total biomass in all years.

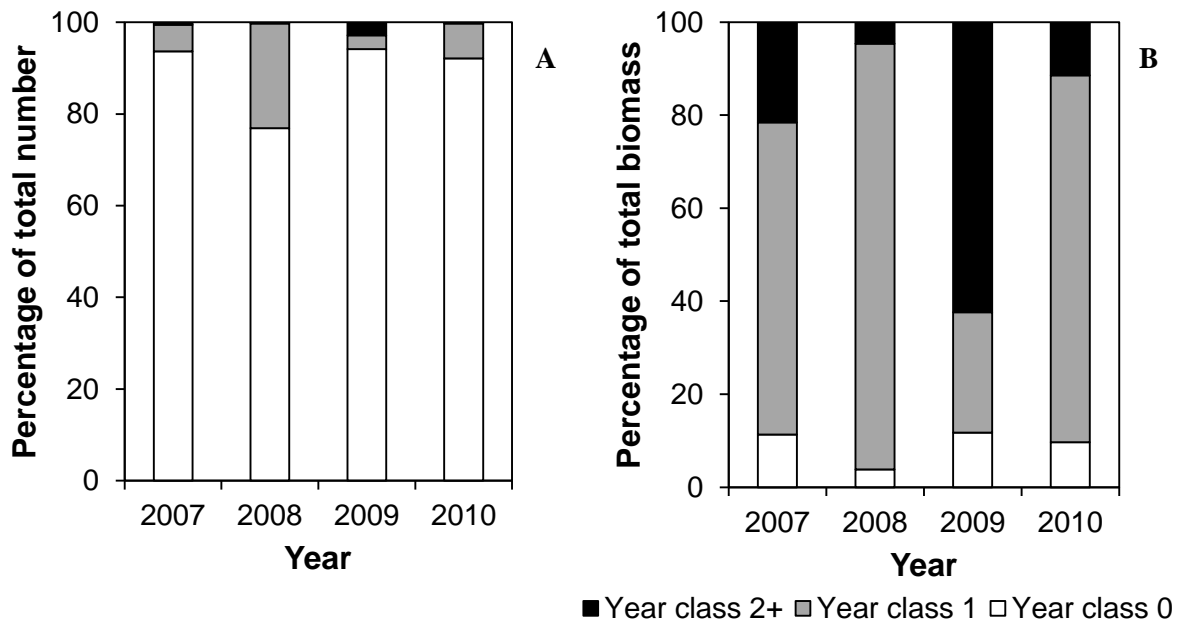


Fig. 6. Percentage contribution of year classes 0, 1 and 2+ of saithe to (A) the total number of saithe, and (B) the total biomass, in pellets from the European shag at Sklinna, central Norway, 2007–2010. Exact values are reported in Appendix 8.

Year class 0

Number of fish per pellet of year class 0 was significantly different between years ($F_{3, 432}=4.2$, $p=0.006^\dagger$, Fig. 7A). The number of fish per pellet of year class 0-saithe was significantly lower in 2008 as compared to all other years (Tukeys test for differences between groups; 2007-2008: $p=0.036^\dagger$; 2008-2009: $p=0.033^\dagger$, 2008-2010 $p=0.007^\dagger$), whereas no significant differences were found between the other comparisons of years (Tukeys test for differences between groups; 2007-2009: $p=0.99^\dagger$; 2007-2010: $p=0.98^\dagger$; 2009-2010: $p=0.98^\dagger$).

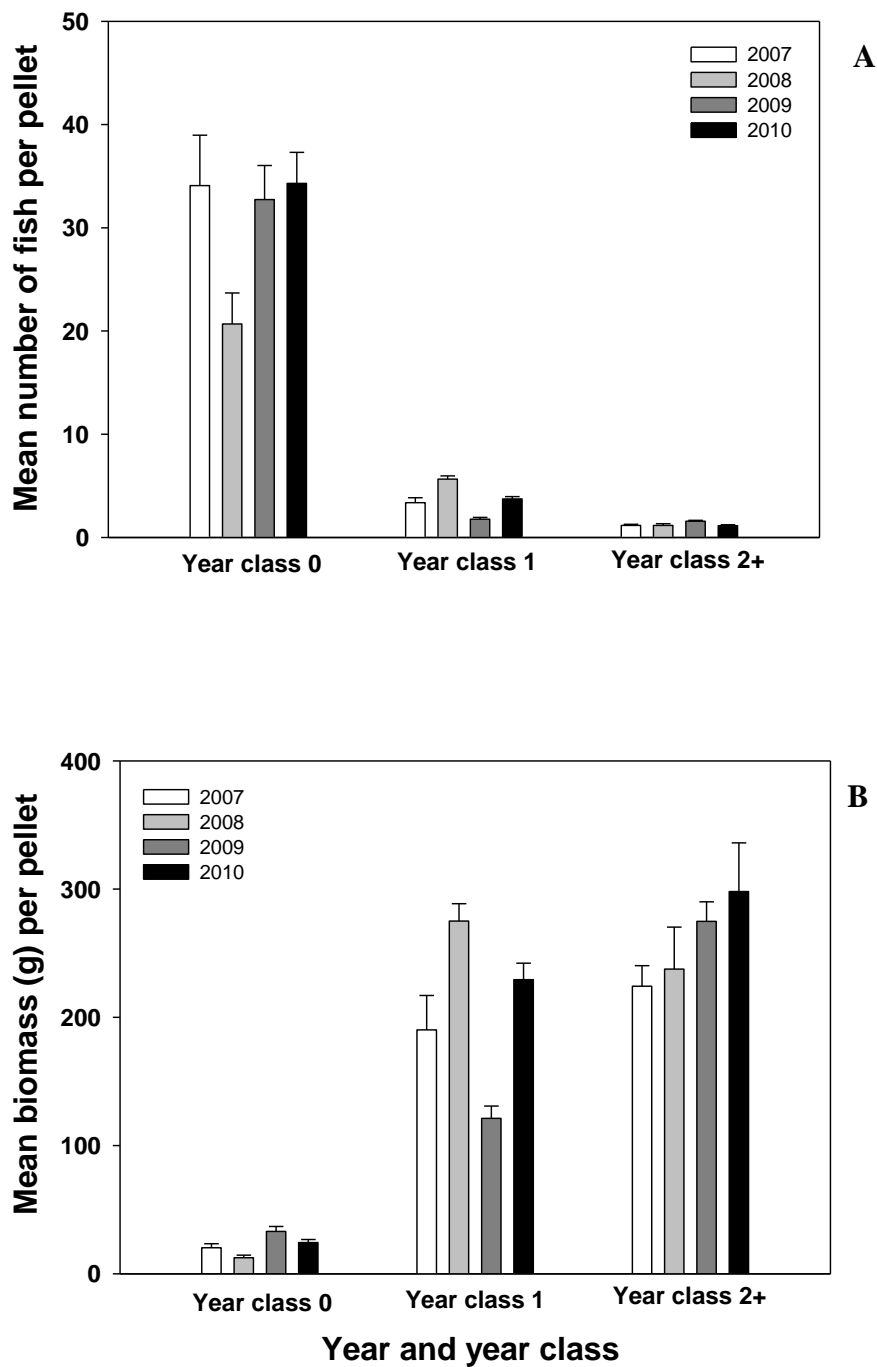


Fig. 7. (A) Mean number and (B) mean biomass per pellet of year classes 0, 1 and 2+ of saithe in pellets from the European shag at Sklinna, central Norway, 2007–2010. Error bars represent SE.

There was a significant difference in fish mass between years for year class 0 (Kruskal-Wallis=228.9, df=3 $p < 0.001$ †, based on median). Specifically, there was a significant difference between all years, except between 2009 and 2010 (based on median, Tables 3–4).

Table 3. Body mass measurements (g) for year classes 0, 1, and 2+ of saithe, in pellets from the European shag at Sklinna, central Norway, 2007–2010.

	Year	Mean	SE	Median	Range	Min.	Max.	N
Year class 0	2007	0.6	0.02	0.4	12.2	0.01	12.2	2374
	2008	0.6	0.02	0.3	11.5	0.00	11.5	1929
	2009	1	0.02	0.3	10.2	0.01	10.2	3529
	2010	0.7	0.01	0.4	8.5	0.01	8.5	5616
Year class 1	2007	56.6	2	52.7	106.7	20	126.6	148
	2008	48.7	0.7	46.4	103.9	13.3	117.2	576
	2009	68.7	2.8	63.3	101.3	22.2	123.4	113
	2010	61.5	0.9	59.6	109	14.4	123.4	466
Year class 2+	2007	192.2	10.3	192.2	115.8	136.7	252.5	14
	2008	203.7	24.5	192.2	189.9	136.7	326.6	7
	2009	174.7	3.3	174.9	145.7	129.9	275.6	107
	2010	260.8	32.2	247.1	394.9	129.9	524.8	16

Table 4. Statistical outcome from pairwise Mann-Whitney U-tests performed for fish mass of different year classes of saithe between years, in pellets from the European shag at Sklinna, central Norway, 2007–2010. Note that the critical significance level used for all pairwise tests was 0.0083.

		2008	2009	2010
Year class 0	2007	Z=-8.1, N ₁ =2374, N ₂ =1929, p < 0.001	Z=-5.5, N ₁ =2374, N ₂ =3529, p < 0.001	Z=-5.7, N ₁ =2374, N ₂ =5616, p < 0.001
	2008		Z=-13, N ₁ =1929, N ₂ =3529, p < 0.001	Z=-13.8, N ₁ =1929, N ₂ =5616, p < 0.001
	2009			Z=-1.3, N ₁ =3529, N ₂ =5616, p=0.2
Year class 1	2007	Z=2.9, N ₁ =148, N ₂ =576, p=0.004	Z=-3.3, N ₁ =148, N ₂ =113, p=0.001	Z=-3.4, N ₁ =148, N ₂ =466, p=0.001
	2008		Z=6.5, N ₁ =576, N ₂ =113, p < 0.001	Z=-11, N ₁ =576, N ₂ =466, p < 0.001
	2009			Z=-1.5, N ₁ =113, N ₂ =466, p=0.1
Year class 2+	2007	Z=-0.08, N ₁ =14, N ₂ =7, p=0.9	Z=-1.6, N ₁ =14, N ₂ =107, p=1	Z=-1.5, N ₁ =14, N ₂ =16, p=0.1
	2008		Z=-1.2, N ₁ =7, N ₂ =107, p=0.2	Z=-0.9, N ₁ =7, N ₂ =16, p=0.4
	2009			Z=-2.8, N ₁ =107, N ₂ =16, p=0.005

Biomass per pellet of year class 0 was significantly different between years (Kruskal-Wallis=8.5, df=3, p=0.036†, based on median). Specifically, biomass per pellet was significantly lower in 2008 (median: 6.2 g (111.3)) as compared to 2010 (median: 9.8 g (175.1)), whereas no significant differences were found between the other comparisons of years (medians; 2007: 7.5 g (106.5), 2009: 8.2 g (149.8)) (Table 5).

Table 5. Statistical outcome from pairwise Mann-Whitney U-test performed on biomass per pellet for year class 0-saithe, in pellets from the European shag at Sklinna, central Norway, 2007–2010. Note that the critical significance level used for all pairwise tests was 0.0083.

	2008	2009	2010
2007	Z=-2, N ₁ =70, N ₂ =94, p=0.05	Z=-0.6, N ₁ =70, N ₂ =107, p=0.56	Z=-0.2, N ₁ =70, N ₂ =163, p=0.8
2008		Z=-2.4, N ₁ =94, N ₂ =107, p=0.02	Z=-2.7, N ₁ =94, N ₂ =163, p=0.008
2009			Z=-0.6, N ₁ =107, N ₂ =163, p=0.6

No significant difference in frequency of occurrence for year class 0 was found between years (pairwise comparisons between years with Bonferroni corrections; 2007-2008: $\chi^2_1=3.5$, p=0.06††; 2007-2009: $\chi^2_1=4.8$, p=0.03††; 2007-2010: $\chi^2_1=0.3$, p=0.6††; 2008-2009: $\chi^2_1=0.1$, p=0.7††; 2008-2010: $\chi^2_1=3.3$, p=0.07††; 2009-2010: $\chi^2_1=5.3$, p=0.02††, Fig. 8).

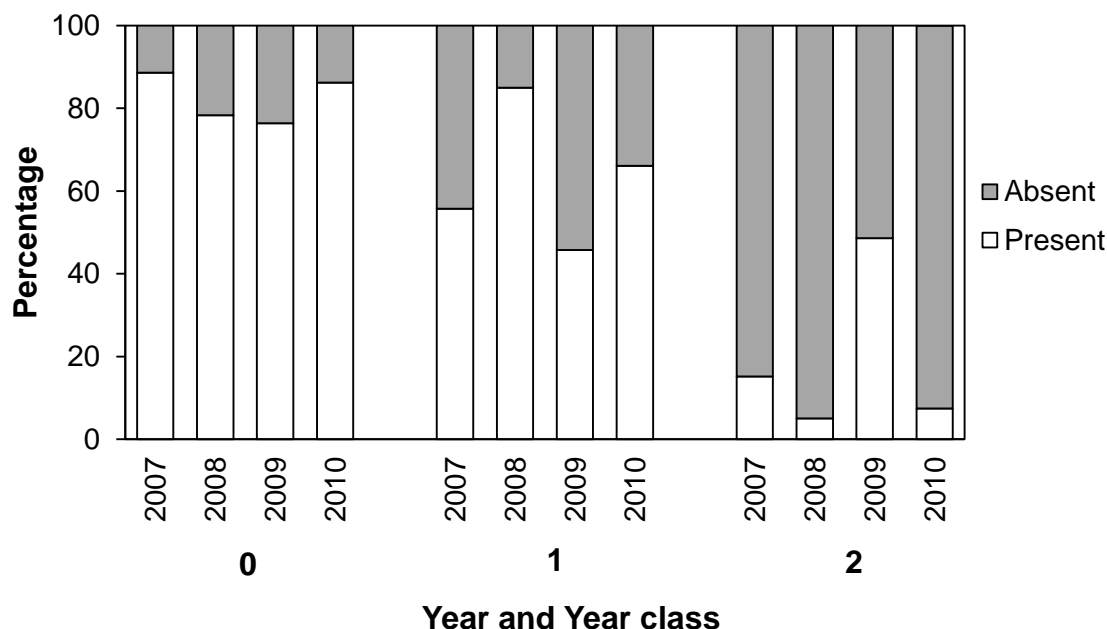


Fig. 8. Frequency of occurrence (%) of year classes 0, 1 and 2+ of saithe in the pellets from the European shag colony at Sklinna, central Norway, 2007–2009. Exact values are given in Appendix 8.

Year class 1

The number of fish per pellet of year class 1 differed significantly between years ($F_{3,331}=41.4$, $p < 0.001$ †, Fig. 7A). Specifically, the number of fish per pellet was significantly higher in 2008 than in all other years (Tukeys test for differences between groups; 2007-2008: $p < 0.001$ †; 2008-2009: $p < 0.001$ †; 2008-2010: $p < 0.001$ †). Further, the number of fish per pellet was significantly lower in 2009 as compared to 2007 and 2010 (as well as compared to 2008, see above) (Tukeys test for differences between groups; 2007-2009: $p < 0.001$ †; 2009-2010: $p < 0.001$ †). There was no significant difference in number of fish per pellet between 2007 and 2010 (Tukeys test for differences between groups; 2007-2010; $p=0.4$ †).

There was a significant difference in fish mass between years for year class 1 (Kruskal-Wallis=131.2, $df=3$, $p < 0.001$ †, based on median). Specifically, there was a significant difference between all years, except between 2009 and 2010 (based on median, Tables 3–4).

The same pattern was found for biomass as for number of fish per pellet. Biomass per pellet of year class 1 was significantly different between years ($F_{3,331}=22.2$, $p < 0.001$ †; Fig. 7B). Specifically, biomass per pellet was significantly higher in 2008 as compared to all other years (Tukeys test for differences between groups; 2007-2008: $p < 0.001$ †; 2008-2009: $p < 0.001$ †; 2008-2010: $p=0.04$ †). Also, biomass per pellet was significantly lower in 2009 as compared to 2007 and 2010 (as well as 2008, see above) (Tukeys test for differences between groups, 2007-2009: $p=0.04$ †; 2009-2010 $p < 0.001$ †). There was no significant difference in biomass per pellet between 2007 and 2010 (Tukeys test for differences between groups; 2007-2010 $p=0.1$ †).

The frequency of occurrence was significantly different between years for year class 1-saithe ($\chi^2_3=45.7$, $p < 0.001$ †, Fig. 8). Specifically, the frequency of occurrence was significantly higher in 2008 as compared to all other years (2007-2008: $\chi^2_1=21$, $p < 0.001$ ††, 2008-2009: $\chi^2_1=43.2$, $p < 0.001$ ††, 2008-2010: $\chi^2_1=13.4$, $p < 0.001$ ††). Also, in addition to being significantly lower than in 2008 (see above) the frequency of occurrence was significantly lower in 2009 as compared to 2010 (2009-2010: $\chi^2_1=13.7$, $p < 0.001$ ††). The frequency of occurrence was not significantly different between 2007 and 2009 ($\chi^2_1=2$, $p=0.2$ ††), and 2007 and 2010 ($\chi^2_1=2.6$, $p=0.1$ ††).

Year class 2+

The number of fish per pellet for year class 2+-saithe was not significantly different between years (pairwise comparisons between years with Bonferroni corrections (Table 6, median=1 for all study years (range=1 in 2007, 2008 and 2010, and 2 in 2009))).

Table 6. Statistical results for pairwise Mann-Whitney U-tests used to test for differences in the number of fish per pellet for year class 2+ between years, in pellets from the European shag at Sklinna, central Norway, 2007–2010. Note that the critical significance level used for all pairwise tests was 0.0083.

	2008	2009	2010
2007	Z < 0.001, N ₁ =12, N ₂ =6, p=1	Z=-2, N ₁ =12, N ₂ =68, p=0.04	Z=-0.2, N ₁ =12, N ₂ =14, p=0.9
2008		Z=-1.5, N ₁ =6, N ₂ =68, p=0.1	Z=-0.1, N ₁ =6, N ₂ =14, p=0.9
2009			Z=-2.3, N ₁ =68, N ₂ =14, p=0.02

There was a significant difference in fish mass between years for year class 2+ (Kruskal-Wallis=10.8, df=3, p=0.013†, based on median). Specifically, there was a significant difference between 2009 and 2010, whereas no significant differences were found between other years (based on medians, Tables 3–4).

Biomass per pellet showed the same pattern as did number of fish per pellet with no significant differences between years (Kruskal-Wallis=1.1, df=3, p=0.8†, based on median; 2007: 215.8 g (190.9), 2008: 221.5 g (199.3), 2009: 236.3 g (471.3), 2010: 263.9 g (394.9)).

However, the frequency of occurrence of year class 2 was significantly different between years ($\chi^2_3=112.4$, $p < 0.001$ †, Fig. 8). Specifically, frequency of occurrence was significantly higher in 2009 as compared to all other years (2007-2009: $\chi^2_1=24.3$, $p < 0.001$ ††, 2008-2009: $\chi^2_1=60.2$, $p < 0.001$ ††, 2009-2010: $\chi^2_1=72.8$, $p < 0.001$ ††), whereas no significant differences were found between other years (2007-2008: $\chi^2_1=6$, $p=0.01$ ††; 2007-2010: $\chi^2_1=3.9$, $p=0.05$ ††; 2008-2010: $\chi^2_1=0.7$, $p=0.4$ ††).

Shag breeding parameters in relation to the proportion of saithe in the diet.

Although there are too few years to do a sound correlative analysis, there appeared to be a positive relationship between the percentage contribution of year class 1 to the total biomass of saithe and different breeding parameters for the shag at Sklinna (Fig. 9A). The breeding population (pairs) at Sklinna co-varied with the strength of this year class between 2007 and 2010. Also, other reproductive parameters seemed to correlate positively with the percentage contribution of year class 1 to the total biomass of saithe, such as clutch size at incubation, clutch size at hatching, hatching success and survival of chicks to day 20 (Fig. 9B-C). The only exception was the survival of chicks to 20 days was at its highest in 2010.

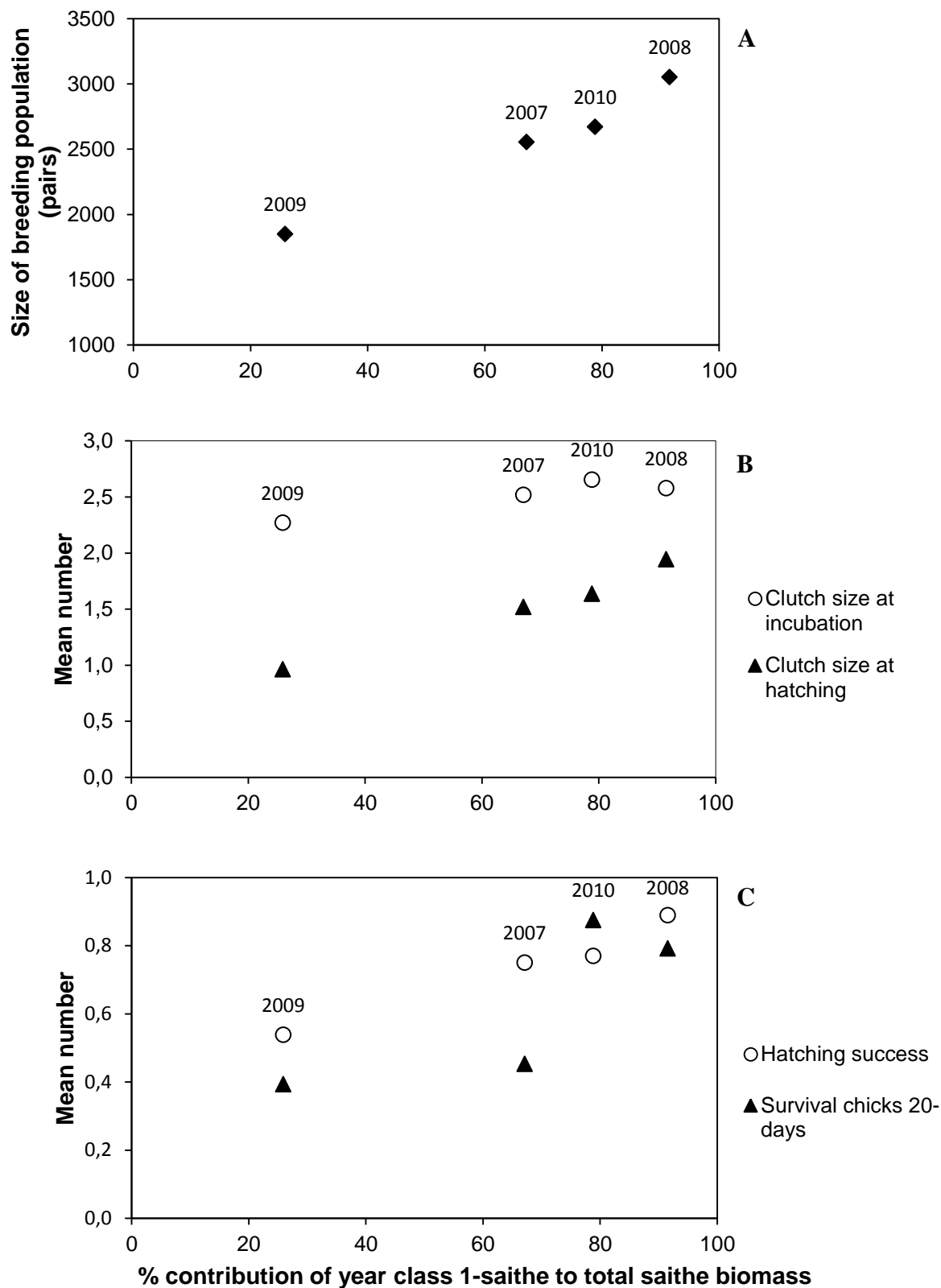


Fig. 9. Correlation between the percentage contribution of year class 1 to the total biomass of saithe and (A) size of the breeding population (pairs); (B) clutch size at incubation and clutch size at hatching; (C) hatching success and survival of chicks to 20 days (in nests where at least one chick hatched), of the European shag colony at Sklinna, central Norway, 2007–2010 (S.-H. Lorentsen, unpubl. data).

Discussion

Dietary composition and the importance of saithe

The European shag at Sklinna fed on a variety of fish species of different sizes during the breeding period, which were mainly associated with kelp- or sandy-bottom demersal habitats (Peton 2005). Fish from the Gadoid family constituted the main prey species throughout the study period. This agrees well with previous findings on the diet of the shag along the Norwegian coast (Barrett *et al.* 1990; Barrett 1991). The Gadoid group included saithe, poor cod and cod, where saithe was the dominant species in all years. The shags thus relied heavily on saithe during the reproductive period in this area.

If the total amount of saithe in the diet was affecting the different variables of reproduction it could be expected that any dietary differences would be particularly apparent at least between 2008 and 2009. The size of the breeding population at Sklinna declined by 40% from 2008 to 2009, and had intermediate values in 2007 and 2010, with correlative patterns in reproductive success (S.-H. Lorentsen, unpubl. data). However, there were no differences in the number of saithe per pellet or frequency of occurrence between any of the four study years. Biomass per pellet for total saithe did, however, differ between years in that there was a significantly higher biomass per pellet in 2008 than in 2007 and 2010, and in 2009 as compared to 2007. The biomass per pellet in 2008 and 2009 did not differ. Thus, while the largest differences in reproductive effort and success were between 2008 and 2009, no differences in numbers, biomass or frequency of occurrence of total saithe were detected between these two years. Also, the biomass per pellet was significantly higher in 2009 than in 2007, while reproductive success was higher in 2007 than in 2009. The reproductive parameters of shags at Sklinna thus appeared not to co-vary with the overall amount of saithe in the diet.

The results in this study may, however, suggest that the size of breeding population and other variables of reproductive success of the European shag correlated specifically with the abundance of year class 1-saithe. This year class was significantly more abundant in pellets in 2008 and significantly less abundant in pellets in 2009, as compared to other years, in both numerical frequency and biomass per pellet. Also, the frequency of occurrence was higher in 2008 than in other years, and lower in 2009 as compared to 2008 and 2010. Although without sufficient number of years with data to do a statistical analysis, the reproductive effort and success appeared to correlate positively with the abundance of this year class in the diet of the

shags. This concurs well with previous studies of a more indirect nature where the estimated abundance of this year class of saithe explained some of the variation in time of laying and clutch size for the shags (Anker-Nilssen 2005).

A previous study on shags found no relationship between reproduction and total sandeel biomass in the region of study (Aebischer & Wanless 1992). However, the reproductive output was found to correlate positively with the size of sandeels in the diet of puffins in the same area, where the sandeels were on average smallest during years with particularly poor reproduction (Aebischer & Wanless 1992). No direct dietary studies were performed for the shag in this particular study, but concurrent studies confirmed that sandeels were indeed the main prey species for these birds, and that there were large inter-annual differences in the proportions of year classes 0- and 1+-sandeels in the diet (Harris & Wanless 1991). This may therefore support the idea that certain size ranges, and as such certain year classes, of the preferred prey species may be more profitable than others for the birds' breeding success.

Year class 0-saithe, although dominating the diet by numerical frequency, contributed little to the total biomass of saithe. Further, both numerical frequency and biomass of year class 0-saithe were significantly lower in 2008 when reproductive output was at its highest of the four study years. The abundance of this year class explained some of the variation in time of laying of shags at Røst and Sklinna (Anker-Nilssen 2005) which suggests a higher importance than what was apparent in my study. However, laying dates were not compared to diet in the current study, and a direct comparison cannot be made.

The number of fish individuals from the different year classes caught by the shags may be influenced by the relative abundance of the different year classes. For example, the significantly lower number of year class 0-saithe caught by the shags in 2008 could be caused by the presence of a strong year class 1, which may be the preferred prey size. However, year class 1 appears to have been very low in abundance in 2009. In 2008 this year class was one year younger (e.g. year class 0) and it is therefore fair to assume that the lower number of year class 0 caught in 2008 was a result of the abundance of this specific year class being very low.

In 2009, when reproductive output of the shag at Sklinna was poor, year class 2+ dominated the biomass of saithe in the diet of the shag. There was no significant difference in numbers or biomass per pellet of this year class between years. The maximum number of fish of this year class in any pellet was three individuals. Individuals of this year class have an estimated

minimum body length of 250 mm, and this large size probably imposes a limit to the number of fish that the shags can ingest in a feeding bout. This may have caused the little variation in the number of individuals in pellets, and be the reason why there were no significant differences in number or biomass per pellet of this year class. However, due to the significantly higher frequency of occurrence of year class 2+, the total percentage contribution to biomass was high in 2009. Although biomass of total saithe was not significantly lower in 2009 as compared to 2008, and year class 2+ thus appeared to compensate for year class 1 in total biomass by a higher frequency of occurrence, this compensation appears not to have been enough for the shag as reproduction in 2009 was poor.

There may be several reasons, or a combination of these, why year class 1-saithe may be the most important in terms of reproduction for the shag; catchability, energy content and digestibility. Firstly, catchability varies with the size of the prey. Swimming speed generally increases with the size of the fish, rendering it more difficult to catch for the shags (Wardle 1975; Ulenaers *et al.* 1992; Van Eerden & Voslamber 1995 and references therein; review by Domenici 2001), including saithe (note that the experiment on saithe were only performed on fish of lengths ≥ 250 mm); He & Wardle 1988; Videler 1993 in Pedersen 2001). Temperature may affect swimming speed of fish (Domenici & Blake 1997), and cormorants have been found to increase swimming speed during the season to compensate for the increased speed reached by its fish prey, probably as a response to increased water temperature. It was hypothesized that a switch to smaller prey size at higher water temperatures occurred at a point when the larger fish became too fast for the cormorant to catch (Van Eerden & Voslamber 1995). Handling time has also been found to increase with size (Uleaners *et al.* 1992). In contrast, acceleration and manoeuvrability often decrease with size, possibly counteracting the effect of speed in predator escape behaviour (Domenici & Blake 1997; Domenici 2001). This makes it difficult to predict which combination is true for catchability of different sizes of saithe and how this possibly affects the interactions between hunting shags and fish of different year classes of saithe. Secondly, the calorific value per gram of a fish increases in a non-linear way, such that larger prey items often represent a higher energy value per biomass due to a lower water content relative to smaller prey items (Hislop *et al.* 1991). Also, fewer individuals of large size need to be caught to achieve a certain amount of food. Therefore, in terms of energy gained per gram of prey caught, larger prey items are generally more energy-efficient to catch for the shag. Thirdly, however, digestion rate decreases with individual prey size, probably due to an decrease in surface:volume ratio of

larger prey items (Hilton *et al.* 1998). Thus, the higher digestion rates of smaller prey items may counteract the benefits from choosing larger prey items, to maximise ingestion rates (Hilton *et al.* 1998). In conclusion, year class 1-saithe may represent the most profitable prey size in terms of catchability, energy content, digestibility, or a combination of these.

The number of breeding pairs of shags was coherent with the subsequent breeding success (clutch size, hatching success etc.). This concurs with previous studies where the abundance or size of a certain prey species appears to affect the entire course of reproduction (Aebischer 1986; Harris & Wanless 1991; Aebischer & Wanless 1992). This suggests that the specific season's food potential is apparent to the birds already very early in the season, as older and more experienced shags may decide whether to breed or not as early as February (Potts *et al.* 1980; Aebischer 1986). This probably depends on the body condition of the shags at the time of decision making, being affected by the food abundance throughout the previous winter. This would agree with the suggestion that year class 1-saithe indeed is of high importance to the shags, as the abundance of this year class may be apparent to the birds throughout the winter and spring (as year class 0) and thus at the time of making the decision whether to make an effort to breed or not, as opposed to for example year class 0-saithe which is not present until later in the breeding season (April–May).

Most studies on dietary composition of seabirds are performed during the breeding season and little is known of the diet during the rest of the year (review in Barrett *et al.* 2007). However, one study on shag did indeed sample pellets throughout the year demonstrating that, although somewhat more varied in winter, the diet was consistently based on sandeels throughout the year (Harris & Wanless 1991). It may therefore be plausible that saithe, and particularly year class 1 (year class 0 during winter) may be the main prey of the shags at Sklinna also during the winter, thus affecting the body condition of the adult shags during the winter, and as such the number of breeding pairs in the subsequent year. The Cape cormorant *Phalacrocorax capensis* was found to increase substantially in body mass prior to the onset of breeding (Berry *et al.* 1979). Further, the great cormorant kept its body mass constant during the breeding period independently of food abundance and thus prioritised own maintenance over the survival of its offspring (Grémillet 1997). These results indicate that body condition prior to the onset of breeding is affected by food abundance and is important to the breeding effort by seabirds. The cormorant, and thus possibly also the related shag, may have a threshold body mass for reproduction and limited abilities to buffer for prey variability through body reserves as opposed to what is true for some other species of seabirds (Grémillet 1997;

Kitaysky et al 1999; Weimerskirch *et al.* 2000 and references therein). If year class 1-saithe is indeed an important prey item for the shags at Sklinna also during winter, it could have an effect on the breeding performance in the subsequent breeding season through an effect on the body condition of the adults at the time of initiating the reproductive season. It would therefore be of interest to examine the dietary composition for shags at Sklinna also during winter to examine whether the diet comprised mainly of saithe, specifically year class-1 (0), also during winter.

In 2010 poor cod and cod contributed more to the total biomass in the pellets as compared to previous years. The biomass of these two species were mainly contributed by year class 1 individuals (own unpublished data) and were therefore approximately of the same length range as year class 1-saithe which may be of a more profitable size for the breeding shags. Interestingly, the survival of chicks was the highest of all years in 2010, although the other parameters of reproduction correlated well with the abundance of year class 1-saithe. This may be attributed to the large proportion of cod and poor cod of year class 1 in the diet, but several more years of data on the breeding parameters and diet of the shags will be vital to elucidate on any such connection. In previous years, such as 2007 and 2009, when the shags' reproduction was at intermediate and low levels, such increases in the catches of poor cod and cod did not occur. It therefore appears that the shag may not always replace the saithe with alternative prey species, depending on abundance and sizes of different prey species in any given year.

Sandeels, along with Gadoids, have previously been found to be important prey for shags in Norway (Barrett *et al.* 1990). However, sandeels appeared to contribute little to the diet of the shags at Sklinna in all study years. Analyses of the diet of Puffins *Fratercula arctica* and Common guillemot *Uria aalge* at Sklinna during the same period indicated that sandeels was more abundant than what was apparent from the dietary composition of shags. Sandeels comprised from insignificant numbers to at times about 50% of the diet by numerical frequency or biomass for the Common guillemot and puffins during the same study period, whereas Gadoid spp. were the most common prey species (Anker-Nilssen *et al.* 2008; Lorentsen & Eriksen 2009; Lorentsen *et al.* 2010). The discrepancy of dietary contribution of sandeels between species of seabirds at Sklinna may be due to the lower recovery rate of sandeel otoliths as compared to Gadoid otoliths from regurgitated pellets (Johnstone *et al.* 1990), whereas the diet of the puffins and guillemots are assessed by direct observations of prey brought to the nest by adults. The true numerical frequency of the sandeel may therefore

very well be underestimated in the diet of the shag. Sandeels do in fact have a higher calorific value per gram than do Gadidae spp., which is an advantage when raising chicks (Barrett *et al.* 1987; Hislop *et al.* 1991), and one may expect that the shag would prefer sandeels to Gadids if present in the area. Also, Puffins and Common guillemots normally do prefer more energy-rich prey species, such as sandeels, herring or capelin (Harris & Hislop 1978; Barrett & Furness 1990; Barrett *et al.* 1990; Barrett 2002; Bugge *et al.* 2010). At Sklinna, the numerical frequency of sandeels in seabirds' diet was generally lower than in other areas in Norway, both for the shag (Barrett & Furness 1990; Barrett *et al.* 1990) and the Common guillemot and Puffins (Barrett & Furness 1990; Barrett *et al.* 1990; Barrett 2002; Bugge *et al.* 2010), and this may therefore reflect a generally low abundance of sandeels in the waters surrounding Sklinna.

The importance of year class 1-saithe for the breeding performance was found to be lower in the colony of shags at Sklinna than in a colony at Røst when using indirect methods, which was hypothesized to be caused by alternative prey such as sandeels being more abundant in the latter region (Anker-Nilssen 2005). This was not supported by the results in this study. Caution should be taken when correlating reproductive variables with the estimated abundance of prey species on a regional scale as this may not necessarily reflect the abundance of species on a local scale (Aebischer & Wanless 1992).

The breeding success of the shag may be affected directly by external factors other than diet. It may be affected by severe weather conditions, such as rainfall or gales (Aebischer 1993; Velando *et al.* 1999; Velando & Freire 2003). This may be due to the direct effect on the survival of chicks or adults (Aebischer 1993; Velando & Freire 2003), or the reduced feeding success of the adults during severe weather (Velando *et al.* 1999). The severe weather conditions in these studies occurred during a very limited period of time and did not affect other variables of breeding such as size of breeding population, laying dates or brood size (Aebischer 1993; Velando *et al.* 1999). In the current study, the different parameters of breeding appeared to co-vary within years, which suggests that the factor(s) affecting these were of a more long-term nature than what shorter periods of bad weather would be.

The NAO-index reflects temperature, winds, and rainfall on a more consistent annual basis (Ottersen *et al.* 2001). The NAO-index was indeed found to directly explain some of the variation in laying dates for shags at Røst and Sklinna (Anker-Nilssen 2005), and this is more consistent with the results that reproductive variables co-varied within years. Whether the link

between environmental conditions or the NAO-index and breeding success is of a direct effect on mortality or of a more indirect nature by affecting the food availability is often difficult to discern (Harris & Wanless 1991; Velando *et al.* 1999; Ottersen *et al.* 2001). The dietary composition for each study year has been collected from late May to mid-July, and may therefore be assumed to be representative for the main breeding season. More detailed studies on seasonal variation in dietary composition during the breeding period in the already collected material, possibly compared with environmental conditions and reproductive parameters, may elucidate any connections in more detail.

Shags have previously been suggested as natural samplers of the younger year classes of saithe and cod (Barrett 1991; Anker-Nilssen 2005). These species are of important commercial value, but their abundance cannot be securely assessed by researchers until they are a minimum of two years old. If fish of year class 1 are indeed the preferred prey of shags, its abundance in the diet of shags may be less affected by the relative strength of other year classes, e.g. 0 and 2+, and therefore the best year class to monitor to assess the strength of recruitment of specific year classes of saithe one to two years later. The data on saithe which is necessary to do such a preliminary comparison is currently unavailable due to the time lag between when the shag feeds on a year class and the time when the fisheries sample this specific year class one to two years later (S. Mehl, pers. comm. 2010).

Adult shags may have a somewhat different diet compared to the chicks as they may feed on a broader or different diet and digest this while searching for food for the chicks at sea (Johnstone *et al.* 1990; Skarprud 2003; Lilliendahl & Solmundsson 2006). Further, non-breeding adults probably have a different diet from breeding adults (Harris & Wanless 1993; Barrett *et al.* 2007). This may be a significant source of bias when analysing the direct link between diet and reproductive success, especially if large annual variations in the proportion of breeding adults in the colony occur. It was not possible to assign specific pellets to a single nest or individual, but the pellets were normally collected between the nests and a large proportion of the pellets may be assumed to stem from reproductively active individuals. The dietary study will thus allow for an examination of the colony and changes in available prey as a whole, and probably be representative for the diet for reproductive shags.

Methodological considerations

Determining at which fish body length to separate the different year classes of saithe was done by evaluating the size-frequency distribution of the estimated fish lengths from otoliths in pellets. The advantage of this method is that the estimation of year classes is more adapted to location and time of year, and also buffers for the fact that otolith lengths will be more or less reduced due to erosion. On the other hand, the disadvantage of this method is that the individuals with body lengths situated in the regions around the boundaries between year classes may be assigned to the wrong year class. This region contains relatively few individuals and this probably represents a minor bias in the data, but an attempt should nevertheless be made to validate the assumptions made on the length distributions of year classes of saithe. The solution would be to age-determine the otoliths as well as measuring length and width (Johansen *et al.* 1999). This is a time-consuming method although an important one. However, by age-determining smaller samples along the entire range of fish lengths in the pellets from the shag, this would provide a better understanding of the length-at-age distribution of the saithe caught by the shag, and thus allow for a better estimate of length ranges of the different age classes.

The recovery rate of a typical Gadidae spp. otolith (saithe and cod, based on otolith shape) in regurgitated pellets, estimated by the number of individuals present after otoliths were paired, was 68%. This is somewhat lower than in previous studies where the recovery rate of cod otoliths (assumed here to be approximately representative for Gadidae spp.) in controlled experiments with the European shag was 73 % (Johnstone *et al.* 1990). An important aspect of the method used in the current study was the pairing of otoliths. There is no standard method advised for this task, and its execution relies much on the experience of the analyst. The lower recovery rate could be a result of the method used in pairing otoliths in this study. However, this could also very well be due to the fact that the mean length of Gadidae otoliths was lower in this study than that of the control study (Johnstone *et al.* 1990). Smaller otoliths are affected more by erosion such that the recovery rate of these may be expected to be lower than that of larger otoliths (Jobling & Breiby 1986; Johnstone *et al.* 1990, compare also to Johansen *et al.* 1999). Further, the formula from Härkönen (1986) used for estimating fish mass from otolith length for year class 0-saithe may underestimate the true mass, as it does with fish length estimated from otolith length (see methods). This is supported by lower estimates of biomass in the current study (Mean=0.73 g, median=0.33 g) than what might be expected for this size group (1-2 g) (Anker-Nilssen 2005; T. Pedersen, pers. comm. 2010). In

conclusion, both numbers and biomass of year class 0-saithe may have been underestimated, and their importance in the diet of the shag may be more significant than what was apparent in this study.

An effort should be made to sample particularly saithe of year classes 0 and 1, as the main prey item in the diet, to estimate a better formula for calculating fish mass from otolith length. Further, saithe and cod have different growth zones in their otoliths which may aid in the differentiation between these two species (Johansen *et al.* 1999). A study on a sub-sample of the otoliths assigned to unidentified Gadidae (< 3 mm otolith length) which were subsequently included in the year class 0-saithe group, using growth zones, would confirm or reject the hypothesis that most of these were indeed saithe.

Conclusion

Today there are large changes occurring in ecosystems and environmental conditions due to human impacts and global climate changes. Many populations of seabirds have undergone large reductions in size during the last decades. Breeding effort and success of seabirds are affected by, and often reflected in, their diet. Dietary composition is therefore an important feature to monitor for these species to elucidate on the putative explanations for the declines.

The European shag at Sklinna fed on a varied diet based on fish species mainly associated with kelp- or sandy bottom, demersal habitats. Sandeels contributed relatively little to the diet of the shags in this colony, which contrasts with studies on this species in other areas, in both Norway and elsewhere. Gadoid species, such as saithe, cod and poor cod, constituted the main prey species for the shags at Sklinna during the main breeding period. Saithe was the most important prey species in all study years. Year class 1-saithe may be of particular importance as there appears to be a positive correlation between the amount and proportion of this year class in the diet and different indicators of reproductive success for the shags. Continued studies on reproduction and diet of the shags, but also on methodology, are vital to conclude on the findings and suggestions in the current study. This study does nevertheless represent an important contribution to the knowledge of the shags and their diet at Sklinna, and form a basis for further studies, including suggestions for improvements on methodological issues.

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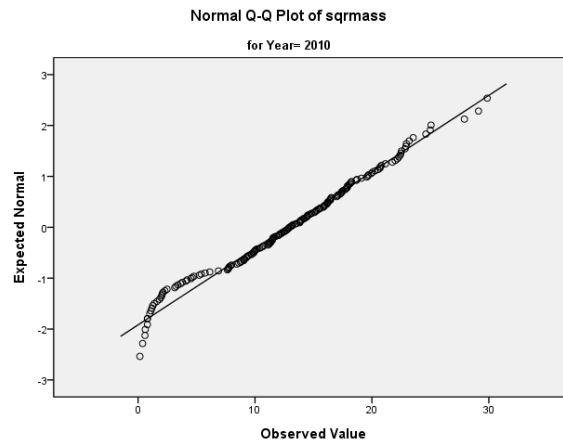
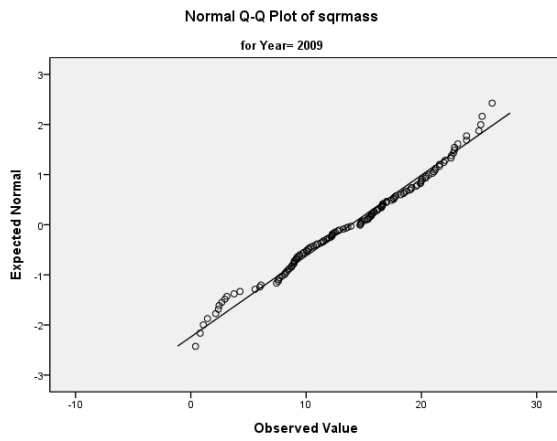
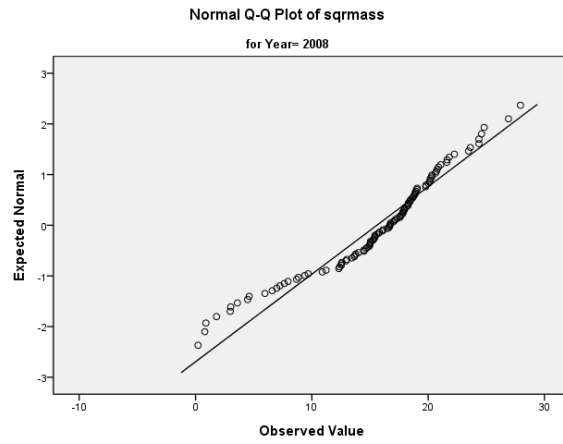
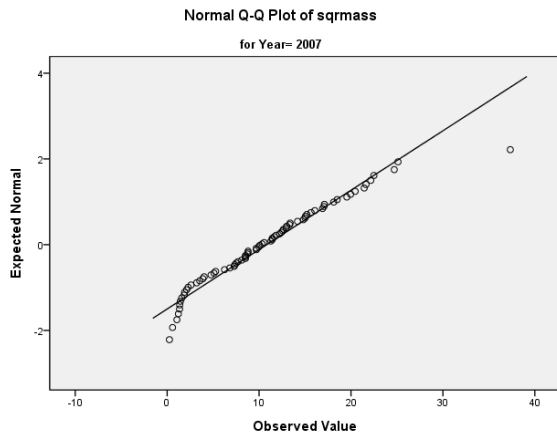
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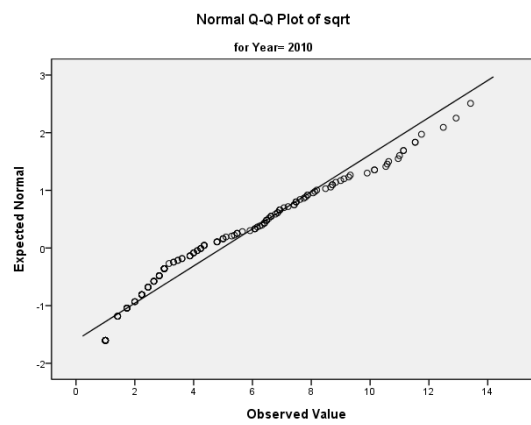
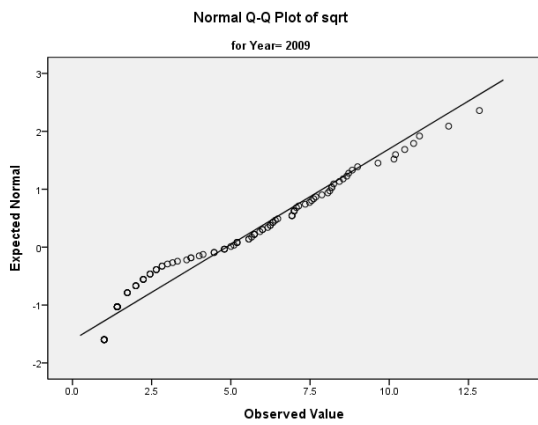
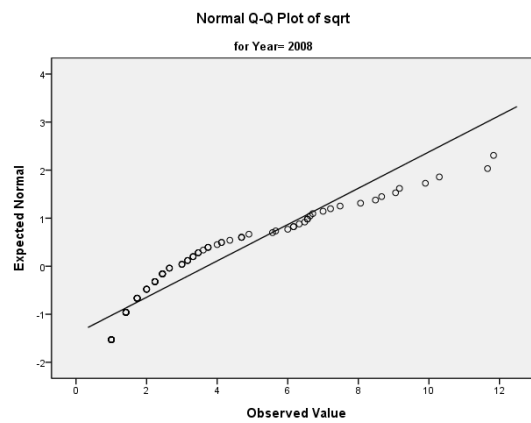
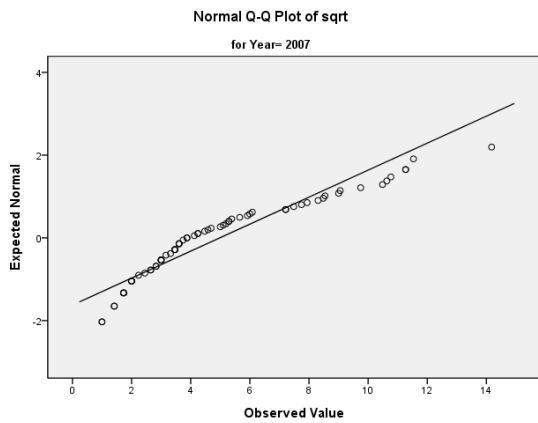
Appendix 1. Equations used to estimate fish length and body mass from otoliths in pellets from European shag at Sklinna, central Norway, 2007–2010. All equations are from Härkönen (1986), except those marked with * which are from Jobling and Breiby (1986), and with ** which are from Leopold *et al.* (Version 1.0). Y-c = year class. OL = otolith length. Equations for length and mass was multiplied with the respective proportion for different species (“percentage – species”) and added together where several equations were used for one taxonomic group.

Species/Family	Fish length (mm)	Fish mass (g)	Percentage - species
Unid. Gadidae OL > 3mm	8.97297 OL ^{1.53} 0.41+22.44 OL* 13.2 OL ^{1.329}	0.007288 OL ^{4.501} 0.006855 OL ^{4.435} 0.01192 OL ^{4.205}	94.2% saithe 5.3% cod 0.5% pollack
Unid. Gadidae OL < 3mm	-4.24+23.5 OL*	0.007288 OL ^{4.501}	Saithe
Saithe	y-c 0: -4.24+23.5 OL* y-c 1+: 8.97297 OL ^{1.53}	0.007288 OL ^{4.501}	
Poor cod	-49.9+28.091 OL	0.003540 OL ^{4.57}	
Norway Pout	-42.6+29.522 OL	0.002805 OL ^{4.729}	
Pollack	13.2 OL ^{1.329}	0.01192 OL ^{4.205}	
Cod	0.41+22.44 OL*	0.006855 OL ^{4.435}	
Tadpole-fish	-20.37+22.96 OL	0.151155 OL ^{2.912}	
Unid. bearded rockling	-74.6+92.29 OL	1.0736 OL ^{3.444}	Five-bearded rockling
Eelpout	-23.65+179.3 OW	12.58 OW ^{4.432}	
Norway Haddock	-14.46+38.81 OL	0.00075 OL ^{5.41}	
Bull-rout	-9.95+34.84 OL	0.2261 OL ^{3.496}	
Sea Scorpion	5.36+33.71 OL	0.6398 OL ^{2.988}	
Unid. Labridae	9.5+39.36 OL -4.76+52.12 OL	1.23 OL ^{2.88} 0.688 OL ^{3.51}	99% goldsinny 1% cuckoo wrasse
Cuckoo wrasse	-4.76+52.12 OL	0.688 OL ^{3.51}	
Goldsinny	9.5+39.36 OL	1.23 OL ^{2.88}	
Butterfish	1.23+173.96 OW	6.11 OW ^{1.421}	
Unid. Ammodytidae	-4.024+56.84 OL 18.76+45.75 OL	0.461 OL ^{2.903} 0.6041 OL ^{2.763}	50% greater sandeel 50% sandeel (<i>Ammodytes tobianus</i>)
Greater sandeel	-4.024+56.84 OL	0.461 OL ^{2.903}	
Unid. Gobiidae	-8.927+42.037 OW -23.36+56.94 OW -3.89+44.93 OW	0.225 OW ^{4.197} 0.1677 OW ^{5.369} 0.3345 OW ^{3.121}	34% black goby 33% sand goby 33% two-spot goby
Black goby	-8.927+42.037 OW	0.225 OW ^{4.197}	
Dragonet	44.29 OL ^{1.412}	0.482 OL ^{4.459}	
Norwegian topknot	55 OL	1.29 OL ^{2.91**}	Note: formula for length is only a rough estimate from Härkönen (1986)
Unid. Pleuronectidae	-3.81+47.63 OL -51.06+59.1 OL -50.96+58.47 OL 10.93+88.46 OL	0.498 OL ^{3.408} 1.578 OL ^{2.899} 0.17 OL ^{4.117} 4.89 OL ^{3.45}	25% plaice 25% flounder 25% dab 25% lemon sole
Lemon sole	10.93+88.46 OL	4.89 OL ^{3.45}	

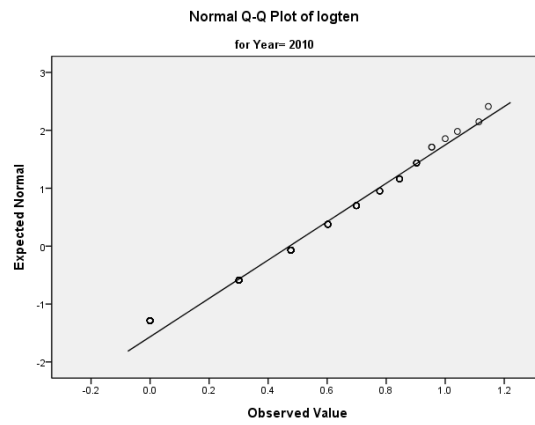
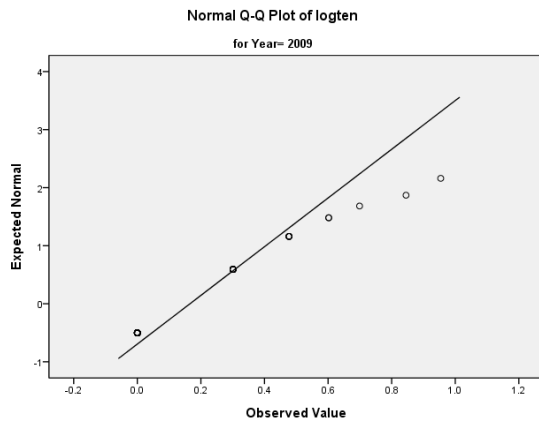
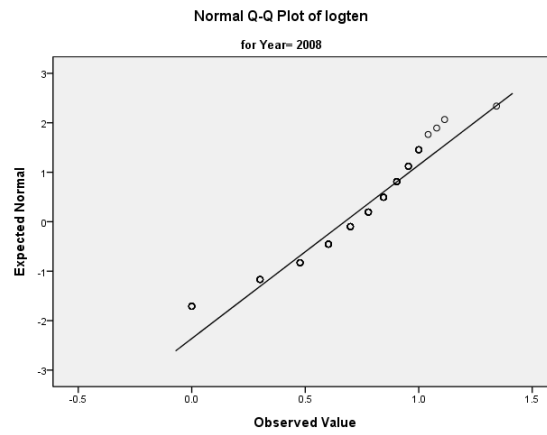
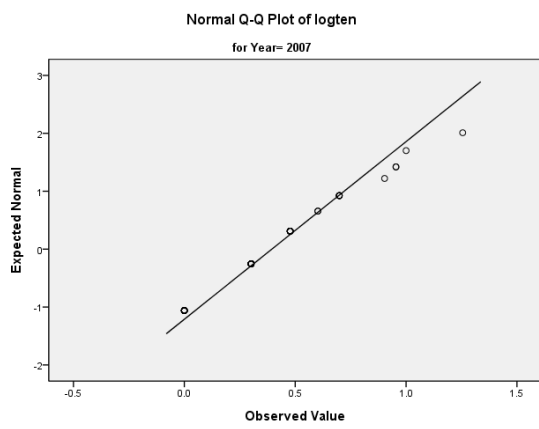
Appendix 2. Normality of data for biomass per pellet for total saithe, in pellets from European shag at Sklinna, central Norway, 2007–2010:



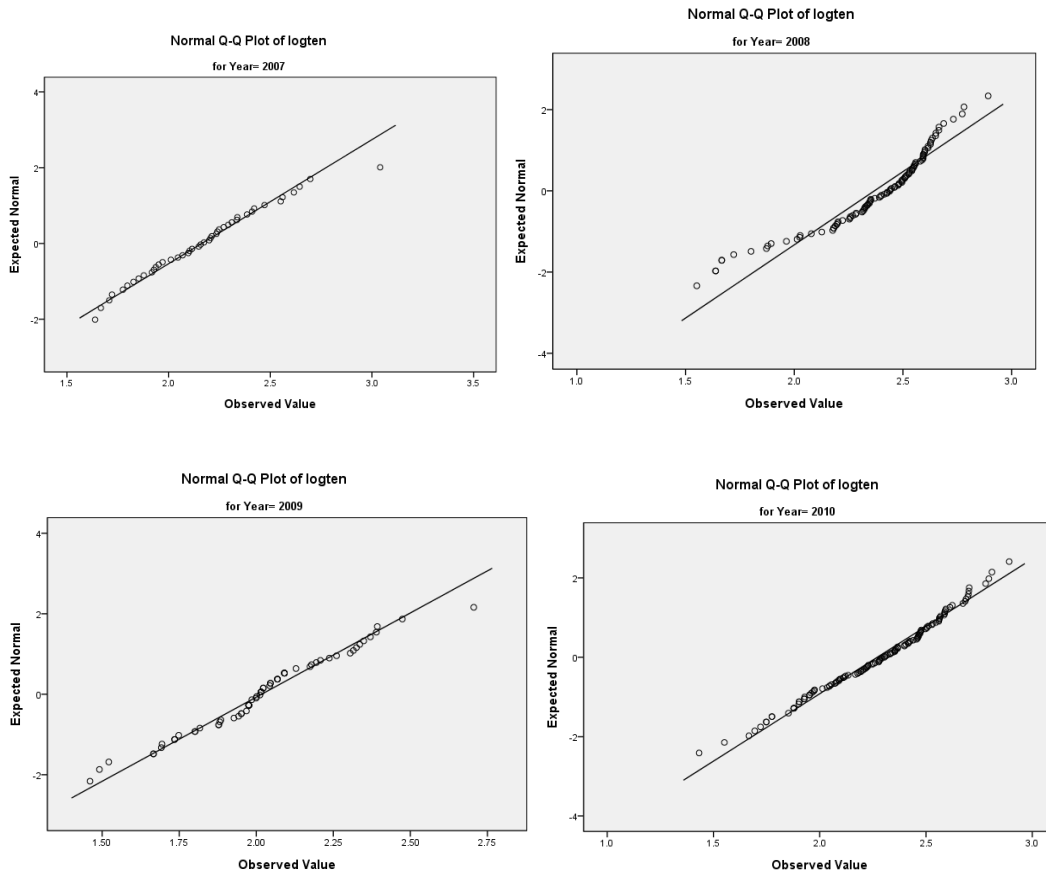
Normality of data for number of fish per pellet for year class 0-saithe, in pellets from European shag at Sklinna, central Norway, 2007–2010:



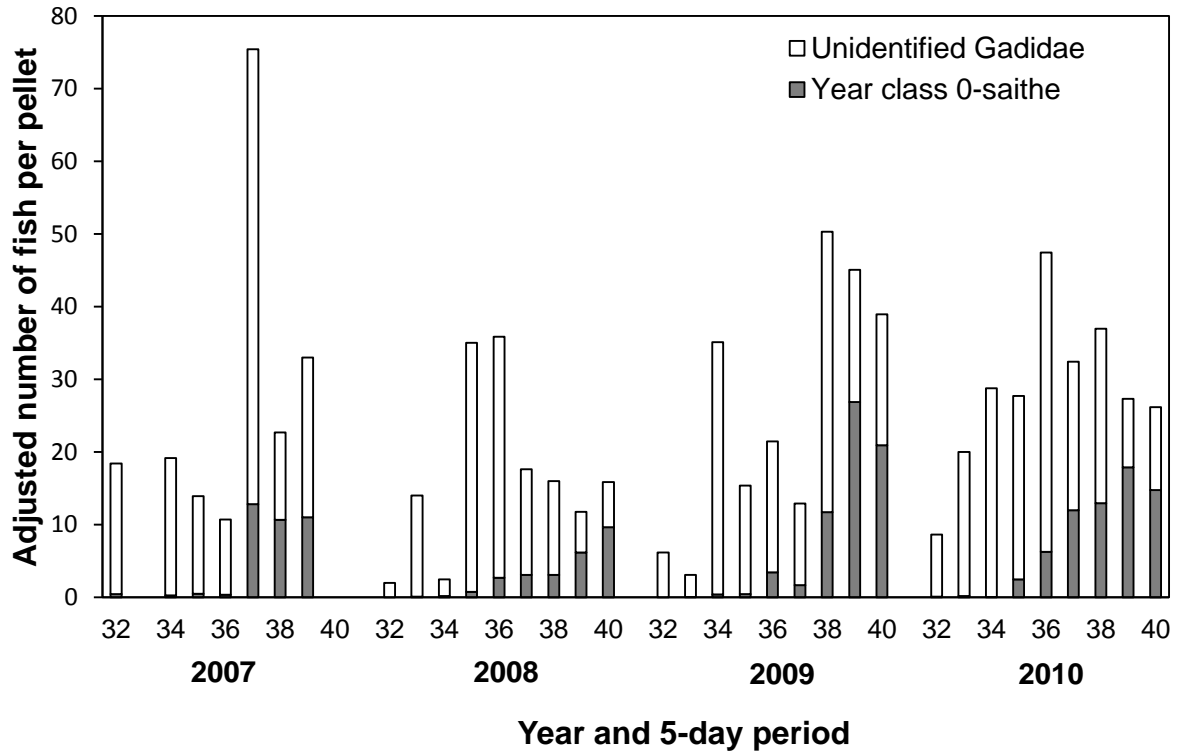
Normality of data on number of fish per pellet for year class 1-saithe, in pellets from European shag at Sklinna, central Norway, 2007–2010:



Normality of data on biomass per pellet for year class 1-saithe, in pellets from European shag at Sklinna, central Norway, 2007–2010:



Appendix 3. Number of year class 0-saithe and unidentified Gadidae at 5-day intervals during the study period (05.06.–19.07), in pellets from European shag at Sklinna, central Norway, 2007–2010. Note that the number of fish have been divided by number of pellets collected in any specific 5-day period to adjust for different number of pellets collected, and thus allow for a relative comparison between periods and years.



Appendix 4. Numerical frequency of prey species in pellets from the European shag at Sklinna, central Norway, 2007–2010. * Present in very small percentage. ** Bearded rockling spp. was either Five-bearded rockling *Ciliat amustela* or Three-bearded rockling *Gaidropsarus vulgaris*. Note that unidentified Gadidae with otolith length < 3 mm have been included in saithe.

Species/Family	2007		2008		2009		2010	
	N	%	N	%	N	%	N	%
Unid. Gadidae	14	0.5	16	0.5	10	0.2	26	0.3
Saithe <i>Pollachius virens</i>	2536	91.7	2512	84.7	3749	82.3	6098	69.7
Poor cod <i>Trisopterus minutus</i>	28	1	67	2.3	57	1.3	767	8.8
Norway Pout <i>T. esmarkii</i>			3	0.1	1	*		
Pollack <i>P. pollachius</i>	1	*	3	0.1	1	*	21	0.2
Cod <i>Gadus morhua</i>	17	0.6	26	0.9	52	1.1	181	2.1
Tadpole-fish <i>Raniceps raninus</i>					2	*		
Unid. bearded rockling**	1	*	4	0.1	3	0.1	9	0.1
Eelpout <i>Zoarces viviparus</i>			2	0.1	2	*	11	0.1
Norway Haddock <i>Sebastes viviparus</i>	1	*					4	*
Bull-rout <i>Myoxocephalus scorpius</i>			1	*	2	*	6	0.1
Sea Scorpion <i>Taurulus bubalis</i>	5	0.2	24	0.8	10	0.2	84	1.0
Unid. Labridae	2	0.1	3	0.1	12	0.3	73	0.8
Cuckoo wrasse <i>Labrus bimaculatus</i>					1	*		
Goldsinny <i>Ctenolabrus rupestris</i>	7	0.3	23	0.8	58	1.3	60	0.7
Butterfish <i>Pholis gunnellus</i>	1	*			3	0.1	5	0.1
Unid. Ammodytidae	2	0.1	3	0.1	10	0.2	58	0.7
Greater sandeel <i>Hyperoplus lanceolatus</i>	4	0.1	15	0.5	13	0.3	4	*
Unid. Gobiidae	1		9	0.3	89	2	111	1.3
Black goby <i>Gobius niger</i>					1	*		
Dragonet <i>Callionymus lyra</i>			1	*				
Norwegian topknot <i>Phrynorhombus norvegicus</i>			8	0.3			2	*
Unid. Pleuronectidae			7	0.2	4	0.1	14	0.2
Lemon sole <i>Microstomus kitt</i>					1	*		
Unid. Polychaeta	6	0.2	25	0.8	37	0.8	140	1.6
Unid. fish	141	5.1	214	7.2	435	9.6	1081	12.3
Total	2767	100	2966	100	4553	100	8755	100

Appendix 5. Estimated biomass (g) for prey species in pellets from European shag at Sklinna, Central Norway, 2007–2010. Latin names are given in Appendix 4. * Present in very small percentage. ** Unidentified bearded rockling was either Five-bearded rockling *Ciliat amustela* or Three-bearded rockling *Gaidropsarus vulgaris*. Note that unidentified Gadidae with otolith length < 3 mm have been included in saithe, and that mass was not estimated for unidentified fish species or the unidentified species of polychaete.

Species/Family	2007		2008		2009		2010	
	Biomass	%	Biomass	%	Biomass	%	Biomass	%
Unid. Gadidae	539.5	3.5	131.5	0.4	102.3	0.3	566.5	0.9
Saithe	12472.8	81.3	30652.9	88.2	29975.5	82.2	36794.2	61.6
Poor cod	791.9	5.2	1110.5	3.2	655	1.8	8187.1	13.7
Norway Pout			8.4	*	3.4	*		
Pollack	37.8	0.2	83.2	0.2	19.3	0.1	1416.3	2.4
Cod	1182	7.7	819.8	2.4	2760.6	7.6	7987.5	13.4
Tadpole-fish					153.9	0.4		
Unid. bearded rockling**	11.7	0.1	483.9	1.4	756.3	2.1	129.1	0.2
Eelpout			25.2	0.1	210.5	0.6	74.8	0.1
Norway Haddock	25.9	0.2					290	0.5
Bull-rout			0.3	*	79.1	0.2	58.6	0.1
Sea Scorpion	34.4	0.2	130.3	0.4	76.2	0.2	481.2	0.8
Unid. Labridae					48.1	0.1	310	0.5
Cuckoo wrasse					81.7	0.2		
Goldsinny	72.1	0.5	304.2	0.9	552.3	1.5	720.9	1.2
Butterfish	2.3	*			8.9	*	13.1	*
Unid. Ammodytidae	2.7	*	9	*	41.4	0.1	458.6	0.8
Greater sandeel	82	0.5	361.5	1	247.6	0.7	86.2	0.1
Unid. Gobiidae	0.2	*	8.9	*	8	*	19.9	*
Black goby					38.3	0.1		
Dragonet			5.1	*				
Norwegian topknot			158.3	0.5			10.6	*
Unid. Pleuronectidae			104.2	0.3	45.4	0.1	174.5	0.3
Lemon sole					115.4	0.3		
Total	15255.3	100	34397.3	100	35979.1	100	57779.1	100

Appendix 6. Frequency of occurrence for prey species in pellets from European shag at Sklinna, central Norway, 2007–2010. Latin names are given in Appendix 4. ** Unidentified bearded rockling was either Five-bearded rockling *Ciliat amustela* or Three-bearded rockling *Gaidropsarus vulgaris*. Note that unidentified Gadidae with otolith length < 3 mm have been included in saithe.

Species/Family	2007		2008		2009		2010	
	N	%	N	%	N	%	N	%
Unid. Gadidae	9	11.4	6	5	6	4.3	19	10.1
Saithe	74	93.7	111	92.5	130	92.9	178	94.2
Poor cod	8	10.1	15	12.5	17	12.1	63	33.3
Norway pout			3	2.5	1	0.7		
Pollack	1	1.3	3	2.5	1	0.7	20	10.6
Cod	12	15.2	20	16.7	36	25.7	93	49.2
Tadpole-fish					2	1.4		
Unid. bearded rockling**	1	1.3	3	2.5	3	2.1	8	4.2
Eelpout			1	0.8	2	1.4	8	4.2
Norway haddock	1	1.3					4	2.1
Bull-rout			1	0.8	2	1.4	6	3.2
Sea scorpion	4	5.1	10	8.3	6	4.3	23	12.2
Unid. Labridae	1	1.3	3	2.5	9	6.4	40	21.2
Cuckoo wrasse					1	0.7		
Goldsinny	6	7.6	15	12.5	24	17.1	29	15.3
Butterfish	1	1.3			3	2.1	4	2.1
Unid. Ammodytidae	2	2.5	3	2.5	8	5.7	20	10.6
Greater sandeel	4	5.1	9	7.5	10	7.1	3	1.6
Unid. Gobiidae	1	1.3	7	5.8	28	20	45	23.8
Black goby					1	0.7		
Dragonet			1	0.8				
Norwegian topknot			3	2.5			1	0.5
Unid. Pleuronectidae			4	3.3	3	2.1	10	5.3
Lemon sole					1	0.7		
Unid. polychaeta	4	5.1	15	12.5	24	17.1	49	25.9
Unid. fish	27	34.2	52	43.3	66	47.1	162	85.7
Total number of pellets	79		120		140		189	

Appendix 7. Length measurements (mm) of fish and polychaete species present in pellets from the European shag at Sklinna, central Norway, 2007–2010. Latin names are given in Appendix 4. ** Unidentified bearded rockling was either Five-bearded rockling *Ciliat amustela* or Three-bearded rockling *Gaidropsarus vulgaris*. Note that unidentified Gadidae with otolith length < 3 mm have been included in saithe, and that length was not estimated for unidentified fish species or the unidentified species of polychaete.

Species/Family	Mean	SE	Median	Range	Min.	Max.	N
Unidentified Gadidae	104.5	6.5	103	335.5	49.3	384.8	66
Saithe	68.7	0.4	52.2	385.2	16.7	401.9	14895
Norway pout	85.6	4	86.7	17.7	75.6	93.3	4
Poor cod	96.9	1.2	82.1	210.7	23.1	233.8	919
Pollack	177.4	10.3	165.4	235.8	115.1	350.8	26
Cod	153.1	1.9	150.8	199.7	70	269.7	276
Tadpole-fish	174.8	2.3	174.8	4.6	172.5	177.1	2
Unid. bearded rockling**	176.8	30.2	128.4	489.1	36.1	525.3	17
Eelpout	141.9	15.5	137.7	233.1	66	299.1	15
Norway haddock	294.9	15.3	292.1	81.5	253.3	334.8	5
Bull-rout	81.8	16.4	77.2	139.4	28.4	167.7	9
Sea scorpion	72.7	1.4	69.4	84.3	39.1	123.3	123
Labridae spp.	71.6	3.0	63.1	130.3	48.8	179.2	90
Cuckoo wrasse	198.5						1
Goldsinny	91.5	1.3	92.2	102.3	52.8	155.1	148
Butterfish	98.8	3.5	105.6	26.1	79.5	105.6	9
Ammodytidae spp.	123.2	4.6	115.1	174.4	63.8	238.2	73
Greater sandeel	204.5	5.8	200.6	170.5	138.1	308.6	36
Gobidae spp.	25.1	0.8	22.7	76.7	7.1	83.8	210
Black goby	134						1
Dragonet	93.7						1
Norwegian topknot	108.4	7.6	115.5	60.5	74.3	134.8	10
Pleuronectidae spp.	78.4	4.5	77.7	95.1	39.7	134.8	25
Lemon sole	232.1						1

Appendix 8. Percentage contribution to the total number of fish and biomass, and frequency of occurrence (%), of different year classes of saithe in pellets from the European shag at Sklinna, central Norway, 2007–2010.

		2007	2008	2009	2010
Numerical frequency	Year class 0	93.6	76.9	94.1	92.1
	Year class 1	5.8	22.8	3	7.6
	Year class 2+	0.5	0.3	2.8	0.3
Biomass	Year class 0	11.3	3.8	11.8	9.7
	Year class 1	67.1	91.5	25.9	78.8
	Year class 2+	21.6	4.7	62.3	11.5
Frequency of Occurrence	Year class 0	88.6	78.3	76.4	86.2
	Year class 1	55.7	85	45.7	66.1
	Year class 2+	15.2	5	48.6	7.4