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Short-term indirect effects of the 'Prestige' oil spill on European shags: changes in availability of prey

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ABSTRACT: In 2003, immediately following the 'Prestige' oil spill in Galicia, Spain, we studied the reproductive performance of European shags *Phalacrocorax aristotelis* at Illas Cíes, the main breeding ground for the species in Spain. Over the 10 yr preceding the spill, we monitored the breeding and the dynamics of the Illas Cíes population. We performed 1000 simulations of the population dynamics using the population parameters and their variability for the pre-spill period. The number of breeding pairs counted in 2003 was lower than any of the values predicted by the simulation models, suggesting that population parameters changed after the 'Prestige' wreck. Environmental conditions cannot explain the observed effects because weather conditions were far from severe in 2003. The analysis of shag casualities showed that despite the extensive oiling of Illas Cíes and nearby waters it is unlikely that shags were killed in large numbers. Nevertheless, the shag feeding grounds around Illas Cíes, which are mainly sandy bottoms, were continuously exposed to oil pollution throughout the shag breeding season as revealed by the high levels of pollutants in sediments, plankton, and other organisms. In the pre-spill years, shags showed low seasonal dietary variation, feeding mainly on sandeels. Nevertheless, in 2003, there was a dietary shift with a lower occurrence of sandeel that, together with sandeel fishery data, indicate lower sandeel availability at foraging areas. In addition, reproductive performance in 2003 was significantly lower and chick condition was poorer compared to the pre-spill years. When all this information is taken into account, the picture that emerges strongly suggests that the European Shag population in Illas Cíes is suffering a negative impact of an indirect nature mediated through a reduction on the availability of a highly preferred forage-fish.

KEY WORDS: European shag · *Phalacrocorax aristotelis* · 'Prestige' · Oil contamination · Population dynamics · Diet · Reproductive performance

INTRODUCTION

Seabirds are long-lived animals and upper trophic level consumers. Thus, seabirds are good candidates to detect changes in the marine ecosystem (Furness & Greenwood 1993), especially as indicators of prey abundance (e.g. Cairns 1987, Barrett et al. 1990, Lewis et al. 2001) and marine pollution (e.g. Becker et al. 1993, Bearhop et al. 2000). Large oil spills are one of the pollution events most likely to have dramatic effects on marine ecosystems. Despite the assumed role of seabirds as marine monitors, the responses of seabird populations to oil spills are poorly documented and remain controversial (e.g. Eppley 1992, Paine et al. 1996, Piatt & Anderson 1996). Direct bird mortality immediately following an oil spill typically attracts the greatest public and scientific concern (e.g. Wiens et al. 1984, Piatt & Ford 1996), although a direct cause and effect relationship between oil spills and seabird population numbers is not easy to demonstrate. In some cases oil slicks have killed great numbers of seabirds but without any apparent consequences at the population level (Dunnet 1982). By comparison, delayed (long-term), indirect or sublethal effects of acute oil pollution on seabird populations have received much less attention. Such effects cannot be ignored because of their potential consequences at the population level (Golet et al. 2002)

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which, in turn may act as indicators of oil pollution disturbance on the marine environment.

Indirect effects, whether delayed or not, include effects through prey availability or habitat conditions and may also be sublethal. Sublethal effects on seabirds, derived from direct exposure to oil and indirect oil incorporation into the marine food chain, include a large array of inflammatory and toxic effects on internal organs (e.g. Fry & Lowenstine 1985, Leighton 1993), as well as damage to the immune system (reviewed in Briggs et al. 1996) and impaired health conditions (e.g. Khan & Ryan 1991, Golet et al. 2002). In the long term, sublethal exposure to oil may result in continued poor body condition, reproduction and survival of waterbirds in heavily oiled areas (Butler et al. 1998, Esler et al. 2000, Golet et al. 2002). For example, in Prince William Sound, Alaska, pigeon guillemots *Cepphus columba* showed unequivocal toxic signs of oil exposure 10 yr after the Exxon Valdez disaster (Seiser et al. 2000, Golet et al. 2002). In addition, oil pollution may reduce food availability through habitat degradation and disturbance, prey decline, trophic cascades, and/or prey behaviour changes (e.g. Peterson 2001, Peterson et al. 2003). Effects of oil spills related to food limitation are poorly documented in seabirds (but see Golet et al. 2002). Nevertheless, seabirds are very sensitive to changes in food supply and respond rapidly with changes in their life history parameters (Cairns 1987, Monaghan et al. 1992). In long-lived species, such as seabirds, current reproductive investment is likely to be regulated by its impact on the future reproduction of the parents (Stearns 1992), therefore adult seabirds should reduce their reproductive effort when food availability is low (Drent & Daan 1980, Velando & Alonso-Alvarez 2003). In fact, seabirds respond most strongly to prey variability with variation in breeding success rather than adult survival rate (Cairns 1987, Montevecchi 1993, Velando & Alonso-Alvarez 2003, but see Oro & Furness 2002).

On 13 November 2002, the oil tanker 'Prestige' started to spill heavy bunker oil off the coasts of Galicia (NW Spain). During the next 6 d the ship followed an erratic course back and forth along the Galician coast, spreading out some 19000 tonnes of oil and finally sinking 130 miles west of Illas Cíes (42° 12′ N, 12° 03′ W). During the following months the wreck further released 40000 tonnes of oil. Wind and currents pushed oil into a vast coastal area, from northern Portugal to Brittany (France), making the 'Prestige' oil spill the biggest large-scale perturbation of its type in Europe. Galicia suffered 3 severe 'black tides' and the most heavily oiled area was Costa da Morte (Fig. 1).

The European shag *Phalacrocorax aristotelis*, a typical inshore seabird, is the second most numerous seabird breeding in Galicia. The breeding population is quite dispersed although Illas Cíes holds the most important colony, approximately 42% of the Iberian population and 2% of the world population (Velando et al. 1999a). At Illas Cíes (Fig. 1), this species shows low seasonal diet variation feeding mainly on sandeels (family Ammodytidae) (71 to 86% of prey items: Velando & Freire 1999). On 3 December, Illas Cíes and the rest of the outer area of the Ría de Vigo (Fig. 1) suffered the impact of the first of a series of large oil slicks and, as a consequence, some areas remained oiled for several months. The European shags breeding at Illas Cíes forage by diving in nearshore habitats at an average distance of less than 20 km away from the breeding colony during the whole year (Velando 1997); thus, potentially they were exposed to oil pollution.

In this study, we examined the short-term effects of the 'Prestige' oil spill on European shags breeding at Illas Cíes. Over the 10 yr preceding the spill, we monitored reproductive performance and population dynamics in this locality (Velando & Freire 2002). We

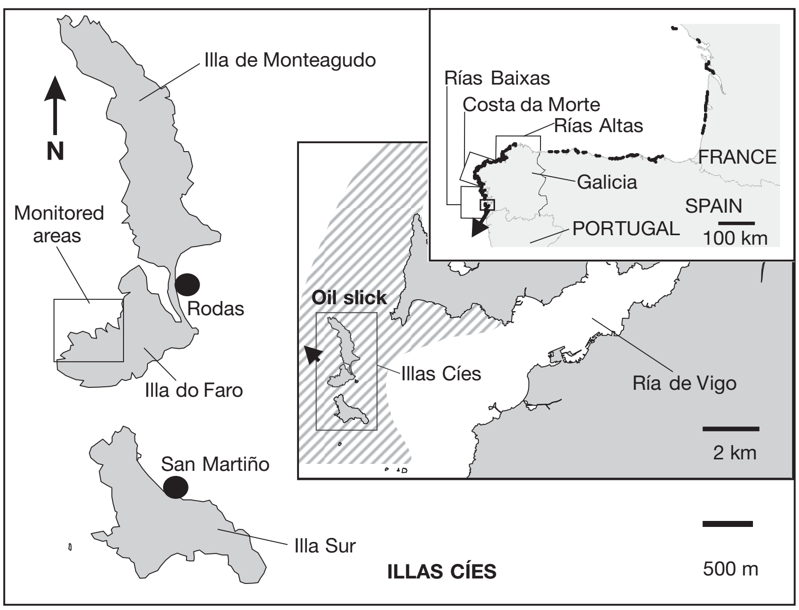

Fig. 1. Monitored breeding areas of European shags *Phalacrocorax aristotelis* at Illas Cíes (Galicia, NW of Spain) and sampling stations for levels of polycyclic aromatic hydrocarbons (PAHs) in sediment, plankton and other organisms (black circles). Inset maps show the main oiled areas in Spain and France and the pathway of the oil slick in the Ría de Vigo

compared this data with population dynamics of the 2003 breeding season, immediately following the 'Prestige' oil spill. Determining the likely effects of this perturbation is crucial in managing and conserving shag populations and can also be useful to evaluate the overall health of nearshore systems in the Ría de Vigo. The 'Prestige' oil spill occurred in winter, when the shags prefer to forage well into Ría de Vigo (Velando 1997), an area which remained relatively unoiled when compared to Illas Cíes and the outer reaches of Ria de Vigo. In fact, few European shags were killed by the oil spill (see 'Results'). Nevertheless, in the breeding season, significant effects derived from continued exposure to persisting oil pollution at foraging areas may be expected because the shags forage much closer to the breeding colonies. Here, we evaluate the potential effects of food limitation due to reductions in the availability of prey to shags related to the oil spill pollution. We analyzed 4 lines of evidence concerning the food limitation hypothesis in the breeding season immediately after the 'Prestige' oil spill: (1) reproductive parameters of European shags that might be expected to be affected by reduced availability of food, (2) presence of oil pollution at foraging areas, (3) availability of sandeels, and (4) changes in the breeding season diet.

MATERIALS AND METHODS

Study site and population dynamics. In Illas Cíes (Fig. 1; 42° 15′ N, 8° 53′ W), the European shags prefer to nest in caves formed by large granite rocks that fall from the cliffs (Velando 1997). Population counts (nests apparently occupied in April/May) were made in Illa do Faro from 1994 to 2003 (Illas Cíes, Fig. 1). We modelled the population dynamics of shags breeding at Illas Cíes using a Leslie matrix model (Velando & Freire 2002) with 3 age classes (first year, second year and adults). In east Britain, Aebischer (1995) showed that 95 % of shags recruited within a radius of less than 8 km from the natal colony. European shags at Illas Cíes also showed a high philopatry, and only 1 bird was recorded in another colony (Illa de Ons, 15 km to the north). No birds ringed in other colonies were recorded in Cíes. Thus, Leslie matrix models for closed populations may be applied to the shag population on Cíes Islands (Velando & Freire 2002). Given that survival is independent of sex (Velando & Freire 2002), and that the males select nest sites and initiate nest-building and that there were documented cases of polygyny (about 4 % of males; A. V. Potts 1968 unpubl. data), the model equated nests with breeding males and operated on cohorts of males (Aebischer & Wanless 1992). A balanced sex-ratio was assumed in the model. Sex ratio did not differ significantly from the 1:1 expectation in the Cíes Islands, (60 males and 67 females; Velando et al. 2002). The demographic parameters used in this model included the estimated annual reproductive success (see below), and the survival and recruitment data estimated during the period 1994 to 1997 (adult survival: 0.72; second year survival: 0.70; first year survival: 0.42; recruitment of second-year olds: 47 %; for details see Velando & Freire 2002). In the years with no data on reproduction the average annual reproductive success was used.

We used the 1000 simulations model with parameters variability of population change in the 2001 to 2003 period to test whether the pre-spill demography fits with the estimated population in 2003 based on nest counts. In these simulations, survival for each year was randomly selected from a normal distribution generated from average and variance estimates (Caughley & Gunn 1996). The estimated survival variance represented the sampling variation rather than true interannual variation (Velando & Freire 2002).

Reproductive parameters. The breeding data set included information on nest-sites in 3 adjacent areas at Illa do Faro (Fig. 1, Illas Cíes) monitored in the period 1992 to 2003. The annual breeding density varied during the study, especially in 1998 when severe winter weather in 1997/1998 produced a low occupation rate with most adults refusing to breed (Velando & Freire 2002). In 1998, some rocks that fell during the winter restricted our access to some nest sites during the breeding season, resulting in a lower sample size after this year. In the study areas, we recorded the laying date of the first egg (n = 12 yr), and for each nest with eggs, clutch size (n = 7 yr), and reproductive success (defined as the number of chicks surviving to 50 d; n = 8 yr) during the period 1992 to 2003 (see Velando et al. 1999b, Velando & Freire 2002 for details). Chicks were weighed and measured within the first week after hatching (between 1 and 7 d post-hatch, n = 5 yr). The wing length is a good age predictor in the first wk of hatching (Velando 1997). We used the residuals from a regression analysis of log body mass on log wing length (linear regression: $R^2 = 0.93$, $p < 0.001$) as an index of chick condition, avoiding the effects of age. The residuals obtained were standardized in a *z*-normal distribution. In order to test for differences between the 2003 season and previous years, we used a *t*-test for the comparison of a single observation with the mean of a sample (Sokal & Rohlf 1995). In addition, we calculated annual differences in reproductive parameters by pair comparisons, using nest as unit of analysis. We used the Mann-Whitney test with sequential Bonferroni correction, following the Dunn-Sidak method for critical value estimation (Sokal & Rohlf 1995), to compare between breeding variables that were not normally distributed (Shapiro-Wilk test). For normally distributed variables we used the Tukey test assuming equal variance (Levene test) and unequal sample size (Sokal & Rohlf 1995).

Direct mortality. Direct mortality of shags due to the 'Prestige' oil spill was estimated as the total number of casualties relative to total shag population. The coastline of Galicia was divided into 3 areas: Costa da Morte, Rías Baixas and Rías Altas (Fig. 1). We used the database provided by the Consellería de Medio Ambiente (Xunta de Galicia) in order to know the number and location of shag casualties up to March 2003. The Consellería de Medio Ambiente keeps a record of all the beached birds that were collected and reported along the coasts of Galicia since the first days of the spill. For the purpose of this study all birds informed to be retrieved (whether dead or moribund) were included in the tally of dead shags. The total size of the shag population within an area was estimated as 3.585 times the number of breeding pairs based on age population structure obtained from a Leslie matrix model (Velando & Freire 2002) and population estimates in 1994 (Velando et al. 1999a).

Environmental conditions. European shags are very sensitive to adverse weather (Aebischer & Wanless 1992, Velando & Freire 2002). In order to test for differences in adverse weather conditions in the 2003 season and the pre-spill years, we analyzed different climatic indexes. There is growing evidence that climatic oscillations such as the North Atlantic Oscillation (NAO) are regulating forces on marine and terrestrial ecosystems (Ottersen et al. 2001). In order to test environmental variability over time, we used the NAO index based on the difference of normalized sea level pressure between Lisbon, Portugal and Stykkisholmur/Reykjavik, Iceland during the winter, December through March (Hurrell 1995). The NAO can be useful to assess winter severity, and positive values indicate high winter temperature and precipitation (Ottersen et al. 2001). To assess weather conditions at the local scale we used the number of gale-days from March to May in the Rías Baixas. This period encompasses from egg laying to chick rearing for the majority of pairs breeding at Illas Cíes (Velando 1997, Velando et al. 1999b). A gale-day was defined as a day with rainfall over 10 mm and winds over 100 km. Climatological data were taken from the Lourizán weather station (Sistema de Información Ambiental de Galicia, Consellería de Medio Ambiente), 15 km away from Illas Cíes.

Foraging areas and oil pollution. During the breeding season, the feeding range of shags on Illas Cíes is typically less than 4 km around the colony and the consumption of sandeels is related to a strategy of group feeding (Velando 1997). The foraging areas were determined from 95 feeding groups observed from land and sea surveys around the islands during the breeding seasons from 1995 to 2002. Typically, the feeding groups were large and conspicuous with group size of approximately 300 to 1000 shags moving around the islands. The feeding groups were located in a 500 × 500 m grid, and the proportion of groups in each cell was calculated. The spatial distribution of shag groups in the Ría de Vigo was mapped by kriging after determining the experimental variogram. In addition, the grid of seabed sediment types was obtained from Instituto Hidrográfico de la Marina (Cadiz, Spain) maps.

We compiled the data on oil pollution at Ría de Vigo after the 'Prestige' oil spill. These data came from 3 main sources: (1) Centro de Control do Medio Mariño (CCMM; Xunta de Galicia; www.ccmm-prestige.cesga.es/): oil presence in seabed by experimental fishing, (2) Instituto Español de Oceanografía (IEO, www.ieo.es/prestige.htm): levels of polycyclic aromatic hydrocarbons (PAHs) in common razor shell *Ensis ensis*, a sand-dwelling benthic organism (Gonzalez et al. 2003, see Fig. 1), and (3) SAVICO project (Ministerio de Ciencia y Tecnología): PHA levels in sediment and plankton (see Fig. 1). The Instituto Español de Oceanografía analyzed the total concentration of 6 PHAs while SAVICO analyzed the total concentration of 45 PAHs levels.

Prey abundance. The sandeel fishery has little importance in Galicia and most of the captures are used as live-bait for long-liners. In our study area the sandeel fishery is a traditional activity restricted to 3–7 small vessels based on the port of Baiona. We used the commercial catch in kg per vessel per day obtained from information held in the database of the 'Confraría de Baiona' (the 'confrarías' are fishers' organisations supervised by the regional government), which started in 1999, as an index of sandeel availability in Ría de Vigo. Sandeel fishing areas in Ría de Vigo were mapped using information gained from personal interviews with fishermen. In 2003, the sandeel fishery was not opened until April due to fishing restrictions related to the 'Prestige' oil spill. We analyzed sandeel catch per effort unit from April to June (incubation and chick rearing periods of European shags at the Illas Cíes). We used Generalized Linear Mixed Models (GLMMs) (Littell et al. 1996) to simultaneously identify the annual differences in sandeel catch per effort unit while controlling for potential non-independence of observations from the same vessel (included as random variable). A post-hoc analysis (Tukey test) was performed for annual pairwise comparisons.

European shag diet. The diet was studied by analyzing pellets collected in the nesting colonies between late March and late June, during incubation and chick rearing. On each sampling occasion, each pellet was taken from a different nest. The hard parts used for prey identification were separated from the other remains in the laboratory and identified to the lowest taxonomic level possible (Velando & Freire 1999). Sandeel numerical importance was expressed as the percentage of sandeels (family Ammodytidae; mainly *Gymnammodytes semisquamatus*; Velando & Freire 1999) in relation to the total number of prey items. Prey items were considered to be a pair of otholiths or at least one pharyngeal tooth in Labrid fishes, and upper beaks in cephalopods. In addition, some pellets were analyzed directly in the field and, for these, only the presence or absence of sandeels was recorded. Sandeel occurrence was expressed as the proportion of pellets with sandeel in relation to the total number of pellets, pooling the data of all pellets. Annual differences in sandeel numerical importance and occurrence were tested using Tukey-type multiple comparisons tests for proportions (Zar 1999).

RESULTS

Population dynamics

In the pre-spill years, the Illa do Faro breeding population decreased at a mean annual growth rate of 5% from 323 pairs in 1994 to 218 pairs in 2001 (Fig. 2a, Velando & Freire 2002). In the season immediately after the oil spill (2003), the population was estimated at 146 pairs, showing a decrease of 40% from 2001. A deterministic Leslie matrix model used to simulate the dynamics of shags breeding at Cíes Islands successfully reproduced the population dynamics before the 'Prestige' oil spill (Fig. 2a, Velando & Freire 2002). Within that period, the colony experienced an almost complete breeding failure in 1998, when the few shags that laid eggs subsequently abandoned their clutches. The failure in 1998 was associated with winter severity and adverse weather during the egg laying period (Velando & Freire 2002) and the model showed that this crash was due to a high proportion of adults failing to breed (see Velando & Freire 2002). The model predicted a population of 220 pairs in 2003, 34% higher than observed (Fig. 2a). Using the population parameters and variability obtained during the pre-spill period, all 1000 simulations predicted a larger breeding population than that observed in 2003 (Fig. 2b).

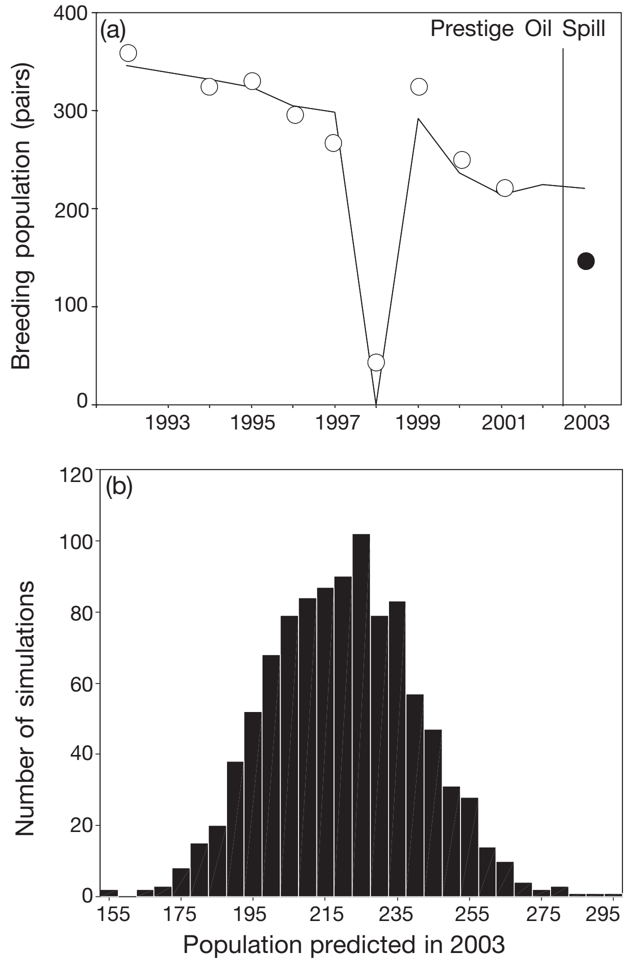

Fig. 2. *Phalacrocorax aristotelis*. Results of simulations of the population dynamics of the European shag population breeding in Illa do Faro, Illas Cíes, between 1992 and 2003, run with the population parameters estimated in the pre-spill period 1994–1997. (a) Simulation with the average population parameters (solid line), O: population size estimated from nest counts; ●: breeding season following the oil spill. (b) Frequency histogram of the population size in 2003 estimated from 1000 simulations run with parameter variability according to pre-spill conditions

Reproduction immediately after oil spill

In 2003, the season immediately after the spill, the laying date of the first egg was March 30. This was a month later than the overall mean for the pre-spill years (Fig. 3a), which showed a significant difference (Table 1). Mean clutch size was 15% lower than the average for previous years (Table 1). Post-spill clutch size was significantly lower than clutch size in 1995, 1996, 1997 and 2000 (Fig. 3b, corrected Mann-Whitney test, $p < 0.05$ in all cases) but not than clutch size in 1993, 1994 and 2001 (Fig. 3b, $p > 0.1$ in both cases).

Chick condition (as shown by residuals of regression of body mass on wing length) during the first week of life varied among years (Fig. 3c, ANOVA: $F_{4,144} = 11.56$, $p < 0.001$), and the post-hoc analysis showed that 2003 was significantly different than all the pre-spill years (Tukey test, $p < 0.001$ in all cases). In 2003, the repro-

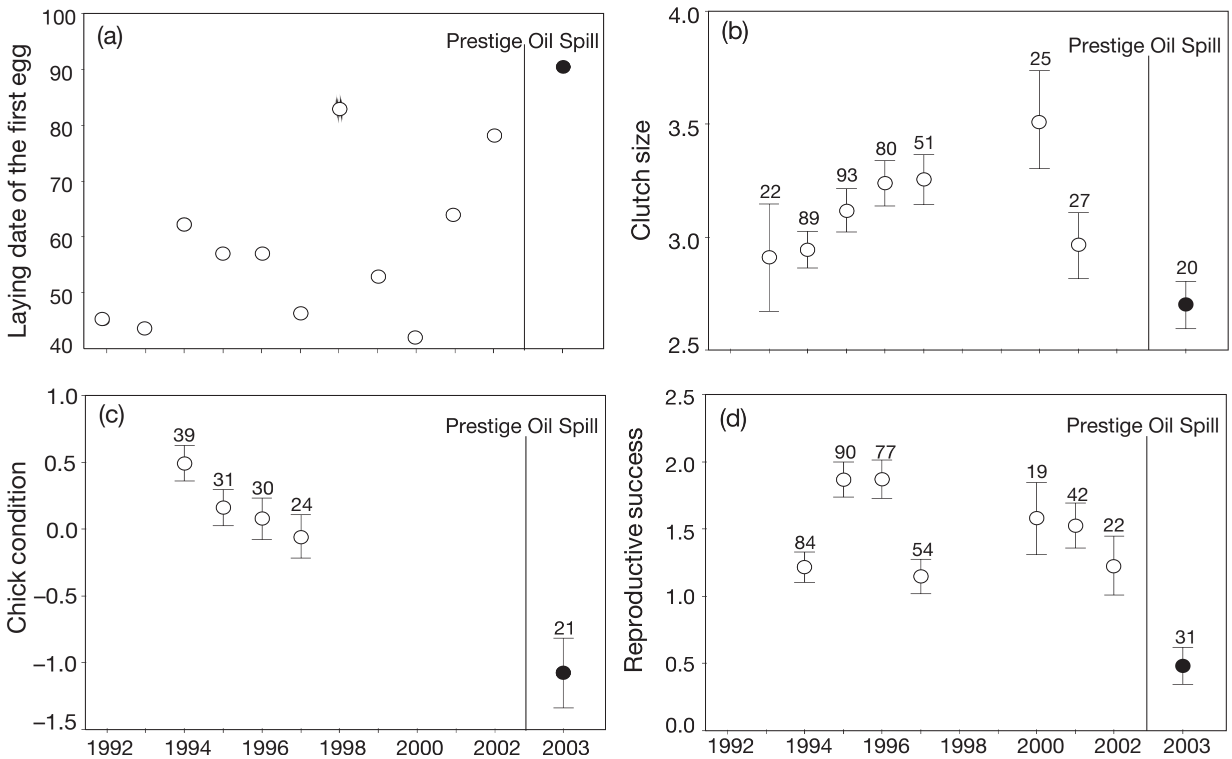

Fig. 3. *Phalacrocorax aristotelis.* Mean (±SE when appropriate) of (a) laying date of the first egg in the monitored nests (day of the year), (b) clutch size, (c) chick condition expressed as *Z*-residuals from a regression analysis of log body mass on log wing length the first week after hatching and (d) reproductive success expressed as number of chicks fledged per pair at Illas Cíes during the 12 yr of the study. Sample sizes are indicated above error bars. Black circles indicate the breeding season following the oil spill (2003)

Table 1. *Phalacrocorax aristotelis.* Mean values of 1992 to 2002 (±SE, range, number of years) and 2003 laying date of the first egg (day of the year), clutch size (number of eggs per clutch), reproductive success (chicks fledged per pair) and sandeel occurrence and numerical importance in the diet of European shags at Illas Cíes. Results of *t*-test for the comparison of a single observation (2003 season) with the mean of 1992 to 2002 are shown

	1992–2002	2003	*t*	p
Reproduction				
Laying date of the first egg	57 (±4, 42–83, 11)	88	2.29	0.023
Clutch size	3.2 (±0.1, 2.9–3.5, 6)	2.70	2.33	0.029
Chick condition	0.07 (±0.16, −0.18–0.49, 4)	−1.07	3.24	0.024
Reproductive Success	1.49 (±0.11, 1.15–1.87, 7)	0.48	3.09	0.011
Diet				
Sandeel occurrence (%)	90 (±3, 77–100, 7)	52	4.51	0.002
Sandeel numerical importance (%)	80 (±6, 63–92, 5)	27	4.11	0.007

ductive success dropped by 32% compared with the average for the 1994 to 2002 period (Table 1). Pairwise comparisons between 2003 and the pre-spill years revealed significant differences in each case (Fig. 3d, corrected Mann-Whitney test, $p < 0.01$ in all cases).

Direct mortality

During the oil spill, from November 2002 to February 2003, 340 shags were collected in the Galician coast as recorded by the Xunta de Galicia database (Table 2). The casualties represented around 5% of the estimated European shag population for Galicia (Table 2). Most of the records where the locality of recovery is known (n = 264) came from Costa da Morte (53%) and Rías Baixas (42%). Within the Rías Baixas, only 24 shags were recorded in the Ría de Vigo (the main wintering area for the shags breeding at Illas Cíes; Velando 1997). Recovery of juvenile shags accounted for 66% of the total number of aged shags (n = 95), indicating that oil mortality was not evenly distributed among age classes ($\chi^2_1 = 10.12$, $p < 0.01$).

Table 2. *Phalacrocorax aristotelis*. Number of European shag recoveries during the 'Prestige' oil spill in Galicia. The Galician coast was divided into 3 main areas (Rías Baixas, Costa da Morte and Rías Altas, see Fig. 1). The percentage of recoveries with respect to population (see 'Materials and methods') in each area is shown

	Recoveries	% of population
Rías Baixas	112	2
Costa da Morte	141	15
Rías Altas	11	2
Unknown locality	76	
Total	340	5

Environmental conditions

The population decline in 2003 cannot be attributed to adverse environmental conditions during the preceding winter or through the egg laying period. There was no evidence of winter severity in 2003 compared with the 1992 to 2002 period according to Hurrell's winter index of NAO (Hurrell's NAO index; 2003: 0.20, 1992 to 2002: 1.19 ± 0.72, range –3.78 to 3.96; $t = 0.4$, $p = 0.35$). In 2003, only 3 gale-days were recorded during the whole breeding period (March to May), well below the average for the rest of the years of our study period (1992 to 2002: 5.00 ± 3.03 gale-days; range 0 to 11). In 1998, the breeding collapse was due to a long episode of severe adverse weather during egg laying (Velando & Freire 2002), with 8 consecutive gale-days starting April 1; the worst climatological conditions during egg laying in the years of our study.

Oil pollution at foraging areas

During breeding, the spatial distribution of European shags at sea was typically limited to the outer area of the Ría de Vigo, less than 4 km around Illas Cíes (Fig. 4a). Feeding groups were located in 85% of the 500 m grid-cells with sand within a radius of 4 km around Illas Cíes (n = 55) suggesting that foraging areas for shags are related to the distribution of sandy sediment bottoms around the islands (Fig. 4b). The oil slick passed across the outer part of the Ría de Vigo affecting the main foraging areas for shags (Figs. 1 & 4). In February 2003, oil was found in 5 of the 15 stations located in the shag foraging areas by CCMM experimental fishing. In January and March, the IEO found high PAH levels in common razor shells, especially in the San Martiño area, Illas Cíes (Fig. 1; San Martiño: January, 132 µg kg^{-1} dry weight, March, 171 µg kg^{-1} dry weight; Rodas: March, 47 µg kg^{-1} dry weight). In May, data from the SAVICO project showed high levels of PAHs in the sediment (Fig. 1, Rodas, 7 m depth: 274.67 µg kg^{-1} dry weight; 20 m depth: 398.25 µg kg^{-1} dry weight), as well as in the plankton (Fig. 1, Rodas, 7 m depth: 17 390 µg kg^{-1} dry weight; 19 m depth: 7086 µg kg^{-1} dry weight).

Sandeel abundance

In 2003, sandeel availability on the Ría de Vigo, measured as commercial catch per vessel per day, was 48% lower than the values for the 1999 to 2002 period (Fig. 5). There were significant differences in sandeel catch per day among vessels (GLMM; $F_{2,8} = 25.0$, $p < 0.001$) and years (GLMM; $F_{4,8} = 8.6$ $p = 0.005$). A post hoc analysis indicated that the sandeel catch per unit effort differed between 2003 and each of the pre-spill years (Tukey test, $p < 0.05$ in all cases), but not among pre-spill years (Tukey test, $p > 0.6$ in all cases). The differences in 2003 cannot be attributed to an increase in fishing effort, because the number of fishing boats decreased (6 to 3) and the total sandeel catch dropped by 78%.

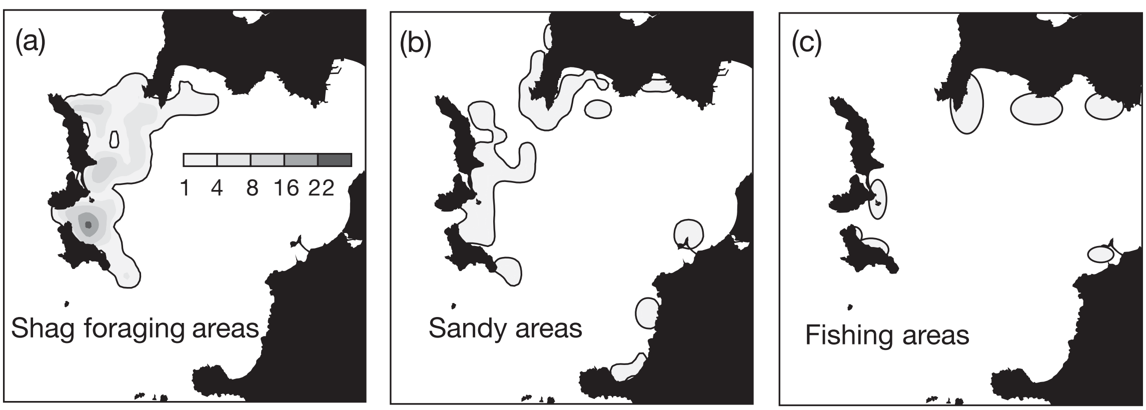

Fig. 4. Ría de Vigo. (a) Breeding season foraging areas of European shags during the 8 yr of the pre-spill period; grey scale indicates the number of feeding groups (n = 95). (b) Location of sandy sea bottoms and (c) sandeel fishing grounds

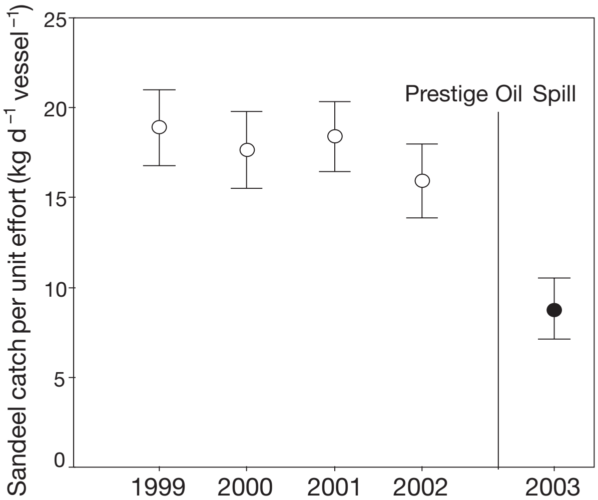

Fig. 5. Mean (±SE) sandeel catch per unit effort in Ría de Vigo. Black circle indicates the season following the oil spill (2003)

European shag diet

During the pre-spill years (1992 to 2002), the proportion of pellets with sandeels varied between 77% and 100% (Fig. 6a) while in 2003, only 52% of the pellets contained sandeels. There was a significant overall difference between the pre-spill years and 2003 in sandeel occurrence (Table 2). Pairwise comparisons in sandeel occurrence between 2003 and each of the pre-spill years revealed significant differences for all years but 1996 (post-hoc test for proportions, $p < 0.05$ in all cases except 1996: $p > 0.05$). In the pre-spill years, the numerical importance of sandeel in pellets varied between 63 and 92% of all prey items (Fig. 6b). In 2003, frequency of sandeel decreased significantly to just 27% of all prey (Fig. 6b, Table 2). The comparison of sandeel numerical frequencies between 2003 and each of the pre-spill years showed significant differences in all cases (post-hoc test for proportions, $p < 0.001$ in all cases). The annual reproductive success correlated with sandeel numerical frequency ($r = 0.89$, $n = 5$, $p = 0.04$), but not with sandeel occurrence ($r = 0.62$, $n = 7$, $p = 0.13$).

DISCUSSION

In the breeding season following the 'Prestige' disaster, the European shag population in Illas Cíes was reduced and showed clear signs of reproductive impairment. The results of the simulation models indicated that the population in 2003 was lower than expected. In addition, all breeding parameters investigated in 2003 differed significantly from pre-spill years (Table 1). Overall, the comparison of the breeding season following the 'Prestige' oil spill with baseline data strongly suggests an important effect on European shags with potential consequences at the population level. Alternatively, natural causes occurring at the same time as the perturbation may potentially help to explain the observed differences (Wiens & Parker 1995). In fact, adverse weather is known to have detrimental effects on the breeding performance of European shags at Illas Cíes (Velando et al. 1999b, Velando & Freire 2002), particularly the combination of strong southerly winds and heavy rains which is typical of winter gales at the western coast of Galicia (that led the population to a breeding crash in 1998; Velando & Freire 2002). During adverse weather events shags are

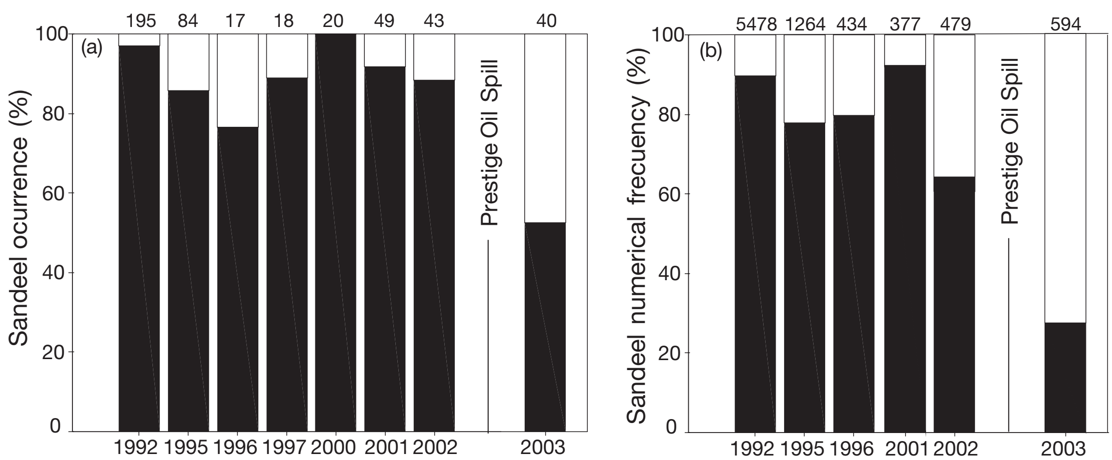

Fig. 6. *Phalacrocorax aristotelis.* Temporal changes in the importance of sandeels in the diet of European shags expressed as (a) the proportion of pellets with sandeel in relation to the total number of pellets and (b) the percentage of sandeels in relation to the total number of prey items pooling the data of all pellets. Sample sizes are included

not able to forage well, due probably to reduced underwater visibility and because the sandeels are buried in the sediment (Velando et al. 1999b). Nevertheless, environmental conditions at Illas Cíes cannot explain the observed effects, because weather conditions were far from adverse in the breeding season of 2003. In 1998, the shag reproduction was the worst recorded in all the colonies studied in the NW of the Iberian Penisula (Álvarez Fernández & Álvarez Laó 2003), indicating that adverse weather works at a large regional level. In contrast, the effects in 2003 were restricted to the oiled area as revealed by a spatial study on the reproductive success and population trends in the NW of the Iberian Peninsula (Velando et al. 2005). The colonies located within the path of the oil suffered greater declines (ca. 10%) when compared with pre-spill trends and with population trends at unoiled colonies. Before the oil spill, population trends were similar between oiled and unoiled colonies (Velando et al. 2005). In addition, in 2003, the breeding success was 50% lower in oiled colonies compared with unoiled ones (oiled: 1.09 ± 0.13 chicks fledged per pair, n = 6 colonies; unoiled: 2.00 ± 0.08 chicks fledged per pair, n = 11 colonies); the data available from prespill years suggest that the annual reproductive success did not differ among colonies before the impact (Velando et al. 2005). Thus, before–after and control-impact comparisons agree and strongly suggest that European shags suffered a negative impact from the 'Prestige' oil spill.

The difference between population estimated and expected in 2003 could be attributed to changes in 3 adult parameters: emigration, survival, or no-breeding. In Illas Cíes, European shags showed high site fidelity (all the marked birds re-nest within 100 m of the nest of the previous year; Velando & Freire 2002). In 2003, no adults ringed at Illas Cíes were seen breeding in other colonies, so a massive emigration appears not to be responsible of the observed decline. Our analysis of shag casualties suggests that despite the extensive oiling of Illas Cíes and nearby waters and shorelines around the mouth of Ría de Vigo it is unlikely that shags at Illas Cíes were killed in large numbers. The recorded death toll for shags at Ría de Vigo was less than 1% of the Illas Cíes population and most shags retrieved were juveniles. In winter, European shags usually forage well into Ría de Vigo (Velando 1997) and out of the oil slick area (Fig. 1), therefore reducing the chance of exposure to oil. Even though, only a small (unknown) fraction of the birds that are killed at sea by oil are retrieved (i.e. Piatt & Ford 1996), it is very unlikely that the population decline in the season immediately after the 'Prestige' wreck can be attributed exclusively to direct mortality. In fact, the Illas Cíes population showed a higher decline than the population of the heavily oiled Costa da Morte (Arcea 2003), where casualties represented a much larger fraction of the population (Table 2). The population decline after the oil spill could also be attributed to the fact that some adults that bred in previous years did not breed this year, a common feature of shag biology (Aebischer & Wanless 1992, Velando & Freire 2002).

In 2003, the breeding parameters analysed (laying date, clutch size, chick condition and reproductive success) were lower than those estimated in the pre-spill years (1992 to 2002). This reproductive impairment in shags after the 'Prestige' oil spill could be attributed to reduced availability of prey. The Cíes population seems to be highly dependable on sandeels as shown by the very high numerical frequency of sandeel in diet throughout the breeding period (Velando & Freire 1999) and the years of the pre-spill period, and that the annual breeding success correlated with the numerical frequency of sandeel in diet. In seabirds, a higher quality (lipid-rich, as are sandeels) diet is known to confer reproductive benefits (Annet & Pierotti 1989). Thus, breeding success is related to availability of sandeels in many seabird species (i.e. Rindorf et al. 2000, Lewis et al. 2001). Our study suggests that the European shags at Cíes had to cope with a significant reduction of the availability of sandeel in the season after the 'Prestige'.

Sandeel availability in 2003, as indicated by data from the sandeel fishery in Ría de Vigo, was significantly reduced. Sandeel catch per unit effort at Ría de Vigo can be used as a reliable index of sandeel availability to shags since most of the fishing is done in areas where the shags forage (Fig. 4). The diet of shags in 2003 showed a strong reduction in both sandeel presence and sandeel numerical importance, also suggesting lower sandeel availability at Illas Cíes following the spill. Sandeels are small, short-lived, lipid rich shoaling fish that have the habit of alternating between lying buried in the substrate and swimming pelagically in well formed schools (Robards et al. 1999). Sandeels depend on sandy bottom environments and these habitats around Illas Cíes were heavily impacted by 'Prestige' oil. For several months after the first strike of the oil slick (early December 2002) the bottoms around Cíes including intertidal and subtidal habitats were covered by sparse oil mats of considerable thickness and size; in 2003, 1912 tonnes of oil were removed from these marine habitats (Organismo Autónomo de Parques Nacionales 2003). Analysis of razor shells, organisms that also live buried in the sand, sampled at Illas Cíes showed high levels of oil contaminants. In May, there were high levels of PAHs in plankton and sediments revealing that sandy areas around Illas Cíes were continuously exposed to oil pollution throughout the shag breeding season.

The effect of oil pollution on sandeel populations results in high rates of mortality, such as occurred in the mass die-off of sandeels after the Torrey Canyon oil spill (see Reay 1970). In addition sandeels can also migrate to avoid contaminated substrates. Experimental evidence has showed that sand lance *Ammodytes hexapterus* avoids oiled substrates (Pinto et al. 1984). EROD activity (7-ethoxyresorufin-O-deethylase, an enzyme related to oil exposure) in sandeel larvae was correlated with water hydrocarbon concentrations in the North Sea, suggesting that sandeels suffer from oil pollution when the water column is contaminated (Stagg & McIntosh 1996). Overall, the changes in the diet of adult shags and the reduction in the sandeel fishery catches suggest a decrease in the abundance of sandeels in the sandy polluted areas around the Illas Cíes where the European shags forage. Sublethal effects on shags, that we did not measure, could partially explain the reproductive impairment of shags but not the reduction in the catch per unit effort statistics from the sandeel fishery. Overall, the decrease of reproductive performance of shags, the changes in the diet and the low sandeel catches best fit with the hypothesis of reduced food availability following the 'Prestige' oil spill. European shags are long-lived birds that should preferentially allocate resources to the maintenance of their body condition at the expense of investment in current reproduction when food availability is scarce (Monaghan et al. 1992, Velando & Alonso-Alvarez 2003). In fact, European shags show a constant adult survival rate (Harris et al. 1994) but annual variations in reproductive parameters and non-breeding events related to environmental conditions and food availability are not uncommon (Aebischer & Wanless 1992, Velando et al. 1999b, Rindford et al. 2000).

Food availability may constrain the recovery of shags at Illas Cíes. It may take several years for an impacted population to recover as sandeels are highly phylopatric (Hobson 1986). In addition to food availability, sublethal effects could be affecting the condition and reproduction of shags. This species is an inshore and coastal feeder and resident throughout the year, so with great opportunities for oil exposure as long as the oil persists in their foraging areas. Signs of continued exposure to oil were clear for Harlequin ducks *Histrionicus histrionicus* (Esler et al. 2000) and Pigeon guillemots *Cepphus columba* (Golet et al. 2002) about a decade after the 1989 'Exxon Valdez' oil spill in Alaska. In the last decade the European shag population at Illas Cíes showed an overall decline at an annual rate of 5%, attributed to elevated rates of adult mortality in gill-nets (Velando & Freire 2002). The pre-spill population dynamics, the continuous exposure to oil and reduction of food availability can constraint the future recovery of shags. Thus, conservation measures should be adopted to effectively protect this species at Illas Cíes.

In conclusion, this study showed that European shags at Illas Cíes were negatively affected by the 'Prestige' oil spill. When compared to the pre-spill years, reproductive performance in 2003 was significantly lower, chick condition was poorer and the number of breeding adults was much less than expected. In addition, we provide evidence of a dietary shift with a lower occurrence of sandeel that, together with sandeel fishery data indicate lower sandeel availability at foraging areas. When all this information is taken into account, the picture that emerges strongly suggests that the European shag population in Illas Cíes is suffering a negative impact of an indirect nature mediated through a reduction on the availability of a highly preferred forage-fish. Our study indicates that to rely on a small number of casualties to conclude that a seabird population will not be likely to suffer from an oil spill could be highly misleading if indirect effects are under way. There is a risk that the impacts of oil pollution on seabirds as well as other marine organisms could be underestimated by overlooking the effects of chronic exposures, delayed impacts or indirect effects driven by ecological processes.

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