

# The demography and ecology of the European shag *Phalacrocorax aristotelis* in Mor Braz, France

Matthieu FORTIN<sup>1,a</sup>, Charles-André BOST<sup>2</sup>, Philippe MAES<sup>3</sup> and Christophe BARBRAUD<sup>2</sup>

<sup>1</sup> Bretagne vivante, SEPNB, Réserve naturelle des marais de Séné, route de Brouël, 56860 Séné, France

<sup>2</sup> CNRS, Centre d'études biologiques de Chizé, UPR 1934, 79360 Villiers en Bois, France

<sup>3</sup> Université de Bretagne Sud, Institut de Géoarchitecture, EA 2219, BP 573, 56017 Vannes, France

Received 14 May 2012; Accepted 29 November 2012

**Abstract** – An integrated research program was initiated to evaluate if the European shag *Phalacrocorax aristotelis* can be used as a robust indicator of the marine environment in Mor Braz, Brittany, France. This program focuses on aspects of the ecology of the shag including its abundance, demography, diet and at-sea distribution measured at three breeding colonies. The annual population growth rate was estimated at 1.01 for the period 1987–2009. The number of breeding pairs (mean: 565) was highly variable from year to year. Part of this interannual variation was explained by variations in sea surface temperature and sea surface height in winter and spring: the number of breeding pairs was negatively related to sea surface temperature and sea surface height. First year, second year and adult survival probabilities were 0.44, 0.76 and 0.81, respectively. Juvenile survival rate varied between colonies, despite the short distances separating these islets. Average productivity was one young fledged per nest, but it varied between years and islets. Density of individuals at sea varied between 1.40 ind.km<sup>-2</sup> during the breeding season and 3.08 ind.km<sup>-2</sup> after the breeding season had ended. Individuals foraged up to 7 km from the nest and performed on average 2.7 foraging trips per day. The average number of dives deeper than 5 m varied from 126 to 400 per day. Mean diving depth, dive duration and time spent at bottom were 13 m, 28 s, and 19 s respectively. Regurgitated pellets were collected regularly. Four fish families (Gadidae, Gobiidae, Atherinidae and Labridae) represented more than 65% of the preys throughout the year, a percentage reaching more than 95% of the prey from May to October. The other fish in the diet were Cottidae, Ammodytidae, and Clupeidae. The diet of the European shag consisted of benthic fish throughout the year, and also included pelagic fish more frequently between June and October. The synchronous variations of productivity between colonies suggest that some common environmental factors affect this demographic parameter at the regional scale. Thus, the European shag has a good potential for being a reliable ecological indicator of the state of this marine environment. Finally, improved knowledge on the foraging ecology of shags will be useful in the process of designing Marine Protected Areas in the Mor Braz to help ensure sustainable management of marine resources and biodiversity conservation.

**Keywords:** Seabirds / Breeding pairs / Population density / Diet / Wildlife surveys / Bay of Biscay / Atlantic Ocean

## 1 Introduction

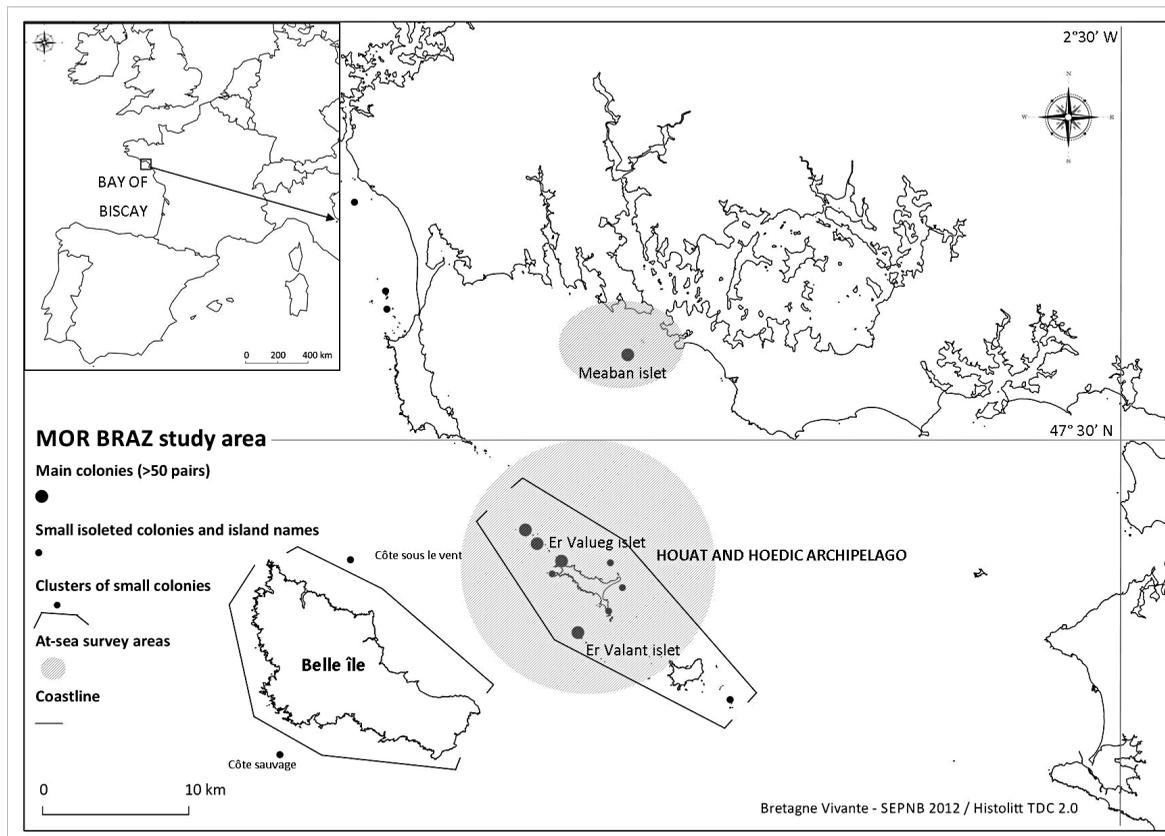
There is an increasing need to develop reliable indicators of the ecological state of the marine environment to support ecosystem-based management of living resources. Seabirds may be useful in this process, since their position at or near the apex of most marine food webs potentially makes them good, reliable sentinel organisms for monitoring changes within marine ecosystems (Furness and Camphuysen 1997; Harding et al. 2005; Piatt et al. 2007). However, producing reliable indicators is challenging and requires a clear definition of the objectives of the indicator, a choice of the seabird species ac-

ording to the objectives, and ideally a good understanding of the ecosystem functioning (Durant et al. 2009).

In 2010, we initiated a research and conservation program (CORMOR) aiming to investigate the use of the European shag *Phalacrocorax aristotelis* (Linnaeus 1761) an inshore generalist bird species, as an ecological indicator of the marine ecosystem of the Mor Braz, Bay of Biscay, France. The main objective of this integrated program is to evaluate whether the European shag can be used as a robust indicator of the marine environment.

The program is based on existing data including: i) long-term data on the abundance of breeding pairs collected annually since the mid-1980s, ii) phenology and breeding performance data collected annually since 2003, iii) multisite capture-mark-recapture data collected annually since 2004, iv)

<sup>a</sup> Corresponding author:  
 matthieu.fortin@bretagne-vivante.org



**Fig. 1.** Map of the study area (Mor Braz) showing the location of the main breeding colonies of the European shag (*Phalacrocorax aristotelis*) and the areas covered by at-sea surveys.

1 diet data collected annually since 2010, and v) at-sea spatial  
 2 distribution data from at-sea based surveys and telemetry. All  
 3 data were collected on islands and islets of the Houat and  
 4 Hoëdic archipelago ( $3^{\circ} 06' - 2^{\circ} 30' W$ ,  $47^{\circ} 30' - 47^{\circ} 18' N$ ,  
 5 Fig. 1), Mor Braz, Brittany. The program also aims to continue  
 6 data collection in the coming years, particularly on diet and at-  
 7 sea spatial distribution data, which will allow an understanding  
 8 of how shags use their oceanographic environment and how its  
 9 variability affects their demography and population dynamics.

10 The aims of this study are threefold. First, we present  
 11 long-term variations in the number of breeding pairs of the  
 12 European shag in Mor Braz and investigate whether these varia-  
 13 tions are related to climatic or oceanographic parameters.  
 14 Second, we provide the first estimates of survival and produc-  
 15 tivity for this population issued from a capture-mark-recapture  
 16 program. Third, we present data on the diet and foraging be-  
 17 haviour and distribution of this shag population, which combin-  
 18 ed with the population parameters, will help to develop a  
 19 comprehensive ecological indicator of this marine ecosystem

## 20 2 Materials and methods

21 Abundance of breeding pairs was estimated from nest  
 22 counts undertaken during annual surveys between March  
 23 and June, performed since 1987. Nest contents (number of  
 24 nests with or without eggs, number of eggs per nest, num-  
 25 ber of chicks per nest, approximate age of the chicks based

on plumage development) were recorded during population  
 26 surveys. We used a log-linear Poisson regression to assess  
 27 between-year changes in the number of breeding pairs using  
 28 logarithms of nest counts with eggs and/or chicks (TRIM soft-  
 29 ware, Pannekoek et al. 2004).  
 30

31 In 2004, we initiated a capture-mark-recapture program.  
 32 Each year in April and May most chicks of pairs breeding on  
 33 three islets, which represent a large proportion (50–60%)  
 34 of the entire breeding population (900 to 1100 breeding pairs),  
 35 were ringed with a stainless steel ring on one leg and with a  
 36 plastic ring on the other leg. Adults were also ringed when  
 37 captured. Each year during surveys, we searched for marked  
 38 individuals over the entire study area. From these capture-  
 39 recapture data, juvenile and adult survival was estimated using  
 40 the software M-SURGE (Choquet et al. 2004).

41 From March 2010 to April 2011, we collected and analysed  
 42 161 pellets collected on roosting sites and at the prox-  
 43 imity of nest sites from one colony (Meaban islet, Fig. 1). A  
 44 total of eight months were sampled. Pellets were dissected un-  
 45 der stereo microscope and otoliths identified by using clas-  
 46 sical identification guides (Härkönen 1986; Campana 2004;  
 47 Lombarte et al. 2006).

48 Mean number of otoliths per pellet, prey frequency and  
 49 the Shannon’s diversity index (Tramer 1969) were calculated.  
 50 The total number of otoliths was divided in half to obtain  
 51 the estimated prey number, assuming that two otoliths corre-  
 52 sponded to one individual fish. A complete one-way analysis

1 of variance (ANOVA) was used to compare the means of total  
 2 prey numbers obtained for different months, after a log trans-  
 3 formation of the data.

4 In 2011, we initiated a study of the at-sea movements of  
 5 breeding individuals that could be easily captured. Birds were  
 6 fitted with GPS tracking devices fixed to their back feathers  
 7 with Tesa tape, and with a temperature depth recorder (TDR)  
 8 fixed to a plastic ring on the leg. Tags were deployed on breed-  
 9 ing individuals with young chicks and recovered 5 days later.

10 We performed transects at sea to get independent data on  
 11 shag foraging distribution during the breeding season. Tran-  
 12 sects covered the entire study area and were performed using  
 13 an inflatable rubber boat. During each transect, all shags de-  
 14 tected on the water were counted and their distance and an-  
 15 gles relative to the measured transect. The density of birds at  
 16 sea was estimated using the software DISTANCE ([http://www.](http://www.ruwpa.st-and.ac.uk/distance/)  
 17 [ruwpa.st-and.ac.uk/distance/](http://www.ruwpa.st-and.ac.uk/distance/), Thomas et al. 2010).

### 18 3 Results

19 The number of breeding pairs was highly variable from  
 20 year to year, ranging from  $370 \pm 34$  to  $780 \pm 51$  with a mean  
 21 of  $565 \pm 250$  (Fig. 2a). The annual population growth rate for  
 22 the period 1987–2009 was estimated at  $1.010 \pm 0.004$ , indi-  
 23 cating that the breeding population size was slowly increasing  
 24 at a rate of 1% per year. However, there was strong inter-year  
 25 variation in the number of breeding pairs, as indicated by the  
 26 low precision of the mean number of breeding pairs (coeffi-  
 27 cient of variation: 44%). Part of this interannual variation was  
 28 explained by variations in sea surface temperature and sea sur-  
 29 face height in winter and spring. Indeed, the number of breed-  
 30 ing pairs was negatively related to a principal component vari-  
 31 able representing variations in sea surface temperature and sea  
 32 surface height from January to April ( $R^2 = 0.50$ ,  $p = 0.0002$ ,  
 33 Fig. 2b). No significant relationship was found between the  
 34 annual number of breeding pairs and the North Atlantic Oscil-  
 35 lation (NAO).

36 From 2004 to 2011, 2 700 individuals were ringed and  
 37 3 400 resightings were made. Resighting probability increased  
 38 with age from 0.20 for one year old individuals to 0.85 for  
 39 five years old and older individuals. As expected, there was  
 40 a strong age effect on annual survival probability. First year,  
 41 second year and adult survival probabilities were respectively  
 42  $0.44 \pm 0.04$ ,  $0.76 \pm 0.07$  and  $0.81 \pm 0.03$ . In addition to age  
 43 effects on survival, island effects were detected, particularly  
 44 on juvenile survival. At Er Valueg islet, juvenile survival was  
 45 lower than at Er Valant islet and Meaban islet ( $0.24 \pm 0.03$ ,  
 46  $0.43 \pm 0.05$ , and  $0.60 \pm 0.08$  respectively), despite the short  
 47 distances separating these islets. No sex effect was detected on  
 48 adult survival.

49 Average productivity was  $1.00 \pm 0.47$  young fledged per  
 50 nest, but varied a great deal between years and islets. The mean  
 51 number of young fledged per nest was particularly low in 2007  
 52 (0.42), and to a lesser extent in 2006 and 2008 (0.87 and 0.97  
 53 respectively). Productivity was lower on one islet than on the  
 54 two other islets, which were monitored regularly, but interan-  
 55 nual variations were highly synchronised between islets.

56 A total of 231 individual shags were observed sitting on  
 57 water or feeding at sea on the 53 transects, which represented a

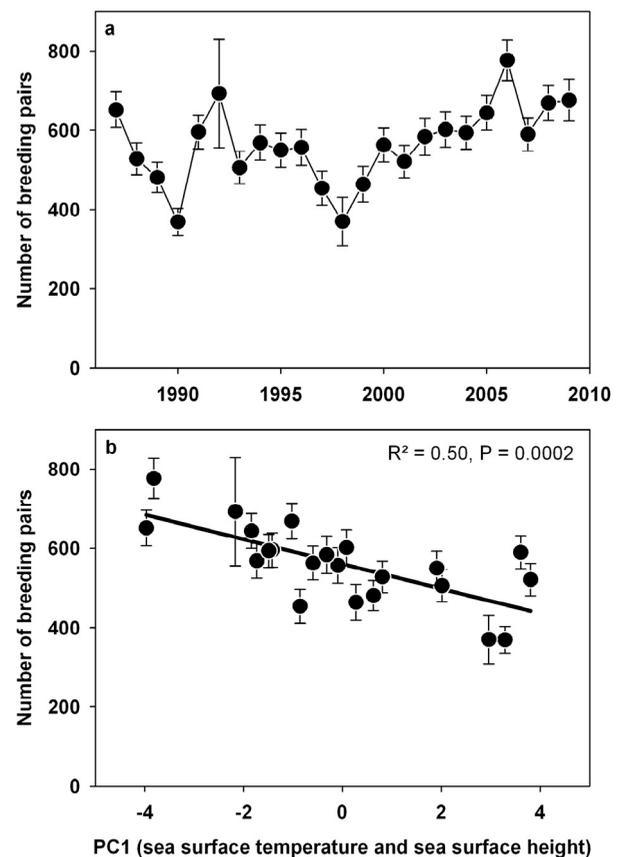
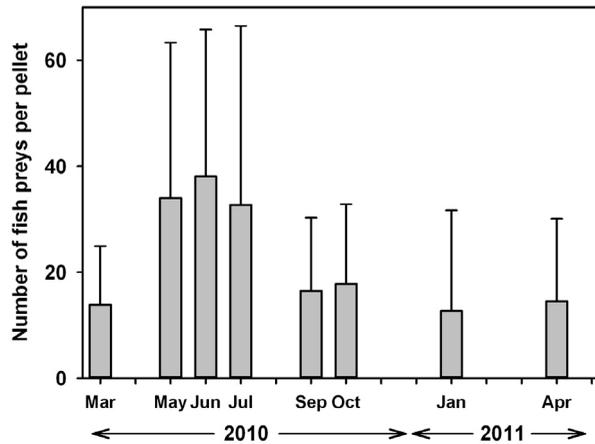


Fig. 2. Number of breeding pairs as a function of (a) year, and (b) a covariate representing variations in sea surface temperature anomalies and sea surface height on a  $1^\circ \times 1^\circ$  rectangle area centred on the study area (B). The covariate was the first axis of a principal component analysis run on monthly sea surface temperature anomalies and sea surface height in January, February, March and April. Errors bars are  $\pm 1$  SD.

total distance covered of 188 km. The probability of detecting  
 shags sitting on the water declined differentially in spring and  
 summer, with increasing distance from the transects: it was re-  
 spectively 0.94, 0.26 and 0.07 at 100 m, 300 m and 600 m from  
 transects in spring, and 0.90, 0.37 and 0.02 at 100 m, 300 m  
 and 600 m from transects in summer. Density of individuals  
 at sea varied between seasons: in spring during the breeding  
 season, it was  $1.34 \pm 0.27$  ind.km<sup>-2</sup>, but this reached  $3.08 \pm$   
 $0.98$  ind.km<sup>-2</sup> in summer following the end of the breeding  
 period.

A total of four breeding individuals raising young chicks  
 (1–2 weeks old) were equipped and recaptured with GPS  
 and TDR in 2011. Preliminary results indicate that on aver-  
 age individuals performed 2.7 foraging trips per day. The aver-  
 age number of dives deeper than 5 m varied from 126 to  
 400 per day. Mean diving depth was 13 m (maximum recorded  
 38 m), mean dive duration was 28 s, and mean time spent at  
 bottom was 19 s. During foraging trips, the maximum recorded  
 distance from the nest was 7 km, but some individuals foraged  
 no further than 1.5 km from their nests.

In Mor Braz, the European shag diet mainly consisted of  
 seven fish families. Three of them are benthic or demersal,



**Fig. 3.** Mean monthly number of preys per pellet of European shags from the colony of Meaban islet, Mor Braz, France. Errors bars are  $\pm 1$  SD.

1 while the other four are schooling pelagic fishes (Table 1).  
 2 This table also compares the abundances of different prey  
 3 types in different sites distributed along the European Atlantic  
 4 coastline from the north of Norway to Corsica (Mediterranean  
 5 sea). It concerns two of the three sub species of the Euro-  
 6 pean shag, *P. a. aristotelis* and *P. a. desmarestii*. Our results  
 7 show that four families represented more than 65% of the  
 8 preys throughout the year: Gadidae, Gobiidae, Atherinidae and  
 9 Labridae; this reached more than 95% from May to October.  
 10 The other fish were, in descending order, Cottidae, Ammodyti-  
 11 dae, and Clupeidae. Results showed that benthic fishes were  
 12 preyed upon throughout the year. Gobiidae represented more  
 13 than 30% of shags' diet during five of the eight months sam-  
 14 pled. Labridae and Cottidae were regularly preyed upon during  
 15 the four seasons and contributed from 1% to 20% of the diet.  
 16 Pelagic fishes were preyed upon more frequently between June  
 17 and October. Gadidae were the main preys in June with a con-  
 18 tribution of 59% of the diet, which then gradually decreased  
 19 to 35% in October. Atherinidae could also reach high percent-  
 20 ages, but represented more than 30% of the diet only during  
 21 two months. The diversity index showed a rather uniform value  
 22 during the studied year (values ranged from 1.01 to 1.67).

23 The monthly mean ( $\pm$ SD) of the total number of preys  
 24 found per pellet was  $22.7 \pm 3.6$ , when calculated over the  
 25 entire time period of the study. However, there were signifi-  
 26 cant monthly differences (ANOVA:  $F_{7,151} = 4.63$ ,  $p < 0.001$ ).  
 27 During the chick-rearing period (from May to July) the aver-  
 28 age number of preys found per pellet was significantly higher  
 29 ( $34.8 \pm 7.4$ ) than in the rest of the year ( $14.4 \pm 3.1$ ). There was  
 30 no significant difference between months within (May to July;  
 31  $F_{2,61} = 0.39$ ,  $p = 0.68$ ) or outside the chick-rearing period  
 32 (August to April;  $F_{4,91} = 0.37$ ,  $p = 0.83$ ).

#### 33 4 Discussion

34 Using long-term monitoring data, our results showed that  
 35 the number of breeding pairs of shags varied from year to year.  
 36 Our analyses suggest that 50% of this interannual variation  
 37 could be explained by environmental variability, particularly

by variations in sea surface temperature and sea surface height. 38  
 As winter and spring sea surface temperatures and sea surface 39  
 height increased the number of breeding pairs decreased. 40

41 At present, the demographic causes of the variations in  
 42 breeding numbers remain unknown, but the high annual sur-  
 43 vival probabilities and their relative stability suggest that a  
 44 change in adult survival is not the main driver. Adult survival  
 45 in our study population was intermediate between adult sur-  
 46 vival estimates obtained in more northerly or more southerly  
 47 breeding populations. For example, adult survival rates were  
 48  $0.72 \pm 0.05$  at Cies Island, north-western Spain (Velando and  
 49 Freire 1999), and  $0.88 \pm 0.01$  in Isle of May, Scotland (Harris  
 50 et al. 1994). As in Frederiksen et al. (2008), first year and  
 51 second year survival appeared more variable than adult sur-  
 52 vival. We suspect variations in breeding probabilities, produc-  
 53 tivity and/or recruitment of breeding individuals to be the main  
 54 drivers of interannual changes in the number of breeding pairs.  
 55 In the near future, we plan to quantify the respective contribu-  
 56 tions of these demographic parameters to the changes in the  
 57 population growth rate, using longer time series and retrospec-  
 58 tive analyses (see Caswell 2001).

59 The ecological mechanisms responsible for the negative rela-  
 60 tionship between the number of breeding pairs and the sea  
 61 surface temperature, are still unclear. As suggested or shown  
 62 in several seabird species (e.g., Kitayski and Golubova 2000;  
 63 Durant et al. 2003; Harris et al. 2005; Bertram et al. 2005),  
 64 we strongly suspect an indirect effect of sea surface tempera-  
 65 tures and food abundance and/or accessibility, which in turn affect  
 66 the birds' energetics and population parameters. In the shag  
 67 population nesting on the Isle of May, attendance of breed-  
 68 ers, timing of breeding, annual chick production and first year  
 69 survival were shown to be linked to herring (*Clupea haren-*  
 70 *gus*) abundance or the size of sandeels (*Ammodytes marinus*)  
 71 taken by puffins (*Fratercula arctica*) breeding on the island  
 72 (Aebischer and Wanless 1992). Furthermore, on this same is-  
 73 land, laying date and breeding success of shags were corre-  
 74 lated with local sea surface temperature (Frederiksen et al.  
 75 2004), and Frederiksen et al. (2007) showed that shag pro-  
 76 ductivity (number of fledged chicks per nest) was positively  
 77 linked to the larval sandeel (the main prey species) abundance  
 78 in the previous spring. However, Frederiksen et al. (2008) also  
 79 showed that, within the same population, survival of second  
 80 year and adult shags was substantially reduced in years when  
 81 high precipitation and strong offshore winds coincided at the  
 82 end of winter. These authors suggested both direct and indirect  
 83 impacts of weather events on shags, with strong winds and  
 84 high precipitation causing mortality, presumably through hy-  
 85 pothemia because shag plumage is not completely waterproof  
 86 (Grémillet et al. 1998), and onshore gales inhibiting foraging,  
 87 perhaps because of increased turbidity during the strongest  
 88 wind episodes (Daunt et al. 2006). Together, these results sug-  
 89 gest that late winter is a stressful period for shags. Studies sim-  
 90 ilar to those conducted in Scotland now need to be conducted  
 91 at more southerly localities, such as our study site, since envi-  
 92 ronmental conditions and diet of shags may differ there.

93 Our tracking study, at-sea observations and previous stud-  
 94 ies on the European shag (Wanless et al. 1991) clearly sug-  
 95 gest that, during the breeding period, individuals forage in  
 96 waters situated in the vicinity of their nests (typically less

**Table 1.** Diet of European shags in different locations of the Atlantic and Mediterranean. Data are expressed as percentage of frequency of occurrence (OF) or of numerical frequency (NF), depending on the method used by the different authors. (–) indicates that a prey group is absent or accounts for less than 0.1%. Completed and modified from Velando and Freire (1999).

Location	Method	Gobidae	Gadidae	Atherinidae	Labridae	Cottidae	Ammodytidae	Clupeidae	Other	Ref. (*)
Hornoy (Norway)	NF	–	40	–	–	–	56	–	3	8
Bleiksoy (Norway)	NF	–	69	–	–	–	15	–	16	8
Rogaland (Norway)	NF	–	50	–	20	–	15	–	15	8
Clyde (Scotland)	NF	3	13	–	1	–	78	0.6	4	2
Farne (Scotland)	NF	–	4	–	–	–	81	–	15	3
Loch Ewe (Scotland)	NF	–	59	–	–	–	41	–	–	4
Shetland (Scotland)	OF	–	–	–	–	–	100	–	–	7
Isle of May (Scotland)	OF	11	45	–	–	–	95	–	15	9
Cornwall (England)	OF	2	4	–	13	–	51	30	14	1
Brittany (France)	NF	–	35	–	16	–	26	–	23	5
Meaban (Morbihan, France)	NF	33	27	19	10	6	2	–	3	This study
Caladonia (Asturias, Spain)	NF	–	11	35	52	–	–	–	2	10
Cies (Galicia, Spain)	NF	6	7	3	5	–	75	–	4	11
Ons (Galicia, Spain)	NF	30	4	20	5	–	38	–	3	11
Corcega (Corsica, France)	OF	–	–	5	78	–	33	–	28	6

(\*) 1 Steven (1933), 2 Lumsden and Haddow (1946), 3 Pearson (1968), 4 Mills (1969), 5 Pasquet (1987), 6 Guyot (1988), 7 Harris and Riddiford (1989), 8 Barret et al. (1990), 9 Harris and Wanless (1991), 10 Alvarez (1998), 11 Velando and Freire (1999).

1 than 10 km). Therefore, at least during the breeding season,  
 2 we might expect site specific effects of local oceanographic  
 3 conditions on foraging performances and possibly on some  
 4 demographic parameters. This idea is congruent with our re-  
 5 sults showing site specific variations in juvenile survival and  
 6 productivity. Although our sample size was relatively small,  
 7 mean diving duration and depths tended to be slightly lower  
 8 than those recorded in other populations, with mean dive du-  
 9 rations varying between 38 s to 70 s and mean depths between  
 10 20 m and 35 m (Wanless et al. 1991; 1997; Grémillet et al.  
 11 1998). This may be due to specific bathymetric characteristics  
 12 of our study site, which has an average depth of 21 m while  
 13 the average depth around the Isle of May is 40 m.

14 The increase in density estimates observed between the  
 15 breeding season and the summer following the end of the  
 16 breeding period has also been observed in the double-crested  
 17 cormorant (*Phalacrocorax auritus*) on the Laurentian Great  
 18 Lakes, using the same approach to estimate density (line tran-  
 19 sect distance sampling, Ridgway 2010). In both cases, the in-  
 20 crease in density may correspond to individuals from areas be-  
 21 yond the study sites moving into the sampled region at the end  
 22 of the nesting period, and/or a reflection of fledging and the  
 23 dispersal of the fledglings from their birth place.

24 Our results confirm that the European shag is an oppor-  
 25 tunistic predator that takes advantage of particular species  
 26 abundance in a given season (Barret 1991), and that the vari-  
 27 ability in its dietary composition in different locations may be  
 28 related to geographical differences in the availability of po-  
 29 tential prey species (Velando and Freire 1999). This was par-  
 30 ticularly obvious in summer, when diet markedly shifted to  
 31 the Gadidae. Assuming that one pellet, on average, is pro-  
 32 duced per day (Johnstone et al. 1990), it may be inferred that  
 33 the number of daily ingested preys more than doubles dur-  
 34 ing the reproductive period, especially during the feeding of

chicks. However, assessing diet from pellets in shags might  
 have underestimated the number and size of prey items taken  
 (Johnstone et al. 1990). At our study site, diet markedly dif-  
 fered from the main prey consumed by shags on the Isle of  
 May and Cíes Islands, where sandeels constitute the domi-  
 nant prey species in the diet of breeding individuals (Wanless  
 et al. 1993; Velando and Freire 1999). However, as observed by  
 Velando and Freire (1999) on the Islands of Ons (NW Spain),  
 we found seasonal changes in diet, where Gobiidae and Gad-  
 iidae were the most frequently consumed prey species in winter  
 (Table 1).

Thus, the synchronous variations of productivity between  
 different colonies suggest that some common environmental  
 factors affect this demographic parameter at the regional scale.  
 This, together with the strong relationship between the num-  
 ber of breeding pairs and sea surface temperature, and the high  
 interannual variability in productivity and number of breed-  
 ing pairs suggest that the European shag has good potential  
 to make a reliable ecological indicator of the state of this  
 marine environment. However, our preliminary results also in-  
 dicate that local factors (at the scale of the islet and its sur-  
 rounding) may also affect demographic parameters. Identifying  
 these factors and the relationships between demographic  
 parameters and environmental factors will be an important step  
 towards developing a long-term indicator. Behavioural data us-  
 ing telemetry further reinforce the potential of the European  
 shag as an ecological indicator, since its foraging distribution  
 during the breeding period appears to be restricted to a few  
 kilometres from the nest.

Improved knowledge on the foraging ecology and demog-  
 raphy of shags will be useful in the process of designing Ma-  
 rine Protected Areas in the Mor Braz, which will help to ensure  
 sustainable management of marine resources and biodiversity  
 conservation. Our results suggest that the European shag

1 could be used as a reliable ecological indicator of the state of  
2 such a Marine Protected Area.

3 *Acknowledgements.* We thank all the fieldworkers involved in the  
4 monitoring of shags in Mor Braz. We thank Yves Desaunay, Jean-  
5 Edouard Legendre, Julien Planchais, Amélie Kergosien, Margaux  
6 Dissais, Amandine Juhel and Nicolas Le Hingrat for their contribu-  
7 tion to the pellet analyses, and Marine Leicher for her help with the  
8 map design. This study was partly supported by *the Agence des Aires*  
9 *Marines Protégées* (AAMP) and *Région Bretagne* (ASOSC plan) as  
10 part of the program CORMOR. We thank two anonymous reviewers  
11 for useful comments that improved the manuscript.

## 12 References

- 13 Aebischer N.J., Wanless S., 1992, Relationships between colony size  
14 and environmental conditions for shags *Phalacrocorax aristotelis*  
15 on the Isle of May, Scotland. *Bird Study* 39, 43–52.
- 16 Alvarez D., 1998, The diet of shags *Phalacrocorax aristotelis* L. in  
17 the Cantabrian sea (North of Spain) during the breeding season.  
18 *Seabird* 20, 22–30.
- 19 Barret R.T., 1991, Shags (*Phalacrocorax aristotelis* L.) as poten-  
20 tial samplers of juvenile saithe (*Pollachius virens* L.) stocks in  
21 Northern Norway. *Sarsia* 76, 153–156.
- 22 Barret R.T., Røv N., Loen J., Montevecchi W.A., 1990, Diets of shags  
23 *Phalacrocorax aristotelis* and cormorants *P. carbo* in Norway and  
24 possible interactions for gadoid stock recruitment. *Mar. Ecol.*  
25 *Prog. Ser.* 66, 205–218.
- 26 Bertram D.F., Harfenist A., Smith B.D., 2005, Ocean climate and El  
27 Niño impacts on survival of Cassin’s auklets from upwelling and  
28 downwelling domains of British Columbia. *Can. J. Fish. Aquat.*  
29 *Sci.* 62, 2841–2853.
- 30 Campana S.E., 2004, Photographic atlas of fish otoliths of the north-  
31 west Atlantic Ocean. *Can. Spec. Publ. Fish. Aquat. Sci.* 133,  
32 1–284.
- 33 Camphuysen C.J., 2005, Understanding marine foodweb processes:  
34 an ecosystem approach to sustainable Sandeel fisheries in the  
35 North Sea. IMPRESS Report, Koninklijk Nederlands Instituut  
36 voor Onderzoek der Zee, Q5RS-2000-30864, Texel.
- 37 Caswell H., 2001, Matrix population models. Sinauer Associates,  
38 Sunderland, MA.
- 39 Choquet R., Reboulet A.M., Pradel R., Gimenez O., Lebreton J.D.,  
40 2004, M-SURGE: new software specifically designed for mul-  
41 tistate capture-recapture models. *Anim. Biodiv. Conserv.* 27,  
42 207–215.
- 43 Daunt F., Afanasyev V., Silk J.R.D., Wanless S., 2006, Extrinsic and  
44 intrinsic determinants of winter foraging and breeding phenology  
45 in a temperate seabird. *Behav. Ecol. Soc.* 59, 381–388.
- 46 Durant J.M., Anker-Nilssen T., Stenseth N.C., 2003, Trophic interac-  
47 tions under climate fluctuations: the Atlantic puffin as an exam-  
48 ple. *Proc. R. Soc. Lond. B Biol.* 270, 1461–1466.
- 49 Durant J.M., Hjermann D.Ø., Frederiksen M., Charrassin J.B.,  
50 Le Maho Y., Sabarros P.S., Crawford R.J.M., Stenseth N.Chr.,  
51 2009, Pros and cons of using seabirds as ecological indicators.  
52 *Clim. Res.* 39, 115–119.
- 53 Frederiksen M., Harris M.P., Daunt F., Rothery P., Wanless S., 2004,  
54 Scale-dependent climate signals drive breeding phenology of  
55 three seabird species. *Global Change Biol.* 10, 1214–1221.
- Frederiksen M., Mavor R.A., Wanless S., 2007, Seabirds as environ-  
56 mental indicators: the advantages of combining data sets. *Mar.*  
57 *Ecol. Prog. Ser.* 352, 205–211. 58
- Frederiksen M., Daunt F., Harris M.P., Wanless S., 2008, The demo-  
59 graphic impact of extreme events: stochastic weather drives sur-  
60 vival and population dynamics in a long-lived species. *J. Anim.*  
61 *Ecol.* 77, 1020–1029. 62
- Furness R.W., Camphuysen K., 1997, Seabirds as monitors of the ma-  
63 rine environment. *ICES J. Mar. Sci.* 54, 726–737. 64
- Grémillet D., Tuschy I., Kierspel M., 1998, Body temperature and  
65 insulation in diving great cormorants and European shags. *Funct.*  
66 *Ecol.* 12, 386–394. 67
- Guyot I., 1988, Relationships between shag feeding areas and human  
68 fishing activities in Corsica (Mediterranean Sea). In: Tasker M.L.  
69 (Ed.) *Seabird food and feeding ecology. Proc. 3<sup>rd</sup> Intl. Conference*  
70 *of the Seabird Group*, Sandy, pp. 22–23. 71
- Harding A.M., Piatt J.F., Sydeman W.J., 2005, Bibliography of liter-  
72 ature on seabirds as indicators of the marine environment. USGS  
73 Alaska Science Centre, Anchorage, available at [http://alaska.](http://alaska.usgs.gov/science/biology/seabirds_foragefish/sai/)  
74 [usgs.gov/science/biology/seabirds\\_foragefish/sai/](http://alaska.usgs.gov/science/biology/seabirds_foragefish/sai/) 75
- Harkönen T., 1986, Guide of the bony fishes of the northeast Atlantic.  
76 Danbiu ApS. Biological consultants. 77
- Harris M.P., Riddiford N.J., 1989, The food of some young seabirds  
78 on Fair Isle in 1986–88. *Scottish Birds* 15, 119–125. 79
- Harris M.P., Wanless S., 1991, The importance of the lesser sandeel  
80 *Ammodytes marinus* in the diet of shag *Phalacrocorax aristotelis*.  
81 *Ornis Scand.* 22, 375–382. 82
- Harris M.P., Buckland S.T., Russell S.M., Wanless S., 1994, Year-  
83 and age-related variation in the survival of adult European shags  
84 over a 24-year period. *Condor* 96, 600–605. 85
- Harris M.P., Anker-Nilssen T., McCleery R.H., Erikstad K.E., Shaw  
86 D.N., Grosbois V., 2005, Effect of wintering area and climate  
87 on the survival of adult Atlantic puffins *Fratercula arctica* in the  
88 eastern Atlantic. *Mar. Ecol. Prog. Ser.* 297, 283–296. 89
- Johnstone I.G., Harris M.P., Wanless S., Graves J.A., 1990, The  
90 usefulness of pellets for assessing the diet of adult shags  
91 *Phalacrocorax aristotelis*. *Bird Study* 37, 5–11. 92
- Kitaysky A.S., Golubova E.G., 2000, Climate change causes contrast-  
93 ing trends in reproductive performance of planktivorous and pis-  
94 civorious alcids. *J. Anim. Ecol.* 69, 248–262. 95
- Lombarte A., Chic Ò., Parisi-Baradad V., Olivella R., Piera J., García-  
96 Ladona E., 2006, A web-based environment from shape analysis  
97 of fish otoliths. *The AFORO database. Scient. Mar.* 70, 147–152. 98
- Lumsden W.H.R., Haddow, A.J., 1946, The food of the shag  
99 (*Phalacrocorax aristotelis*) in the Clyde sea area. *J. Anim. Ecol.*  
100 15, 35–42. 101
- Mills D., 1969, The food of the shag in Loch Ewe, Ross-Shire.  
102 *Scottish Birds* 5, 264–268. 103
- Pannekoek J., van Strien A.J., Roby D., 2004, TRIM (Trends and  
104 indicators for monitoring data). Statistics Netherlands, Vooburg. 105
- Pasquet E., 1987, Relationships between Brittany shags and seawa-  
106 ters resources. Muséum National d’Histoire Naturelle, Centre de  
107 recherches sur la biologie des populations d’oiseaux, Paris. 108
- Pearson T.H., 1968, The feeding ecology of sea-bird species breed-  
109 ing on the Farne Islands, Northumberland. *J. Anim. Ecol.* 37,  
110 53–102. 111
- Piatt J.F., Harding A.M.A., Shultz M., Speckman S.G., van Pelt T.I.,  
112 Drew G.S., Kettle A.B., 2007, Seabirds as indicators of ma-  
113 rine food supplies: Cairns revisited. *Mar. Ecol. Prog. Ser.* 352,  
114 221–235. 115
- Ridgway M.S., 2010, Line transect distance sampling in aerial sur-  
116 veys for double-crested cormorants in coastal regions of Lake  
117 Huron. *J. Great Lakes Res.* 36, 403–410. 118

- |   |  |  |
|---|--|--|
| <p>1 Steven J., 1933, The food consumed by shags and cormorants around<br/>                 2 shores of Cornwall (England). J. Mar. Biol. Assoc. UK 19,<br/>                 3 277–292.<br/>                 4 Thomas L., Buckland S.T., Rexstad E.A., Laake J.L., Strindberg S.,<br/>                 5 Hedley S.L., Bishop J.R.B., Marques T.A., Burnham K.P., 2010,<br/>                 6 Distance software: design and analysis of distance sampling sur-<br/>                 7 veys for estimating population size. J. Appl. Ecol. 47, 5–14.<br/>                 8 Tramer E.J., 1969, Bird species diversity: components of Shannon’s<br/>                 9 formula. Ecology 50, 927–929.<br/>                 10 Velando A., Freire J., 1999, Intercolony and seasonal differences<br/>                 11 in the breeding diet of European shags on the Galician coast<br/>                 12 (NW Spain). Mar. Ecol. Prog. Ser. 188, 225–236.</p> | <p>Velando A., Freire J., 2002, Population modelling of European shags<br/>                 (<i>Phalacrocorax aristotelis</i>) at their southern limit: conservation<br/>                 implications. Biol. Conserv. 107, 59–69.<br/>                 Wanless S., Harris M.P., Morris J.A., 1991, Foraging range and feed-<br/>                 ing locations of shags <i>Phalacrocorax aristotelis</i> during chick<br/>                 rearing. Ibis 133, 30–36.<br/>                 Wanless S., Harris M.P., Russell A., 1993, Factors influencing food-<br/>                 lead sizes brought in by shags <i>Phalacrocorax aristotelis</i> during<br/>                 chick rearing. Ibis 135, 19–24.<br/>                 Wanless S., Harris M.P., Burger A.E., Buckland S.T., 1997, Use of<br/>                 time-at-depth recorders for estimating depth and diving perfor-<br/>                 mance of European shags. J. Field Ornithol. 68, 547–561.</p> | <p>13<br/>14<br/>15<br/>16<br/>17<br/>18<br/>19<br/>20<br/>21<br/>22<br/>23<br/>24</p> |
|---|--|--|