STATUS AND DIET OF THE EUROPEAN SHAG (MEDITERRANEAN SUBSPECIES) *PHALACROCORAX ARISTOTELIS DESMARESTII* IN THE LIBYAN SEA (SOUTH CRETE) DURING THE BREEDING SEASON

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ABSTRACT

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During 2010–2012 we collected data on the population status and ecology of the European Shag (Mediterranean subspecies) *Phalacrocorax aristotelis desmarestii* on Gavdos Island (south Crete), conducting boat-based surveys, nest monitoring, and diet analysis. The species' population was estimated at 80–110 pairs, with 59% breeding success and 1.6 fledglings per successful nest. Pellet morphological and genetic analysis of otoliths and fish bones, respectively, showed that the shags' diet consisted of 31 species. A total of 4 223 otoliths were identified to species level; 47.2% belonged to sand smelts *Atherina boyeri*, 14.2% to bogues *Boops boops*, 11.3% to picarels *Spicara smaris,* and 10.5% to damselfishes *Chromis chromis*. Our results revealed that, during the breeding season, the European Shag feeds mainly on small demersal species that are of low commercial value, posing no significant threat to the conduct of local fisheries.

Keywords: breeding biology, diet, Gavdos Island, European Shag, Mediterranean subspecies

INTRODUCTION

The European Shag *Phalacrocorax aristotelis* resides in the northeastern Atlantic Ocean and Mediterranean Sea basin. It has been divided into three subspecies with breeding ranges that do not overlap: the nominal *P. a. aristotelis* (in the Atlantic), *P. a. riggenbachi* (in North Africa) and *P. a. desmarestii* (in the Mediterranean and the Black Sea) (del Hoyo *et al.* 1992, Aguilar & Fernadez 1999, Nelson 2005). The species' European population is relatively small (<81 000 pairs; BirdLife International 2004) and considered to be stable. The Mediterranean subspecies has decreased substantially, with an estimated population size of <10 000 pairs of which *ca.* 7 000 pairs are found in the western Mediterranean islands (i.e., Balearics, Sardinia, Corsica, and Lampedusa), plus 1 000 pairs in the Black Sea (Guyot 1993, Aguilar & Fernandez 1999, Bazin & Imbert 2012). In the eastern Mediterranean, the subspecies has been poorly studied, although the coast of Greece is regarded as a stronghold for its population, as significant breeding colonies are located in the north and central Aegean Sea. In the 1990s, the Greek population was estimated at 600–1 000 individuals (Handrinos 1993, Handrinos & Akriotis 1997), although a recent survey found that >1 500 breeding pairs reside in Greek waters, probably as a result of better monitoring rather than a population increase (Velando & Freire 2002, Bazin & Imbert 2012, Thanou 2013). The subspecies has been listed in Annex I of the EU "Birds" Directive 2009/147/EC (Council of the European Union 2006) because of a general view that its numbers and breeding distribution have decreased and because of its vulnerability to oil spills, mortality as bycatch in fishing gear, dinoflagellate blooms, and prolonged adverse weather that impedes foraging (Aguilar & Fernandez 1999, Taylor 2000, Mitchell *et al.* 2004, Velando *et al.* 2005, Thanou 2013, Karris *et al*. 2013, Žydelis *et al.* 2013, Berdalet *et al.* 2015). Monitoring its population and conducting research on its biology are considered the top priorities for ensuring the long-term protection of its breeding colonies and feeding grounds (Aguilar & Fernandez 1999).

The European Shag is strongly linked to coastal waters and is largely sedentary. It breeds colonially in rocky areas, showing high nest-site fidelity, but it can occupy numerous sub-colonies that are well spaced over several kilometers of coast, which make it difficult to delineate and monitor colonies (del Hoyo *et al.* 1992, Snow & Perrins 1998, Nelson 2005). In addition, significant fluctuations in breeding numbers have been noted from year to year in several Mediterranean colonies, related to food availability. Thus, censuses in certain regions are quite difficult and need to be well co-ordinated (Guyot 1993).

In the present study, we collected data during 2010–2012 on European Shag population size, including aspects of its breeding biology and foraging ecology at the limit of the subspecies' geographical distribution in the Mediterranean, on the island of Gavdos (south Crete). The study area constitutes the extreme southern extension of the species' European range; no systematic study has been carried out in this area, and our knowledge has been limited to species presence and its sedentary character. The objectives of our study were to (a) determine the subspecies' status in terms of breeding distribution and population size; (b) assess breeding phenology, success rates, and productivity; and (c) investigate its diet and any interactions with the small-scale coastal fishery that is practiced in Crete. Important to the latter is that fact that shags forage at a radius of 4–17 km from their breeding colonies and in depths ranging between 7 and 80 m (Wanless *et al.* 1991, Kirby *et al.* 1996, Velando *et al.* 2005).

STUDY AREA

Gavdos Island (34°51′N, 24°5′E) is a remote insular area with 60 human inhabitants, located 48 km south of Crete and ~260 km from the African coast, in the Libyan Sea (Fig. 1). It covers an area of 29.6 km^2 and has a triangular shape, with its longest distance being 10 km from northwest to southeast. It has sandy beaches as well as limestone rocks that form high vertical cliffs reaching 362 m above sea level in the south-southwestern part of the island. The climate of the island is subtropical-Mediterranean, with a long, dry, hot summer and a short, mild winter with insignificant transition seasons. The average summer temperature is 21 °C, with August being the hottest month (mean temperature 30 °C but often exceeding 40 °C) and July the driest. In winter, February is the coldest month with an average daily temperature of 14 °C. Precipitation is trivial, occurring mainly during winter months, and annual rainfalls rarely exceed 300 mm (1992–2003 range 130–550 mm). The prevailing winds are west-northwest almost all year round (Dimitriou *et al.* 2006, http://gavdos.meteokrites.gr/). The study area covered the coasts of both Gavdos Island and the rocky, flat islet (100 m above sea level, 2 km^2) of Gavdopoula, 7.2 km northwest of Gavdos.

METHODS

Population status

European Shags nest in distinct habitat within the study area, among and under rock boulders and in caves and ridges on sea cliffs. This is a major drawback to researchers, as it makes nest searches from land impossible. In addition, all shag species (*Phalacrocorax* spp.) exhibit a prolonged and highly variable breeding cycle, in which nests might be occupied from December to August and pairs might lay a replacement or double-clutch within a breeding season (del Hoyo *et al.* 1992, Saenz & Thayer 2007, Chilvers *et al.* 2015). This phenomenon makes certain nest survey methods and population estimates difficult or even impractical (Johnson & Krohn 2001, Mitchell *et al.* 2004, Chilvers *et al.* 2015). However, where shags breed extensively along the coastline, as in the study area, surveys of lengths of the coast are recommended (Walsh *et al.* 1995). For the aforementioned reasons, censuses were pursued during the incubation and chick-rearing period, when colony attendance was expected to be greatest. In particular, boat-based surveys were conducted in the morning until 10h00 (i.e., before shags foraged) by sailing slowly (2–4 knots) around the islands at a distance of 50–150 m from the coast (Tasker *et al.* 1984, Mitchell *et al.* 2004). The coastline was divided into sectors (n = 26) that were noted on a 1:50 000 topographic map using a global positioning system (GPS Magellan, Meridian Colour) and specific landmarks that were easily recognizable in the field (e.g., capes, prominent rocks, lighthouses, etc.). Therefore, sectors were readily identified during successive visits. During these surveys, we mapped and tallied all off-duty adult birds standing on rocks, considering them as signals for the presence of "apparently occupied sites" (AOS) (Wanless & Harris 2004, Bibby *et al.* 2005). The census unit was pre-defined as individual shags, assuming that observations of one or more adult birds on a coastal spot corresponded to a breeding territory or cluster (Snow 1960, Aebischer & Wanless 1992, Aebischer *et al.* 1995). The two study islands were visited at least twice per month during November–September in all study years; the birds' location was noted by GPS and transferred into geographic information system (GIS) software (QGIS Development Team 2014).

Breeding biology

Data on breeding phenology and reproductive success were collected from a number of accessible nests that were monitored during the study period starting in early November each year (n = 24 pair-years). The nests were visited as infrequently as possible in order to avoid disturbance, and the breeding data were collected by a combination of methods (Both & Visser 2005, Wesołowski & Maziarz 2009, Dariusz 2011). Specifically, the onset of egg-laying, hatching, and fledging were calculated by back-counting, whereas breeding parameters were calculated by direct observations to estimate: (a) breeding success, i.e., the number of fledglings per nest per year (Murray 2000); (b) fledging success, i.e., the number of fledglings per successful nest; and (c) productivity, i.e., number of fledglings per territorial pair per year. The latter parameter was evaluated indirectly by the ratio of juvenile to breeding territories by recording newly fledged birds in post-breeding surveys during April and May.

Diet and foraging

For diet analysis, 40 regurgitated pellets were collected and examined using a combination of two methodological approaches: a) morphological identification of diet remains based on fish otoliths extracted from pellets by comparing them to a reference database from the Aegean region (Duffy & Laurenson 1983, Johnstone *et al.* 1990, Granadeiro & Silva 2000); and b) genetic

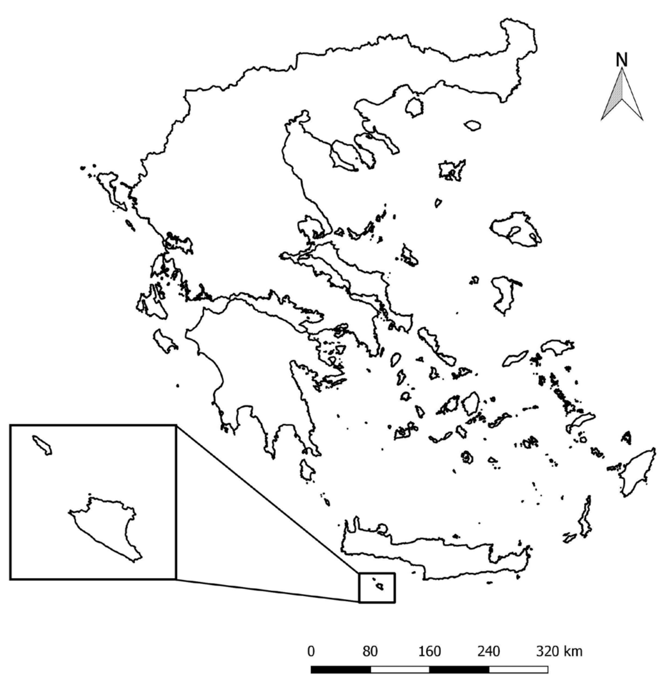

Fig. 1. Map of the study area: Gavdos and Gavdopoula islands.

analysis (DNA metabarcoding) using next-generation sequencing technology (Jarman 2002, Katzner 2006, Dunshea 2009, Pompanon *et al.* 2012). For each pellet, the number of otoliths per species was recorded and the results were statistically analyzed with the software Primer 7 (Santalucia 2007, OLIGO 2010). After the morphological identification, the remains of 20 pellets (apart from otoliths) that contained mainly fish bones were genetically identified. Initially, each pellet was immersed in liquid nitrogen and crushed to powder with mortar and pestle. Then, 90 mg of the powder was used for DNA extraction with the Qiagen DNeasy Blood & Tissue kit. The whole procedure was performed in a UV-sterilized hood; before the processing of each sample. the mortar and pestle were cleaned with a 10% bleach solution, rinsed with distilled water and ethanol, and sterilized in UV. Then, a portion of about 110 bases of the mitochondrial gene 16S rRNA was PCR-amplified using primers Chord_16S_F and Chord_16S_R (Deagle *et al.* 2009), to amplify all chordates. For this reason, a modified primer (blocking primer) was used to prevent the amplification of the shag DNA present in large quantities in the pellet. A PCR was performed, and the samples were sequenced in the genetic analyzer GS-FLX (454, Roche). The produced sequences were bioinformatically analyzed and grouped, on the basis of their similarity, into molecular taxonomic units (MOTUs). These were taxonomically identified by Blast search in the US National Center for Biotechnology Information nucleotide database. To compare the morphological and genetic data, the relative frequency of each species per pellet was calculated as well as the average relative frequency from the 20 pellets that were analyzed by both methods. Scientific names of fish, unless indicated, are contained in Table 1.

The feeding range of shags was investigated by scanning the sea area around the coast from the top of vertical sea cliffs of known altitude. The distance from the shore of single, floating birds was quantified using a laser range-finder or (when on cliffs) calculated trigonometrically with the additional aid of a clinometer (Johnson 2002, Kees *et al.* 2004, Maguire *et al.* 2006, Bolduc *et al.* 2011, Digger & Hulka 2011). The foraging pursuits of shags (e.g., underwater diving-bout duration and depth) were studied by radio-tracking four individuals, i.e., three juveniles and an adult captured at two accessible nests two weeks after egg-hatching and 10–12 d before fledging during the breeding seasons in 2011 and 2012, respectively. Radio-tags (tail mounts) consisted of VHF transmitters (Biotrack Ltd) weighting 14.5 g with a life expectancy of six months. The maximum detection range was up to 15 km in line of sight.

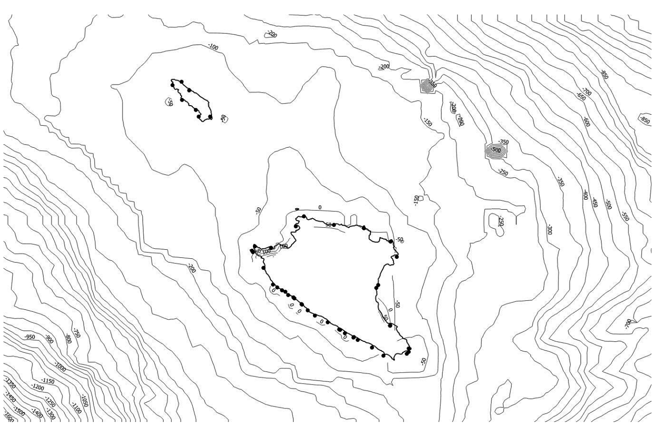

Fig. 2. European Shag breeding clusters (dots) and 50 m isobaths in the coastal area of Gavdos-Gavdopoula islands.

From coastal vantage points, radio-equipped shags were tracked a total of 52 h with a hand-held receiver (Communication Specialists, USA) and a directional three-element Yagi antenna (White & Garrot 1990). Diet composition was also used in the determination of the foraging depth and range (as there are no fisheries discards in the area). Prey fish species were classified according to their ecological preferences as a) surface pelagic (0–3 m), b) mid-water column pelagic (3–18 m), c) demersal (18–25 m), and d) benthic (25-120 m; Morat *et al.* 2011); the depth range of these fish species was obtained from a global fish information system (www.fishbase.org). Their dwelling depth was also compared with bathymetric maps acquired from a relevant portal of the European Marine Observation and Data Network (EMODnet, http://portal.emodnet-bathymetry.eu/depth-contours).

RESULTS

Overall, 43 field trips (lasting 65 d) were conducted, and 47 different AOS were identified. In some of them, more than two adult birds were recorded in all subsequent visits; thus, referring to these AOS as "breeding clusters" was more appropriate. Overall, the minimum population size was estimated at 78 breeding pairs (Fig. 2). Egg-laying took place in mid- to late December, egg-hatching was initiated in mid-January, and fledging occurred from the last week of April until mid-May. Clutch size was 1.9 eggs/nest (range = 1–4, n = 10) although in 50% of the cases single-egg clutches were detected. Breeding success was 0.59 fledglings/nest/year, and fledging success was 1.6 fledglings/successful nest/year. Based on the 32 active breeding territories and the observed ratio of fledglings to adults, presumably parent birds (i.e., 1:3 and 1:4 in the two study years, respectively), productivity ranged between 0.43 to 0.62 fledglings/breeding territory/year.

Regurgitated pellets contained on average (mean ± standard deviation) 105.6 ± 114.3 otoliths (range = 22–525) and 6.9 ± 2.6 fish species (range = 1–14). In total, 4223 otoliths were obtained and morphologically determined to 31 fish taxa (mostly species). Four fish taxa represented 83% of shag diet: 47.2% sand smelts, 14.2% bogues, 11.3% picarels, and 10.5% damselfishes. In addition, 21 other species were identified at frequencies of <3% each (Table 1). The classification of diet items into main categories according to their ecology showed that 47% of the prey fish species were pelagic (mainly *Atherina* spp.), 38% demersal-pelagic (mainly bogue, picarel, and damselfish), 12% demersal, and only 3% benthic. Genetic analysis was more accurate in the identification of small taxa (e.g., Atherinidae and Gobidae families) and added eight more fish species in the prey list. This produced different results in the estimate of relative frequencies for some species (Table 2). A significant discrepancy was the presence of the ornate wrasse (average relative frequency of 15.3%) and peacock wrasse (average relative frequency of 5.6%) in the genetic analyses, which were not found by the otolith analysis (Table 2). Comparison of results per pellet hints that, at least for the ornate wrasse, there was probably misidentification in the otolith analysis (as bogue).

The foraging distance of shags from the coast averaged 425 m (range = 20–1985 m, n = 35), although most shags (71.4%) were seen diving at a distance <350 m from the coastline (median = 202 m). Radio-tagged birds foraged underwater for 57 ± 15 s on average (range = 30–104, n = 45), at a diving rate of one pursuit per 26.5 ± 12 s.

TABLE 1
Relative frequency of fish otoliths and bones found in 40 and 20 pellets, respectively, of the European Shag on Gavdos Island (south Crete) during the breeding season

Species	Otoliths			DNA
	N	% in total	% per pellet	% per pellet
Atherina spp.	1 993	47.19	20.41	
Sand smelt *Atherina boyeri*				8.24
Mediterranean sand smelt *Atherina hepsetus*				0.36
Bogue *Boops boops*	600	14.21	23.62	5.31
Picarel *Spicara smaris*	478	11.32	16.83	11.09
Damselfish *Chromis chromis*	444	10.51	15.54	35.74
Mediterranean sand eel *Gymnammodytes cicerelus*	120	2.84	3.70	3.54
Blackspot seabream *Pagellus bogavareo*	119	2.82	4.84	
Blotched picarel *Spicara flexuosa*	92	2.18	2.81	
Mediterranean rainbow wrasse *Coris julis*	89	2.11	3.36	2.58
Gobiidae	73	1.73	2.06	
Slender goby *Gobius geniporus*				2.82
Bucchich's goby *Gobius bucchichi*				1.50
Rock goby *Gobius paganellus*				0.46
Red-mouth goby *Gobius cruentatus*				0.04
Common two-banded seabream *Diplodus vulgaris*	48	1.14	1.81	0.10
Diplodus spp.	35	0.83	1.05	
Black goby *Gobius niger*	21	0.50	0.60	
Axillary seabream *Pagellus acarne*	18	0.43	0.56	
Common Pandora *Pagellus eruthninus*	15	0.36	0.35	
Comber *Serranus cabrilla*	11	0.26	0.30	0.44
Sparidae spp.	11	0.26	0.28	
Ophidium spp.	10	0.24	0.24	
Annular seabream *Diplodus annularis*	6	0.14	0.16	
Brown comber *Seranus hepatus*	6	0.14	0.17	
Fries's coby *Lesuerigobius friesii*	4	0.09	0.11	
Small red scorpionfish *Scorpaena notata*	4	0.09	0.15	
Salema *Sarpa salpa*	4	0.09	0.15	
Trachurus spp.	4	0.09	0.10	
Horse mackerel *Trachurus trachurus*	4	0.09	0.14	
Blackfin snake blenny *Ophidium barbatum*	3	0.07	0.25	
Thickback sole *Microchirus variegates*	2	0.05	0.12	
Greater Weever Trachinus draco	2	0.05	0.06	
Brown meager *Sciaena umbra*	2	0.05	0.10	
Painted comber *Seranus scriba*	2	0.05	0.06	
Peacock wrasse *Symphodus tinca*	2	0.05	0.10	
Chub mackerel *Scomber japonicus*	1	0.02	0.00	
Ornate wrasse *Thalassoma pavo*				12.97
Symphodus spp.				6.80
Parrotfish *Sparisoma cretense*				4.16
Blotched picarel *Spicara maena*				0.48
Triplefin blenny *Tripterygion tripteronotus*				0.89
Large-scaled gurnard *Lepidotrigla cavillone*				0.15
Wide-banded hardyhead *Atherinomorus lacunosus*				0.18
Surmullet *Mullus surmuletus*				0.15
Curled picarel *Centracanthus cirrus*				0.06

DISCUSSION

This is the first study that attempted to estimate the population of the Mediterranean subspecies of the European Shag in the southernmost point of its distribution in Europe. Usual population counts from the land, i.e., finding active nests (Walsh *et al.* 1995), were impossible, since many nests were located on the ledges of steep cliffs and would be certainly overlooked. However, the methodology used in the present study might also underestimate population size by up to 30%, primarily by missing early breeding failures and non-breeders (Wanless & Harris 2004, Mitchell *et al.* 2004). In addition, taking into consideration the observed adult-to-juvenile ratio, the species population size should range between 80 and 110 breeding pairs, or 200–300 individuals.

Regarding its reproductive phenology, the European Shag exhibits high fluctuations in breeding population and plasticity in its breeding cycle, with great inter-annual variations related to food availability and the experience of the breeders (Greenstreet *et al.* 1993, Guyot 1993). Considering that the shag is a species with a prolonged breeding season (December to June; Mitchell *et al.* 2004, Thanou *et al.* 2010), its breeding phenology on Gavdos Island appears to be one the earliest and most temporally stable in Europe. Clutch size was similar to that reported for Atlantic and Mediterranean colonies, although the single-egg clutch was the dominant frequency on Gavdos. Likewise, the study population showed a rather low breeding success compared with other colonies within the species' range. This finding probably reflects the fact that the oligotrophic coastal waters of Crete are a poor marine environment, in contrast to the north Mediterranean regions (e.g., Gulf of Lion, the Adriatic Sea, the north Aegean Sea), where massive phytoplankton blooms often occur (, Ignatiades 1998, Velando *et al.* 1999, Duineveld *et al.* 2000, Zenetos *et al.* 2002, Daunt *et al.* 2007, Thanou 2013).

TABLE 2
Diet of the European Shag at Gavdos Island (south Crete) during the breeding season, based on the morphological analysis of fish otoliths and genetic analysis of fish bones in pellets (*n* =20)

Species	DNA (%)[a]	Otoliths (%)[a]
Bogue	6.1	25.6
Sand smelt	4.9	22.4
Damselfish	34.9	15.5
Picarel	11.7	14.0
Mediterranean rainbow wrasse	2.5	5.0
Blotched picarel	0.6	4.3
Blackspot seabream	0	4.2
Mediterranean sand eel	2.9	1.6
Common two-banded seabream	0	1.5
Gobies[b]	5.9	1.8
Axillary seabream	0	0.8
Comber	0.2	0.4
Small red scorpionfish	0	0.1
Horse mackerel	0	0.1
Peacock wrasse	5.6	0
Surmullet	0.2	0
Ornate wrasse	15.3	0
Other species	9.1	2.8

[a] Results are given as mean relative frequencies (%).
[b] The Gobiidae are given at the family level because they could not be identified at the species level in the morphological analysis.

The species' diet has received attention because of widespread concern about the impact of the shags on fisheries and how predation may affect the stock sizes of commercially exploited fish species (Barret *et al.* 1990, Bearhop *et al.* 1999, Cowx 2003). Although deducing this effect is problematic, as no data are available on the population size of prey species, through most of the entire Atlantic range shags rely primarily on Raitt's sand eel *Ammodytes marinus*, while bull-rout *Myoxocephalus scorpius*, young gadoids (Gadidae), and Atlantic herring *Clupea harengus,* depending on the location and season (Mills 1969, Barret *et al.* 1990, Harris & Wanless 1991, Grémillet *et al.* 1998, Velando & Freire 1999, Velando *et al.* 2005, Lilliendahl & Solmundsson 2006). The most pronounced exception to the aforementioned pattern is reported in the northernmost latitudes, where gadoids constitute the dominant food source (Hillersøy 2011). In contrast, relevant studies in the Mediterranean region show that the species' dietary spectrum is more diverse. Specifically, Shags feed principally on gobies *Gobius* spp., bogues, sand smelt, damselfish, picarel, red mullet *Mullus* spp., and Mediterranean rainbow wrasse *Coris julis* during the chick-rearing period (Brichetti *et al.* 1992, Cosolo *et al.* 2011, Drechsel 2012, Al-Ismail *et al.* 2013, Morat *et al.* 2011, 2014); and on sand smelt, brown comber *Serranus hepatus*, peacock leopard wrasse *Macropharyngodon bipartitus,* Mediterranean rainbow wrasse, red mullet, European pilchard *Sardina pilchardus,* and salema *Sarpa salpa* during the non-breeding season. In the Aegean Sea (Greece) three fish species have been found to dominate the diet of breeding shags: sand smelt, black goby *Gobius niger* and Mediterranean rainbow wrasse (Thanou 2013).

In the current study, we used two "non-destructive" diet-analysis methods to examine regurgitated material. Although pellets are easy to collect with minimum disturbance to the birds and can contain large numbers of otoliths, the status of the birds being sampled might be unknown and otoliths of different fish families might be digested at different rates (Harris & Wanless 1993). These facts can cause problems in interpretation of the results. However, in this case, pellets were collected solely throughout the incubation/chick-rearing period and from rocks where most roosting birds were in adult plumage. Thus, our results should be regarded as representative for the species' diet during the breeding season. Pellet genetic analysis gave similar results in terms of species composition, but there were differences, particularly in relative abundance. These differences may be due to various reasons, such as a) bias in favor of some species in the DNA amplification by PCR, b) the fact that genetic data are proportionate to biomass and not to the number of species in the diet, as assessed by the otolith analysis, c) incorrect taxonomic determination in the otolith analysis, and d) incorrect taxonomic determination in the genetic analysis due to an incomplete genetic reference database. Genetic analysis showed that ornate wrasse, which was not recognized in the otolith analysis (probably misidentified as bogue), is also a significant component of the shag's diet.

In any case, the diet analysis in the present study showed that shags feed mainly on small pelagic-demersal fishes commonly found near the coast and in relatively shallow waters. The morphological identification of otoliths showed that four fish species (sand smelt, bogue, picarel, and damselfish) were the most common in the diet, with an average relative frequency per pellet of more than 10% each. These findings are in agreement with the existing references for the European Shag, confirming a generalist diet but opportunistic predation in relation to geographical distribution (Velando & Freire 1999, Cosolo *et al.* 2011, Morat *et al.* 2011).

Similarly, underwater foraging bouts of shags were comparable to those detected in other Mediterranean or Atlantic regions (Wanless *et al.* 1991, Camphuysen & Garthe 2004, Camphuysen 2005, Sponza *et al.* 2010). Given that the species is a pursuit-diver (Wanless & Harris 1997), moving directly to the foraging depth with an underwater velocity of 1.3–1.9 m/s (Wanless *et al.* 1991, 1997, Grémillet *et al.* 1998, Velando & Friere 2002, Camphuysen 2005, Watanuki *et al.* 2008), the maximum vertical diving depth of shags in the study area (regardless their age) should range between 74.8 and 109.2 m. Bathymetric maps show that the potential foraging range of the species covers a maximum area of 250 km^2 around the island of Gavdos, or a foraging distance of ~5 km from its coast (Fig. 2). The dwelling depth of prey species imply that most of shags forage 20–25 m below the sea surface, at a foraging distance of <1 km from the coastline. This figure does not differ much from the distance estimated by direct observations of floating and diving birds around the coast.

Overall, shags feed on bentho-pelagic and demersal resources, but water depth and habitat characteristics near their colonies and the stage of their breeding cycle appear to strongly influence their diet (Cramp & Simmons 1997, Wanless *et al* 1997, Grémillet *et al.* 1998, Velando & Freire 1999, Watanuki *et al.* 2008, Sponza *et al.* 2010, Cosolo *et al.* 2011). In this case, the high frequency of a limited number of prey species implies that shags have a rather narrow diet spectrum during the breeding season, concentrating upon demersal fish species. On the whole, the study confirms that the European Shag is a coastal-feeding seabird that selects rocky coasts with rather swallow waters and depends on food availability (Barrett 1991, Al-Ismail *et al.* 2013, Morat *et al.* 2014). On Gavdos Island, the main fish species of the shags' diet are of low commercial value, mainly species caught by coastal trawls. However, this type of fishery is now banned in the coastal zone, while non-commercial species (e.g., damselfish) are not fished with commercial fishing gear (Council of the European Union 2006, Notti *et al.* 2016). Moreover, smelts have been fished with a special type of net, the use of which is prohibited in shallow waters (<50 m depth) and near the coast (<300 m) (Martin 2006). In general, the past and contemporary fisheries in south Aegean and Crete have not altered the structure of the fish community or modified the prey availability for shags. During the last two decades, fish stocks in shallow waters have been exploited in a sustainable way, and a general upward trend has been noted in commercial landings in Greece as well as in the biomass of demersal species, particularly at the depth of 10–50 m (Stergiou *et al.* 1997, Tserpes & Peristeraki 2002, Papaconstantinou & Farrugio 2000). The prohibition of bottom trawling within 1.5 nautical mile from the coast (regardless of depth) implemented in Greece in 2011 in accordance with EC Regulation 1967/2006, has shifted the fishing pressure toward deep waters, thus benefiting shags. Therefore, it appears that there is no significant competition for fish resources between coastal fisheries and European Shags in the Gavdos marine area.

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