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Intercolony and seasonal differences in the breeding diet of European shags on the Galician coast (NW Spain)

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ABSTRACT: The seasonal and spatial variations in the diet of the European shag *Phalacrocorax aristotelis* were studied during the breeding period, based on the analysis of 202 adults' pellets (February to June, 1995) and 30 regurgitations of chicks (April, May and June, 1995 and 1996) taken from 2 colonies located in close proximity to one another (<15 km) on the coast of Galicia (NW Spain; Islands of Cíes and Ons). The diet of birds from the Cíes Islands consisted mainly of sandeels (family Ammodytidae), which make up over 70% of the prey during all months. These fishes went practically unreported in a number of previous studies of fish communities in the region, probably due to the low catchability of trawl nets and the possibility that the habitats of sandeels where shags forage, shallow (<10 to 15 m) sandy bottoms, were not sampled adequately. Seasonal changes were found on the Island of Ons, where in winter (February and March) the diet was based on gobids (family Gobiidae) and sand smelts *Atherina presbyter*, while in spring the dominant prey were the Ammodytidae (in May and June they made up over 86%). The consumption of sandeels established an increased similarity in diet between the colonies throughout the breeding cycle, and they were the only prey whose abundance was negatively correlated with the diversity of each pellet. This study highlights the high plasticity in prey and feeding habitats (both pelagic and benthic with different types of substrates) used by the European shag. It should be noted, however, that the main prey during chick rearing are sandeels. Differences were found in the mean sizes of the different prey consumed, but the modal size for all of them throughout the season was around 9 to 11 cm in total length. The range of sizes available in the environment is greater than the range chosen by the European shag, which suggests that this bird selects a narrow range of prey sizes.

KEY WORDS: Diet · Breeding · Seasonal changes · Spatial changes · Fish prey · Prey size · European shag · Galicia (NW Spain)

INTRODUCTION

Seabirds are upper trophic level consumers and there has been increasing interest in the roles they play in marine ecosystems and in their predator-prey relationships (e.g. Croxall et al. 1985, Schneider et al. 1985, Croxall 1987). Thus, seabirds have been used in several geographical areas to detect ecosystem changes (e.g. Barret & Schei 1977, Ollason & Dunnet 1983, Harris & Wanless 1990, Huntley et al. 1991, Aebischer & Wanless 1992, Monaghan 1996, Montevecchi & Myers 1996, 1997) and as indicators of prey abundance (Cairns 1987, Barret et al. 1990, Hatch & Sanger 1992, Montevecchi & Myers 1995).

The European shag *Phalacrocorax aristotelis* has a distribution restricted to the Western Palearctic, from the North Cape (Norway) to the coast of Morocco (Lloyd et al. 1991). The nominal subspecies (*P. aristotelis aristotelis*) breeds on the Atlantic coast and its distribution limit is located on the Iberian Peninsula (Bernis 1948). Galicia (NW Spain) has a population of approximately 2000 pairs, 85% of which are concentrated on the Islands of Cies and Ons (Velando 1997).

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The European shag is the most abundant bird on the Galician coasts that has exclusively marine feeding habits.

European shags typically use foot propulsion (Ashmole 1971) to feed on the bottom (Wanless et al. 1993a), although shags spend about half their time in pelagic dives (Grémillet et al. 1998). Foraging areas have depths ranging between 7 and 80 m (Guyot 1988, Barret & Furness 1990, Wanless et al. 1991a, 1993a), with a mean of approximately 20 to 30 m (Wanless et al. 1997), and have mean and maximum radii of 7 and 17 km from colonies (Wanless et al. 1991b). Many studies have focused on the diet composition of the European shag. The first study was carried out by Steven (1933), who used an analysis of stomach contents in an attempt to determine the impact of this species on stocks of commercial fish. The diet of the European shag has been used to assess the recruitment and abundance of fish populations (Barret et al. 1990, Barret 1991). This species feeds on a wide-ranging variety of benthic, demersal and schooling pelagic fish, which is the reason for its classification as opportunistic in its feeding habits (Barret 1991, Grémillet et al. 1998). The most common prey during the breeding season are different species of sandeel (family Ammodytidae) (Steven 1933, Lumsden & Haddow 1946, Snow 1960, Pearson 1968, Rae 1969, Harris & Wanless 1991), although gadids are also important components of their diet in Norway (Barret et al. 1990). The diet of the European shag varies depending on annual changes in prey availability (Carss 1993) and, to a lesser extent, on location. Data presented by Lumsden & Haddow (1946) show that specific composition of the diet varied depending on the type of marine substrate where the prey had been caught, suggesting that the type of bottom determines the type of fish that will be found in a particular location. The diet of adults of this species has been well documented on Arctic coasts (Barret et al. 1990), British coasts (Steven 1933, Lumsden & Haddow 1946, Pearson 1968, Mills 1969, Harris & Riddiford 1989, Harris & Wanless 1991, 1993), and in the Mediterranean (Guyot 1988). On the Iberian Peninsula, however, there is no information available on the diet of this species, except for preliminary information from Asturias (N Spain) (Álvarez 1998).

The present study examines the diet composition of the European shag throughout the breeding cycle and the differences between the 2 Galician colonies in close proximity to one another (<15 km). The dietary study was based on analysis of the regurgitations of chicks and the pellets of adults. These methods were chosen because they offer the possibility of acquiring a wealth of information with a minimum of disturbance to the population and, although they are limited indicators of diet, they have been recognized as appropriate methods for the temporal and spatial comparison of the diet of the European shag (Duffy & Laurenson 1983, Barret et al. 1990, Barret 1991).

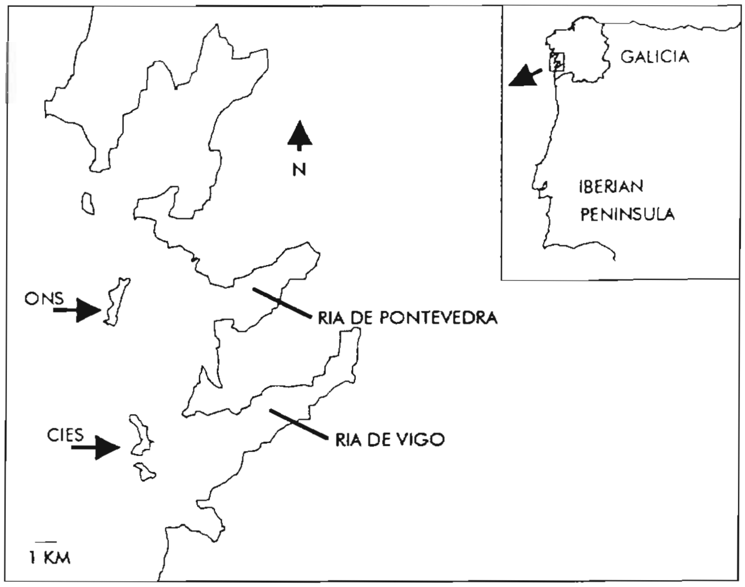

Fig. 1. Location on the Iberian Peninsula of the colonies of European shag *Phalacrocorax aristotelis* on the Islands of Cíes and Ons, where the dietary study was carried out

MATERIALS AND METHODS

The study was carried out on 2 breeding colonies in Galicia (NW Spain): (1) the Cíes Islands (42° 15' 04" N, 8° 53' 30" W), which are located in the outer area of the Ría de Vigo and are the breeding grounds for over 1000 pairs, and (2) the Island of Ons (42° 21' 05" N, 5° 15' 35" W) located in the Ría de Pontevedra, where over 600 pairs breed (Fig. 1). The egg laying season of the European shag on these islands in 1995 and 1996, the years in which the study was carried out, reached its peak on 25 and 20 March, respectively, and the chicks began feeding a month later (Velando 1997).

The diet was analyzed by collecting pellets every 15 d on the Cíes Islands and monthly on the Island of Ons between February and June 1995, and regurgitations of the nestlings only in the Cíes Islands in April, May and June of 1995 and 1996. A total of 202 pellets (127 on the Cíes Islands and 75 on the Island of Ons) and 30 spontaneous regurgitations were collected. All of the pellets were fresh and showed no signs of deterioration

or drying. On each sampling occasion each pellet was taken from a different nest. Hard parts in the pellets were separated from the other remains and identified with a stereoscopic microscope, to the lowest taxonomic level possible. Fish prey were identified using sagittal otoliths and pharyngeal teeth by means of the otolith keys of Bauza (1962) and Härkönen (1986) and our own collections of otoliths and pharyngeal teeth for labrids. Otoliths have been used in many studies to identify fish prey and to estimate their body sizes and biomasses (e.g. in Duffy & Jackson 1986, Härkönen 1986, Jobling & Breiby 1986, Pierce & Boyle 1991).

Diet composition was expressed as the proportion of items belonging to each prey type, such as otoliths, pharyngeal teeth, upper beaks in cephalopods, etc., considering items as paired structures for identification. In the case of crustaceans, of which only gammarid amphipods were observed, the number of prey was counted.

The level of taxonomic resolution for identification was different for each prey type. The family Ammodytidae was treated as 1 category, as the species that make up this family are difficult to identify because the otoliths are very similar and the slight impression of the saculus is lost when they are partially eroded. The small number of otoliths belonging to this family identified at the species level were mainly *Gymnammodytes semisquamatus* and, to a lesser extent, *Hyperoplus lanceolatus*. The species of the genus *Gobius* and *Lesueurigobius friesii* were included within the category *Gobius* spp. The category *Symphodus* spp. was comprised of *S. cinereus* and *S. melops*. Both species have very similar otoliths and pharyngeal teeth, but they can be differentiated from *S. bailloni*. *Trisopterus* spp. may include both *T. luscus* and *T. minutus*, although the few otoliths that were identified pertained to *T. luscus*. Non-cephalopod molluscs were not included in the analysis as in most cases only the shell was present, and these could serve as gastroliths like the stones found in many pellets.

The partial erosion of otoliths caused by digestion could result in the underestimation of the sizes of prey consumed (Johnstone et al. 1990). In order to reduce this effect, only those otoliths that did not show signs of excessive erosion were measured by means of an image analysis system (Electron Microscopy Unit, Universidade da Coruña). The measurements obtained using this system did not differ significantly from those found using a stereoscopic microscope with a graduated eyepiece. The mass and total length of each prey was estimated by means of published equations that relate otolith size to the body size and mass of fish (Härkönen 1986). For the sand smelt *Atherina presbyter* the equations were calculated from unpublished data provided by S. Lens (Instituto Español de Oceanografía, Vigo). In taxa that included several species, the equation pertaining to the most frequent species in the diet was used. In order to estimate the mass of prey with deteriorated otoliths, a mean value of the mass of all analyzed samples was assigned to that prey. For prey without mass equations, a mean value of the mass obtained for all prey was assigned.

The importance of each prey in the diet was estimated as numerical frequency (%N, the total percentage of items constituted by each category) and percentage of biomass (%B, as compared to the total biomass). The numerical frequency of the different types of prey was compared between months and islands using the *G*-test (Sokal & Rohlf 1995). To compute this test, different prey species were grouped by family, including 2 groups of uncommon prey ('invertebrates' and 'other fishes'). The standardized residuals in the tests made it possible to identify prey categories which determine the quantitative importance of the differences between samples.

The Shannon-Wiener diversity index (Tramer 1969) was used to describe the diversity of diet:

$$H' = -\sum p_i(\ln p_i)$$

where p_i is the proportion of all the items in the sample belonging to category *i*. Individual diversity (H'_{ind}) for each pellet, and population diversity (H'_{pop}), referring to the total number of pellets, were calculated. A mean estimate of population diversity (H'_{jack}) was obtained by using the jackknife procedure (Krebs 1989). Both the similarity and diversity indices were calculated using the prey groups that had the highest identification level.

Both parametric and non-parametric statistical tests were used, depending on the normality of the samples (Kolmogorov-Smirnov tests). The individual diversity index was compared between locations and among months using the Kruskal-Wallis and Mann-Whitney tests. Spearman rank correlations were established between individual diversity and the frequency of each prey in the pellet. The indices obtained by the jackknife method were compared between locations and among months with a 2-way ANOVA. The LSD test (least significant difference) was used as an *a posteriori* 1-way ANOVA (Sokal & Rohlf 1995). A correspondence analysis was carried out using each pellet analyzed as a case and the natural logarithm of the number of items of each prey as variables. Prey consisting of over 1% of the total items were selected and the rare categories were downweighted. The following prey were selected: Ammodytidae (Am), *Atherina presbyter* (Ath), *Gobius* spp. (Gob), *Gobiusculus flavescens* (Gbs), *Symphodus* spp. (Sym), *Symphodus bailloni* (Syb), *Trisopterus* spp. (Tri) and *Pollachius pol-*

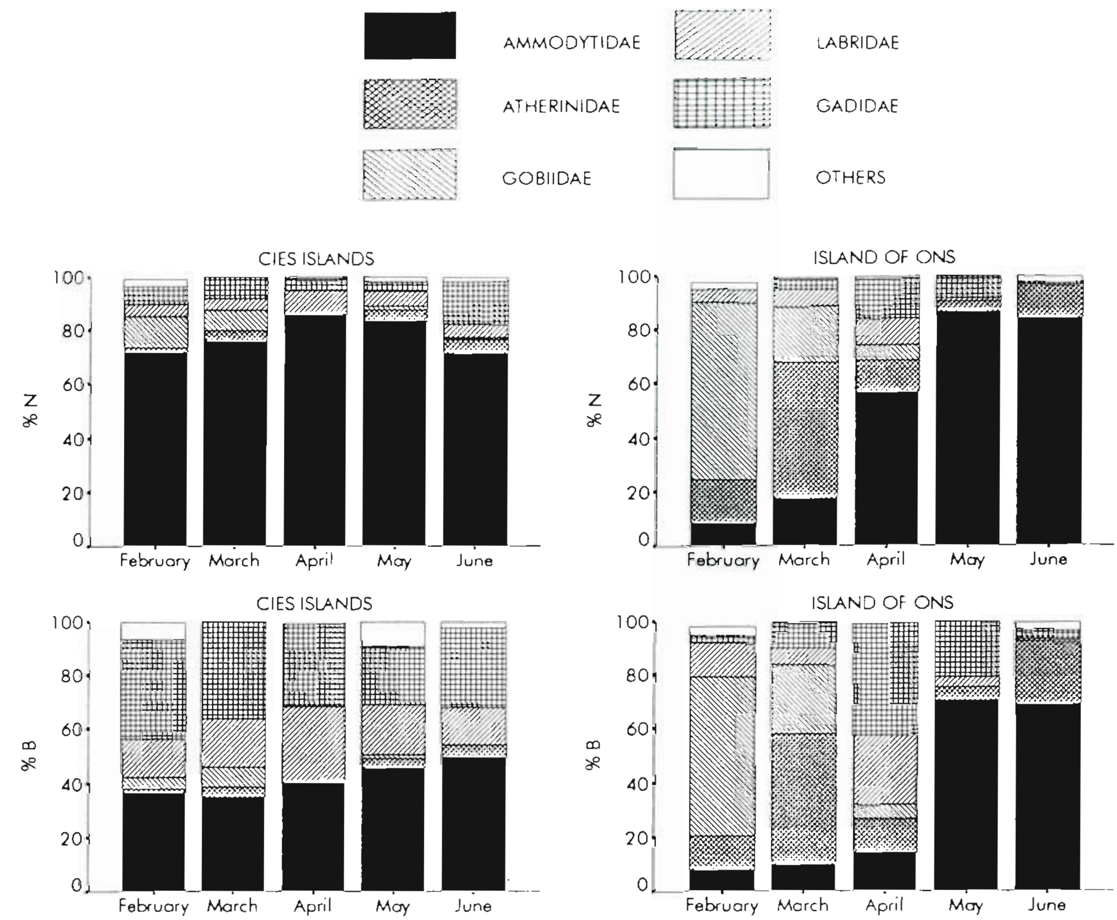

Fig. 2. *Phalacrocorax aristotelis*. Temporal evolution of the diet composition (expressed as numerical frequency, %N) and percentage of mass (%B) of the European shag on the Islands of Cíes and Ons during the study period

lachius (Pll). The correspondence analysis was carried out with the software CANOCO v. 3.11 (ter Braak 1988).

Measurements of undigested otoliths were used to calculate prey size frequency distributions. A 2-way (month and island) ANOVA was carried out in addition to the LSD test as an *a posteriori* 1-way ANOVA (Sokal & Rohlf 1995).

RESULTS

The examination of 202 pellets revealed 6396 identified items (Appendix 1). The most numerous prey came from the family Ammodytidae, accounting for 56% of all prey. Sandeels occurred in 73% of the pellets examined. The next most important prey were *Atherina presbyter*, which were present in 30% of the pellets and accounted for 10% of the prey, and the Gobiidae, which appeared in 16% of the pellets.

Additionally, 30 regurgitations of chicks were examined, of which 28 contained only sandeels (Ammodytidae), with a total of 44 individuals. The other 2 contained sandeels, a specimen of *Symphodus cinereus* and one of *Callionymus lyra*.

The diet composition was significantly different on the 2 islands ($G = 1449$, df = 6, $p < 0.0001$). The main difference was due to the consumption of sandeels on the Cíes Islands, where they comprised 76% of the prey and 42% of the biomass, whereas on the Island of Ons, they only made up 38% of the prey and 25% of the biomass. The differences in diet composition between Cíes and Ons (Fig 2, Appendix 1) were significant during all months (Table 1). However, the differences between the islands decreased significantly as the reproductive season progressed (Spearman correlation between time in the breeding season and *G*-statistic: $r_s = -0.90$, df = 5, $p < 0.05$), with May being the month showing the greatest similarity in diet.

Table 1. *G*-statistic (***$p < 0.0001$) obtained by the monthly comparison of the diet of the European shag *Phalacrocorax aristotelis* (in terms of numerical frequency) between the Islands of Cíes and Ons. Also shown are the significant standardized residuals ($p < 0.05$) corresponding to each important prey (ns: $p > 0.05$)

	Ammodytidae	Atherinidae	Gobiidae	Labridae	Gadidae	*G*
Feb	16.5	8.1	15.1	ns	5.7	1370***
Mar	10.9	11.6	4.7	ns	2.2	642***
Apr	3.3	4.3	3.0	ns	2.9	117***
May	ns	ns	ns	3.0	2.1	45***
Jun	ns	2.5	ns	2.7	4.9	112***

Spatial differences in the consumption of sandeels decreased during the breeding period (Table 1), to the point where there were no significant variations in numerical frequency between the 2 islands in May and June (>70% on both islands). The differences found at the beginning of the breeding period were due to the low appearance of sandeels on the Island of Ons in February (8%), March (18%) and April (57%), as compared to the high frequency on the Cíes Islands during the same period (>70% in all months). The Gadidae were the only group of prey that had significant differences between the 2 islands in all months. Gadids were more frequent in the diet of the European shag in February, March and June on the Cíes Islands and in April and May on the Island of Ons. The variability in consumption of *Atherina presbyter* and Gobiidae between Cíes and Ons was significant during February, March and April. *A. presbyter* accounted for 57% of the diet on the Island of Ons in March, while on the Cíes Islands it did not reach values of over 5%. The gobids accounted for 66 and 21% of the diet in February and March, respectively, on the Island of Ons, while on the Cíes Islands they comprised less than 10% of the diet (the main prey species in this case was *Gobiusculus flavescens*). Labrids were present in the diet with the same frequency on the Islands of Cíes and Ons in February, March and April, but showed significant spatial differences in May and June. Other prey, both fish and invertebrates, did not make any significant contributions to the differences in diet of the birds between the 2 colonies.

Table 2 presents the diversity indices (H') of the diet of the European shag on the Islands of Cíes and Ons throughout the breeding season. Individual diversity (H'_{ind}) varied significantly among months (Kruskal-Wallis test: $\chi^2 = 11.78$, df = 4, $p < 0.05$), but not between the 2 islands (Mann-Whitney test: $U = 422$, $p > 0.05$). Sandeels were the only prey whose abundance correlated negatively with the individual diversity index (Spearman rank correlation, $R_s = -0.70$, $p < 0.05$, N = 202), which implies that they tend to appear as the sole prey in the pellets. The rest of the prey correlated positively and significantly ($p < 0.05$) with the diversity index, the highest corresponding to *Symphodus* spp. ($R_s = 0.59$).

The population diversity index obtained using the jackknife method (Table 2) did not differ significantly between the islands (ANOVA: $F_{1,204} = 0.01$, $p > 0.1$); however, there was a significant difference among months ($F_{4,204} = 2.35$, $p < 0.05$), with a significant interaction between both factors ($F_{4,204} = 3.55$, $p < 0.01$). On the Cíes Islands, the temporal changes were not significant ($F_{4,129} = 1.57$, $p > 0.1$), though they were on the Island of Ons ($F_{4,74} = 6.34$, $p < 0.001$). On the latter island the diversity in June differed significantly from the values found in February, March and April, and the diversity in May differed from that in March and April (LSD test, $p < 0.05$).

Table 2. Indices of individual (H'_{ind}) and population (H'_{pop}) dietary diversity of the European shag *Phalacrocorax aristotelis*, and the population index obtained using the jackknife method (H'_{jack}). H'_{ind} and H'_{jack} are expressed as mean ± SE

	February		March		April		May		June		Total	
	Cíes	Ons	Cíes	Ons	Cíes	Ons	Cíes	Ons	Cíes	Ons	Cíes	Ons
H'_{ind}	0.60 ±0.49	0.52 ±0.39	0.31 ±0.38	0.44 ±0.38	0.20 ±0.30	0.73 ±0.46	0.30 ±0.43	0.33 ±0.33	0.40 ±0.40	0.27 ±0.29	0.39 ±0.44	0.47 ±0.40
H'_{pop}	1.20	1.15	0.98	1.41	0.55	1.40	0.78	0.57	1.01	0.49	1.08	1.51
H'_{jack}	1.35 ±1.40	1.03 ±1.05	1.1 5 ±1.56	1.52 ±0.75	0.38 ±0.81	1.51 ±1.04	0.89 ±1.38	0.59 ±0.56	1.11 ±0.78	0.26 ±0.30	1.05 ±1.29	1.02 ±0.93

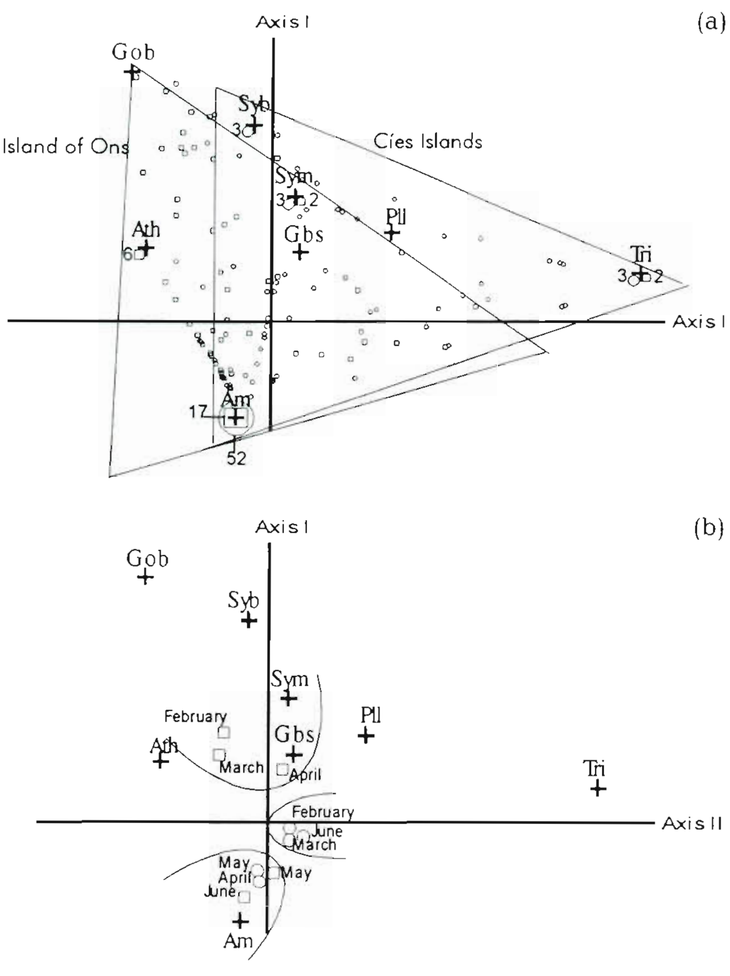

Fig. 3. *Phalacrocorax aristotelis*.Representation of Axes I and II extracted from the correspondence analysis of the diet of the European shag: (a) for all pellets (the numbers represent pellets with coinciding scores, and (b) for the mean scores corresponding to each month and location. (o) Samples from the Cíes Islands; (□) samples from the Island of Ons. See prey codes in Appendix 1

A correspondence analysis was carried out on the diet of the European shag taking into account information on the numerical frequency of the dominant prey in the pellets (Fig. 3). The first 3 axes extracted explain 61% of the variance. Axis I (26%) contrasts Ammodytidae with *Gobius* spp. and, to a lesser extent, with *Symphodus bailloni*. Axis II (20%) is defined in its negative part by the pellets with high frequencies of *Gobius* spp. and *Atherina presbyter* and by *Trisopterus* spp. in its positive part. Axis III (16%) contrasts *Gobiusculus flavescens* and, to a lesser extent, *S. bailloni* with *A. presbyter*. On the plane formed by Axes I and II, some of the pellets from the Islands of Cíes and Ons showed a similar diet due to the great abundance of Ammodytidae, but on the Island of Ons *Gobius* spp. and *A. presbyter* had a higher frequency of occurrence. In contrast, the diet on the Cíes Islands tended to include more gadids, such as *Pollachius pollachius* and *Trisopterus* spp. Three groups of samples may be established in terms of the mean score for each month at the 2 locations (Fig. 3b). The first would be represented by early dates in the breeding season on the Island of Ons (February, March and April), which would have high positive scores on Axis I. The second group would include the early months (February and March) and June on the Cíes Islands, with intermediate scores on both axes. The third group, located in the negative area of Axis I, with a diet based on Ammodytidae, would be made up of the late months on the Island of Ons (May and June) and of the intermediate months on the Cíes Islands.

The mean size (total length) (±SE) of the prey caught by the European shag was 98.5 ± 0.5 mm, and was higher on the Cíes Islands (104.0 ± 0.7 mm) than on the Island of Ons (91.9 ± 0.7 mm) ($t = 11.74$, $p < 0.01$).

The sizes of the different species of fishes caught as prey by the European shag varied significantly (Fig. 4; ANOVA: $F_{4\ 6153} = 298.9$, $p < 0.0001$), and there were significant differences in the sizes of all species (LSD test, $p < 0.05$), except between *Symphodus* spp. and Ammodytidae. However, if we compare the size-frequency distributions of each species on the archipelago, it is possible to observe that all cases present a modal size of 10 to 11 cm. There were no significant differences between locations in the size of the sandeels consumed (ANOVA: $F_{1,3685} = 1.41$, $p > 0.05$), but there were differences among months ($F_{4,3685} = 22.1$, $p < 0.001$); moreover there was a significant interaction between both factors ($F_{4,3685} = 22.3$, $p < 0.001$). The modal size of this prey was around 9 to 10 cm in all the months (Fig. 5).

DISCUSSION

The main group of prey of the European shag on the Islands of Cíes and Ons is the family Ammodytidae, which accounts for 73% of the total number of prey consumed. The otoliths of this family are small and possibly more digestible and more difficult to recover in the samples than those of species having larger otoliths (Johnstone et al. 1990, Harris & Wanless 1993), which implies that their numerical importance might

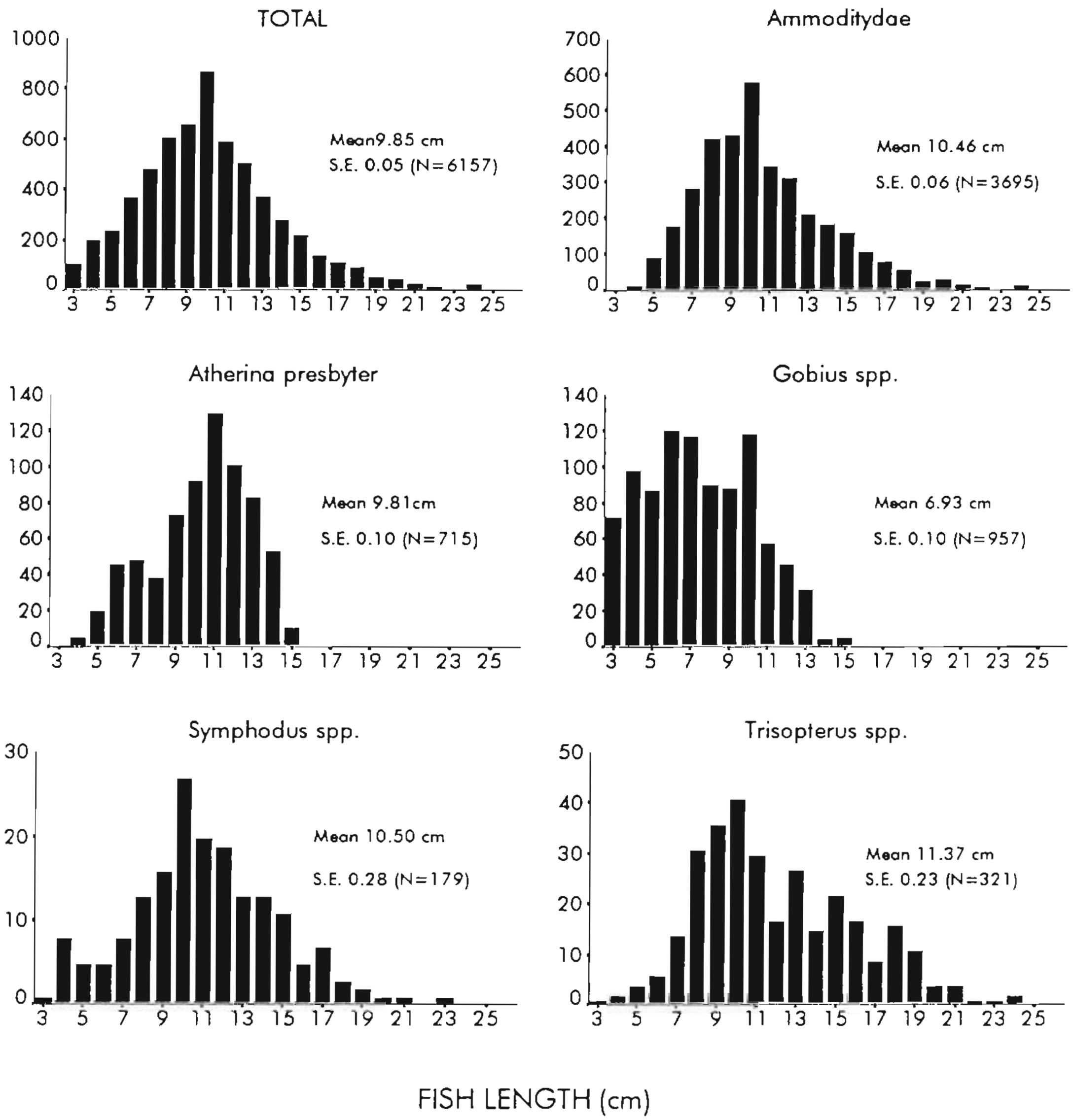

Fig. 4. *Phalacrocorax aristotelis.* Size-frequency distributions (total length, cm) of the different categories of fishes consumed by European shags from February to June 1995 on the Islands of Cíes and Ons. The mean (±SE) size of each prey is given

be underestimated by sampling pellets regurgitated by shags. Ammodytidae are also the dominant prey in British populations of the European shag, and it is consistently present in the diets of shags in all locations studied in the NE Atlantic and Mediterranean, except in the case of the coast of Asturias (N Spain) (Table 3).

It has been suggested that the European shag is an opportunistic predator (Barret 1991) and that the variability in its dietary composition in different locations (Table 3) may be related to geographical differences in the availability of potential prey. Our study shows that the European shag has a high plasticity of feeding habitats, feeding on fish that are found in a diversity of habitats, including pelagic fish (such as *Atherina presbyter*), semipelagic fish from sandy bottoms (such as the family Ammodytidae), benthic species from sandy-mud bottoms (such as the family Gobiidae), as well as demersal and benthic fishes that live on rocky and sandy bottoms (such as *Trisopterus* spp. and the family Labridae). The dominant prey of the European shag in all geographical areas are Ammodytidae and Gadidae, although the Labridae acquire increasing importance in more southern locations (in the Mediterranean and in Asturias, N Spain). *A. presbyster* only appears as prey on the coasts of the Iberian Peninsula and in the Mediterranean, and is locally abundant.

Table 3. *Phalacrocorax aristotelis*. Diet of the European shag in different locations of the NE Atlantic and Mediterranean. Data are expressed as percentage of frequency of occurrence (*) or of numerical frequency (**), depending on the method used by the different authors. (–: absence of prey or present in less than 0.1%)

Location Source	Ammodytidae	Atherinidae	Gobiidae	Clupedidae	Labridae	Gadidae	Other prey
Cornwall (England)* Steven (1933)	51	–	2	30	13	3	14
Farne (Scotland)** Pearson (1968)	81	–	–	–	–	4	15
Clyde (Scotland)** Lumsden & Haddow (1946)	78	–	3	0.6	1	13	4
Loch Ewe (Scotland)** Mills (1969)	41	–	–	–	–	59	–
Shetland (Scotland)* Harris & Riddiford (1989)	100	–	–	–	–	–	–
Isle of May (Scotland)* Harris & Wanless (1990)	95	–	11	–	–	45	15
Hornøy (Norway)** Barret et al. (1990)	56	–	–	–	–	40	3
Bleiksøy (Norway)** Barret et al. (1990)	15	–	–	–	–	69	16
Rogaland (Norway)** Barret et al. (1990)	15	–	–	–	20	50	15
Corcega (Corsica)* Guyot (1988)	33	5	–	–	78	–	28
Caladoria (Asturias, NW Spain)** Álvarez (1998)	–	35	–	–	52	11	2
Islands of Cíes (Galicia, NW Spain)** This study	75	3	6	–	5	7	4
Island of Ons (Galicia, NW Spain)** This study	38	20	30	–	5	4	3

Despite the variability observed in the colonies, the present study shows that the diet converges towards the family Ammodytidae during chick provisioning (primarily in May but also in April and June; Fig. 3), which would bring about a reduction in dietary diversity. Moreover, there is a negative correlation of the diversity of each pellet with the presence of Ammodytidae and a positive correlation with the remainder of the prey. This would appear to indicate that the European shag forages mainly for sandeels on these islands, which coincides with what has been observed in other areas (Table 3). The fish belonging to this family form schools which have a high density in late spring on the British coasts (Reary 1973) and a large number of seabirds depend on these fishes (see Furness 1990, Wright 1996). The seasonal changes in the abundance of schools might explain the temporal changes in diet, giving rise to a greater specialization when this resource is abundant. Harris & Wanless (1993) report that chicks are fed exclusively *Ammodytes tobianus* on the Isle of May (Scotland). On the Cíes Islands the diet observed in the pellets is more diverse than the regurgitations of the chicks, which are made up almost exclusively of sandeels. This implies that parents feed on prey different than those they provide to chicks.

The European shag has a greater dietary diversity in February and March. The diet consumed on the Cíes Islands is similar throughout all the months, though on the Island of Ons during the winter the diet is based on *Atherina presbyter* and *Gobius* spp. There are very few studies on *A. presbyster*, but it appears to be one of the most abundant species of coastal pelagic fish in the waters off the Galician coasts (Lens 1986). The family Gobiidae is dominant in the rías of Arousa and Pontevedra (Chesney & Iglesias 1979, Iglesias 1981, Igle-

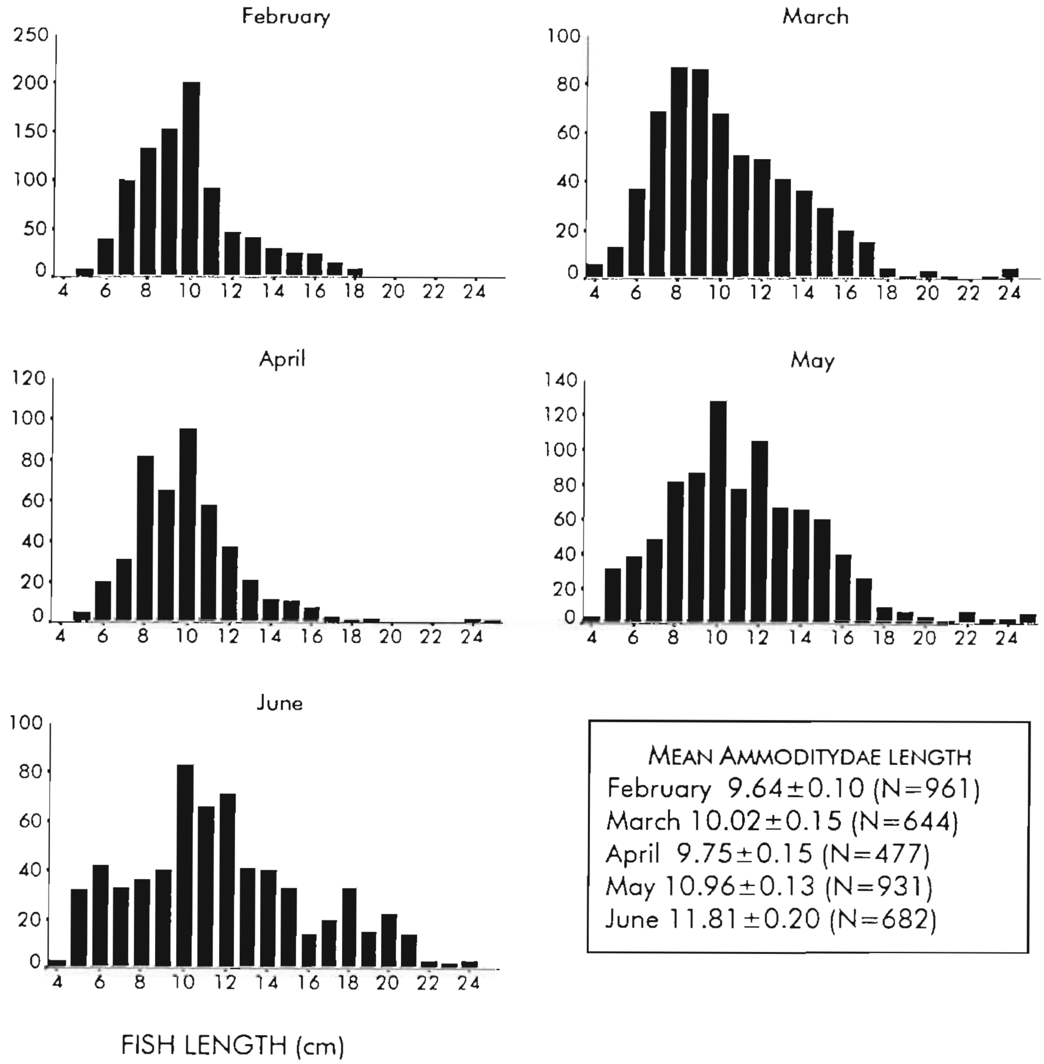

Fig. 5. *Phalacrocorax aristotelis*. Temporal evolution of the size-frequency distributions (total length, cm) of the sandeels consumed by European shags from February to June 1995 on the Cíes Islands and the Island of Ons. The mean (±SE) size is given for each month

sias & González-Gurriarán 1984), with *Lesueurigobius friesii* being the most abundant species (in this study *L. friesii* is included with *Gobius* spp.). Fernández (1994) observed maxima in the abundance of this species in January and August in the Ría de Arousa, and Iglesias & González-Gurriarán (1984) reported densities as high as 0.57 individuals m^{-2} in the Ría de Pontevedra in February. The abundance of this species during the winter could explain why it is consumed by European shags on the Island of Ons. Iglesias & González-Gurriarán (1984) located this species in the outer area of the Ría de Pontevedra, which is used as a feeding area by shags from the Island of Ons (Velando 1997), while *Gobius niger* is found in the inner area of the ría.

Seasonal changes in diet may also be attributed to a change in feeding grounds (Lumsden & Haddow 1946). Sandeels occupy large sandy areas (Reary 1973) and therefore European shags catch this fish only where sand banks are near colonies (Lumsden & Haddow 1946, Wanless et al. 1991b). Ammodytids are poorly documented on the Galician coast, with the most abundant species being *Hyperoplus lanceolatus* and *Gymnammodytes semisquamatus* (see review in Solórzano et al. 1988). These species are likely to have been underestimated in studies of fish communities because of the type of trawl nets used in the samplings (for example, Iglesias 1981, Guerra & Pérez Gándaras 1987). The present paper indicates that this family is abundant in the 2 rías and the adjacent coast, probably

linked to the sandy areas surrounding both islands (Vilas et al. 1995, 1996). The evident contradiction between studies of fish communities and the present analysis of the shag's diet may be due to 2 main reasons: (1) the low ability of the trawl nets used for fish community studies to catch sandeels, related to the benthopelagic habits of sandeels; and (2) previous studies have overlooked habitats characteristic of sandeels which occupy restricted areas but play an important role in the coastal ecosystem, as the present study documents. The last point corroborates the value of studies of seabird diet as indicators of prey abundance (Cairns 1987, Barret et al. 1990, Hatch & Sanger 1992, Montevecchi & Myers 1995).

The family Gadidae, particularly *Trisopterus* spp., is an important element in the diet of European shags, especially in terms of its contribution to the biomass consumed. Although it accounts for only 5% of the prey, it comprises 16% of the biomass. The genus *Trisopterus* is abundant in Galician rías, showing a maximum abundance in summer (Iglesias 1981). It has abundance peaks in the diet in April on the Island of Ons and in June on the Cíes Islands (13 and 15% of the numerical frequency, respectively).

The estimated mean size of prey from the Islands of Cíes and Ons is 9.8 cm, which is similar to the size of 9.7 cm estimated on the Isle of May (Wanless et al. 1993b), although the mean prey size in this location varies from year to year (Wanless et al. 1993a). In contrast, Barret et al. (1990) reported variations in mean prey length among Norwegian populations, Ammodytidae ranging from 10 to 12 cm and the gadids from 6 to 14 cm.

In our study, for all prey species from the 2 islands the modal length was 10 cm. In Norway, the modal prey length varied with species: 9 cm in *Ammodytes* sp. and from 6 to 14 cm in gadids, depending on the colony (Barret et al. 1990). On the Isle of May, the modal prey lengths were 6 and 8 cm (Wanless et al. 1993b). The prey length on the Cíes Islands suggests that European shags selected a restricted range of prey size, especially during April and May, when there were no prey size differences between the 2 islands. Moreover, the available sizes of prey differ from those selected by the shags. The lengths of gobiids eaten by shags differ from those of *Lesueurigobius friesii* in the Ría de Arousa. European shags consume gobiids ranging mainly between 4 and 10 cm, with a bimodal distribution with modes of 6 to 7 and 10 cm. The population of *L. friesii* in the Ría de Arousa has a dominant modal group of around 7 cm, while the 10 cm group is much less abundant (Fernández 1994). The mean length of *Trisopterus luscus* individuals caught on the continental shelf off Galicia was 19 cm, with the most abundant modal class being 23 cm in length (López-Veiga et al. 1976, 1977). Individuals in the rías have much larger mean lengths than those in the diet of shags (J. E. Ortega-Ruano & J. Freire unpubl. data), as the shag captures primarily juveniles measuring less than 11 cm with a bimodal distribution with modes of 10 and 15 cm. European shags appear to select small fish. Shags capture fishes with bills which work like tweezers (Lumsden & Haddow 1946), and there is a strong sexual dimorphism in size (males weigh 22% more than females), although the bill does not show dimorphism. This fact has been suggested as a possible selective force for an optimum bill size in both sexes (Velando et al. unpubl.), which is determined by the need to capture prey of a particular size.

Our study highlights differences in the diets of the European shag in 2 colonies near to one another. The diet was found to have greater divergence and diversity during the winter, which could be a reflection of the greater diversity in feeding grounds used by this species in winter. During this season, the competition between individuals and the scarcity of prey may give rise to a more opportunistic diet, especially if we consider that these birds are able to exploit areas further away from the colonies. In contrast, during the months when the chicks are being provisioned, the diet centers around the family Ammodytidae, and the birds exploit a resource which is abundant in the sandy areas that surround the islands. The feeding grounds on the Cíes Islands are located within a radius of less than 2 km from the colonies, on sandy bottoms at mean depths of less than 14 m (Velando 1997). Additionally, the distribution in size of the prey consumed points to the selection of prey by size (since the size-frequency distribution in the field is different). Therefore, this study has found that the European shag presents characteristics typical of an opportunistic feeder, but is highly selective in its use of a specific resource, depending on the ecological conditions, during the chick feeding period.

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Appendix 1. Seasonal patterns in dietary composition of the European shag *Phalacrocorax aristotelis*, expressed as numerical frequency (%N), on the Cíes Islands and Island of Ons during the period under study in 1995. Prey codes used in Fig. 3 are given in parentheses

	February		March		April		May		June		Total	
	Cíes	Ons	Cíes	Ons	Cíes	Ons	Cíes	Ons	Cíes	Ons	Cíes	Ons
No. of pellets	30	18	28	17	14	14	30	14	25	12	127	75
No. of items	1246	1078	711	653	300	389	650	469	578	322	3485	2911
Ammoditydae (Am)	71.2	8.5	75.8	17.6	86.0	57.3	83.2	86.6	71.4	87.3	75.7	38.5
Atherinidae												
Atherina presbyter (Ath)	2.0	16.0	4.2	50.1	–	11.6	4.1	4.0	5.5	9.3	3.2	20.3
Gobiidae												
Gobius spp. (Gob)	2.0	65.8	7.4	21.0	–	5.9	1.4	–	0.2	–	2.5	29.8
Gobiusculus flavescens (Gbs)	9.6	–	0.1	–	–	–	–	–	0.3	–	3.5	–
Labridae												
Symphodus spp. (Sym)	2.7	4.2	3.2	2.6	8.3	7.2	4.5	1.0	3.1	0.3	3.7	3.2
Symphodus bailloni (Syb)	1.4	0.4	0.7	4.0	–	2.6	1.1	–	2.1	–	1.2	1.4
Labrus spp.	0.5	0.2	0.4	0.5	0.3	0.3	–	0.2	–	–	0.3	0.2
Gadidae												
Trisopterus spp. (Tri)	4.4	0.1	5.6	2.8	4.0	13.1	2.6	6.0	15.2	0.6	6.1	3.4
Pollachius pollachius (Pll)	2.2	0.2	2.0	0.6	0.7	1.3	0.9	2.3	0.3	–	1.5	0.7
Cilia mustelata	0.2	–	0.1	0.1	–	–	0.3	0.2	–	–	0.2	0.1
Micromesistius spp.	–	–	–	–	–	–	–	–	0.3	–	0.1	–
Other fishes												
Sardina pilchardus	0.1	–	–	–	0.7	–	0.1	–	1.2	2.1	0.3	0.2
Chelon labrosus	–	2.5	–	–	–	–	–	–	–	–	–	0.9
Callionymus lyra	1.6	–	–	–	–	0.5	0.3	–	–	–	0.6	0.1
Scomber scombrus	0.3	–	–	–	–	–	0.5	–	–	–	0.2	–
Scorphaena spp.	0.2	–	–	–	–	–	–	–	–	–	0.1	–
Unidentified	0.2	0.1	0.3	0.5	–	0.3	1.0	–	0.2	0.3	0.3	0.2
Crustacea	0.5	1.0	–	0.3	–	–	–	–	–	–	0.2	0.4
Cephalopoda	0.2	1.0	–	–	–	–	–	–	–	–	0.1	0.4

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