

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

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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⁻² during the breeding season and 3.08 ind.km⁻² 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)

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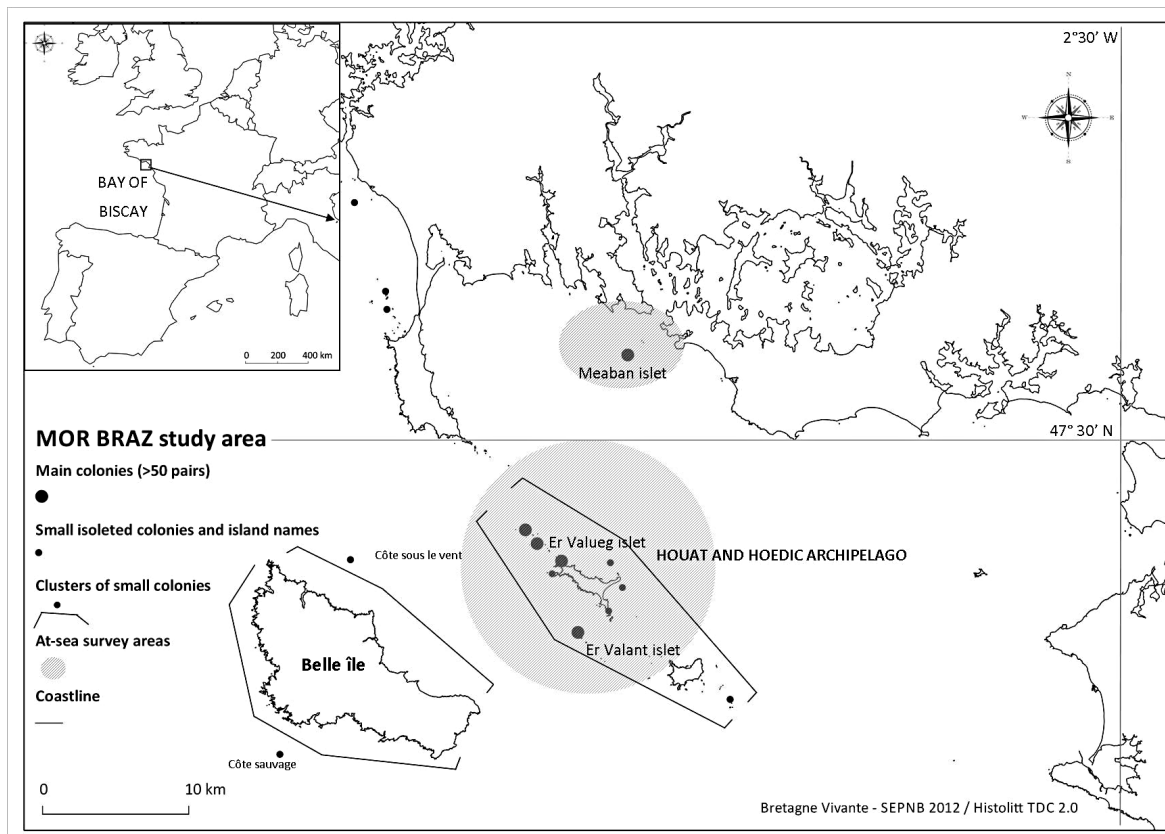


Fig. 1. Map of the study area (Mor Braz) showing the location of the main breeding colonies of the European shag (*Phalacrocorax aristotelis*) and the areas covered by at-sea surveys.

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.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 ± 34 to 780 ± 51 with a mean
 21 of 565 ± 250 (Fig. 2a). The annual population growth rate for
 22 the period 1987–2009 was estimated at 1.010 ± 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 ± 0.04 , 0.76 ± 0.07 and 0.81 ± 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 ± 0.03 ,
 46 0.43 ± 0.05 , and 0.60 ± 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 ± 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

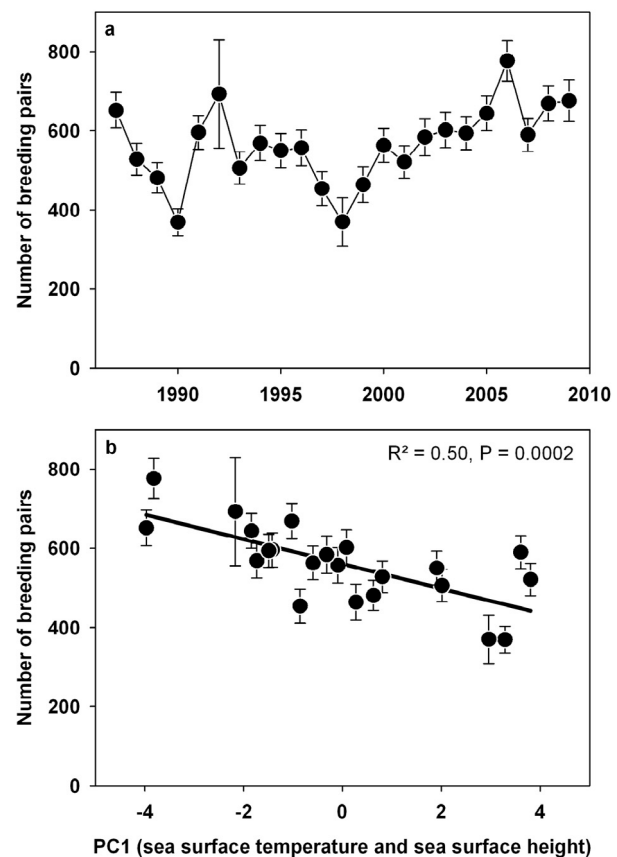


Fig. 2. Number of breeding pairs as a function of (a) year, and (b) a covariate representing variations in sea surface temperature anomalies and sea surface height on a $1^\circ \times 1^\circ$ rectangle area centred on the study area (B). The covariate was the first axis of a principal component analysis run on monthly sea surface temperature anomalies and sea surface height in January, February, March and April. Errors bars are ± 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 ± 0.27 ind.km⁻², but this reached $3.08 \pm$
 0.98 ind.km⁻² 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,

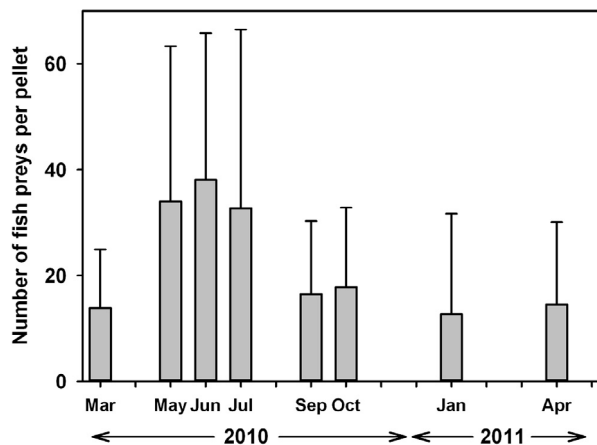


Fig. 3. Mean monthly number of preys per pellet of European shags from the colony of Meaban islet, Mor Braz, France. Errors bars are ± 1 SD.

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 ± 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 ± 7.4) than in the rest of the year (14.4 ± 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 ± 0.05 at Cies Island, north-western Spain (Velando and
 49 Freire 1999), and 0.88 ± 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.

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