

# **Diet of Mediterranean European shag, *Phalacrocorax aristotelis desmarestii*, in a northwestern Mediterranean area: a competitor for local fisheries?**

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**Abstract.** The diet of shag *Phalacrocorax aristotelis desmarestii* was studied in a NW Mediterranean archipelago (Marseilles, France) through the analysis of 109 regurgitation pellets during the non-breeding period (April to September) from 2004 to 2007. A total of 2 462 pairs of fish otoliths was found in pellets. These fishes belong to 12 families and 25 species. Six fish families (Atherinidae, Pomacentridae, Labridae, Centranchthidae, Sparidae and Serranidae) composed 92% of the shag diet. The diet remained stable during the four year study, but monthly variations were detected. These variations could result from diet changes at the end of the chick rearing period or from seasonal changes of fish community composition. The depth at which shags caught their prey was also determined. Shags mainly fish above or in *Posidonia oceanica* seagrass meadows, and mainly targeted small fishes (~10 cm TL). The mean fish biomass eaten daily by shag (280 g) was lower than that consumed by this species in the northern areas of its distribution range. The fish biomass eaten by the shag colony was estimated at only 7.4% of the total biomass caught by fishermen in the area. Thus, shags size captures did not strongly overlap with local fishing activities.

**Keywords:** seabird, feeding, fishes, seagrass beds, Mediterranean.

**Résumé.** Alimentation du cormoran huppé de Méditerranée, *Phalacrocorax aristotelis desmarestii*, dans une zone de la Méditerranée Nord-Occidentale : un compétiteur pour les pêcheries locales ? Le régime alimentaire du cormoran huppé (*Phalacrocorax aristotelis desmarestii*) a été étudié, sur un archipel de Méditerranée Nord-Occidentale (Marseille, France), par l'analyse de 109 pelotes de réjections collectées hors période de reproduction (avril à septembre) entre 2004 et 2007. 2 462 paires d'otolithes de 12 familles et 25 espèces de téléostéens ont été trouvées dans les pelotes. 6 familles

(Atherinidae, Pomacentridae, Labridae, Centracanthidae et Serranidae) ont représenté 92 % de l'alimentation. Malgré des variations mensuelles, le régime alimentaire est resté stable durant les 4 années étudiées. Ces variations reflètent soit des changements d'alimentation à la fin de la période de nourrissage des poussins, soit des changements saisonniers de la composition des communautés de poissons. Les cormorans ont capturé de petits « poissons » (~10 cm de LT) sur ou à proximité des herbiers à *Posidonia oceanica*. La biomasse moyenne consommée par jour (280 g par individu) est inférieure à celle estimée dans le Nord de son aire de répartition. Pour l'ensemble de la colonie, elle n'a représenté que 7.4 % de la biomasse totale capturée par les pêcheurs dans la zone d'étude. La taille des proies des cormorans n'a pas montré de fort recouvrement avec celle ciblée par les pêcheries.

**Mots clés :** oiseaux marins, alimentation, poissons, herbier de posidonie, Méditerranée.

## Introduction

Seabirds play an important role in food webs of marine and coastal ecosystems due to their high trophic level (Schneider *et al.*, 1986; Cairns, 1987; Piatt *et al.*, 2007)<sup>1</sup>. Their diet composition has been used in several studies for detecting changes in ecosystem functioning (Harris et Wanless, 1990; Velando et Freire, 1999; Barquete *et al.*, 2008) and prey abundance (Barrett et Furness 1990; Barrett *et al.*, 1990; Velarde *et al.*, 1994; Furness et Tasker, 2000; Robinette *et al.*, 2007). Several studies demonstrate that cormorant has a small foraging radius, usually ranging between 4 and 17 km (Wanless *et al.*, 1991; Velando *et al.*, 2005) and can severely impact local fish stocks (Birt *et al.*, 1987; Kirby *et al.*, 1996), whereas other authors show strong interactions with fisheries and aquaculture systems (Glahn et Stickley, 1995).

The European shag, *Phalacrocorax aristotelis* (Linnaeus, 1761) is composed by three subspecies. *Phalacrocorax aristotelis aristotelis* is distributed from the Barents Sea to Spain Atlantic coast, *P. a. riggenbachi* is distributed in the Northwest African coasts, and *P. a. desmarestii* is observed in Mediterranean Sea islands and along Black Sea coast (Cramp et Simmons, 1977). The shag's diet was studied in several countries, such as Norway, Iceland, Scotland, England and Spain (Lack, 1945; Barrett *et al.*, 1990; Wanless *et al.*, 1991; Velando et Freire, 1999; Furness et Tasker, 2000; Rindorf *et al.* 2000; Lilliendahl et Solmundsson, 2006). These studies focus on the subspecies *P. aristotelis aristotelis* and show that most of its diet consists of pelagic fishes (Ammodytidae and Gadidae) (Barrett *et al.*, 1990; Grémillet

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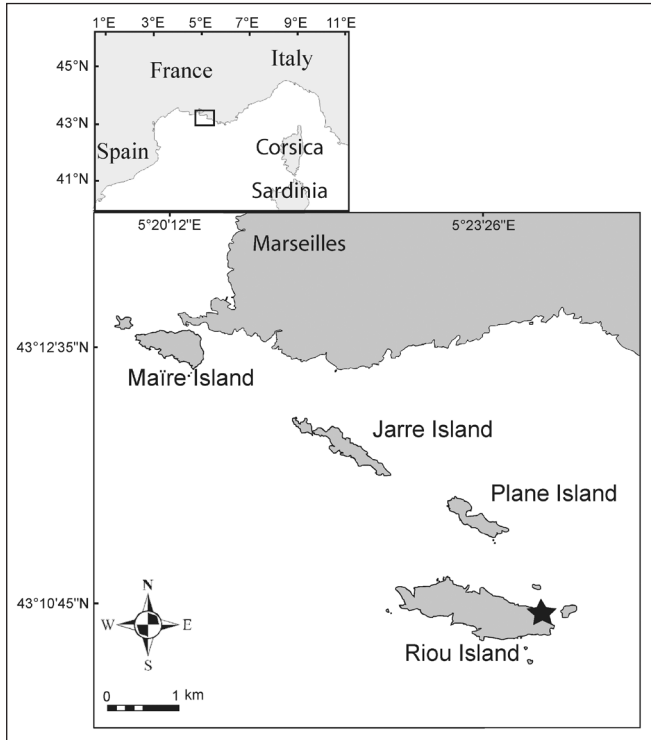
*et al.*, 1998; Velando et Freire, 1999). The diet of the Mediterranean subspecies (*P. aristotelis desmarestii*) was studied only in Corsica, where two fish families, the Labridae and Ammodytidae, represent the main prey, respectively 78% and 73% in frequency of occurrence (Guyot, 1985a; 1988).

On the French Mediterranean coasts, reproductive colonies are known only in Corsica and in Riou Archipelago, near Marseilles. In 2006, a reproductive couple was also observed in Levant Island near Hyères (Issa *et al.*, 2007). In Riou Archipelago, the first breeding adult was observed in 1994 and the first reproduction occurred in 1999 (CEEP, 2007; Delauge *et al.*, 2008). Until 2007, this colony was the first and only breeding colony on the French continental Mediterranean coasts. Over the past few years, the Riou population has increased and has currently reach 5 pair of breeders and a total of about 70 individuals (CEEP, 2007; Delauge *et al.*, 2008). The impact of predation on local fish populations may increase with the colony size, and the study of its diet is thus important in an area where recreational and artisanal fisheries are important. The diet of shag from Riou Archipelago was studied by the analysis of regurgitation pellets for (1) determine the diet composition of *Phalacrocorax aristotelis desmarestii* in Riou Archipelago, (2) look for possible temporal variations (monthly and inter-annual) in the diet composition, and (3) assess the interaction with fishing activities near the archipelago.

## Material and Methods

### Study area and sampling

The Riou Archipelago is located at 43°10.45' N - 05°23.26' E, south of Marseilles in the NW Mediterranean Sea. This archipelago is constituted by four main islands of relatively small size: Maire, Plane, Jarre and Riou which covers ~ 90 ha (Fig. 1). The colony is localised on Riou Island. Three principal types of marine substrates can be found around the archipelago in a Natura 2000 zone (Bonhomme *et al.*, 2005): *Posidonia oceanica* seagrass meadows (18.0%), rocky (11%), and sandy bottoms (71%). The North of the archipelago presents a shallow depth (< 50 m) with *Posidonia oceanica* seagrass meadows and sandy bottoms. *Posidonia oceanica* beds have high fish diversity with 53 recorded species in the studied area (Harmelin-Vivien, 1982; Harmelin-Vivien *et al.*, 2000). The South of the archipelago presents a high depth range (> 80 m) with mostly rocky substrates. This is favourable to abundant small pelagic fishes (Harmelin-Vivien *et al.*, 2000). These two types of habitats are distributed alternatively in the Marseilles area and could constitute a source of prey for shag.



**Figure 1.** Location of Riou Archipelago near Marseilles in the NW Mediterranean Sea. The colony is localised by a star.

Many studies show that shag regurgitate pellets daily (Ainley *et al.*, 1981; Jobling et Breiby, 1986; Barrett *et al.*, 1990; Johnstone *et al.*, 1990). They are constituted by undigested elements (i.e. tooth, pharyngeal teeth, scales, vertebral spines and otoliths) enveloped by mucus. Regurgitation pellets ( $n = 109$ ) were collected during the non-breeding period between April and September each year from 2004 to 2007, winter was avoid in for not interfere with reproduction (Guyot, 1985b). Pellet sampling depended on meteorological conditions and was performed when landing at Riou Island was possible. Only fresh pellets with mucus were collected irrespective of individual bird status (non-breeding and breeding adults).

### Diet analysis

Pellets were hydrated, mucus was removed and all the remaining elements were dissected under a binocular microscope. Fish preys were identified by the shape of otoliths (*sagittae*), an organ of fish reception and equilibration which is species specific

(Campana, 2005; Mériqot *et al.*, 2007). The identification of otoliths was achieved by photographic comparison with an identification book (Campana, 2004) and with an online database (Lombarte *et al.*, 2006), and on the basis of knowledge of local fish communities (Bell et Harmelin-Vivien, 1982; Ruitton, 1999; Harmelin-Vivien *et al.*, 2000). Otoliths were sorted by species, paired and counted, and then single otoliths are added.

The diet composition was used to determine the depth range of shag fishing areas. Fish species were classified into four categories according to their ecological preference: surface pelagic fishes, mid-water column pelagic fishes, seagrass meadows or rocky substrate demersal fishes and benthic fishes (Harmelin-Vivien, 1982; Harmelin-Vivien *et al.*, 2000). The overlap with human fishing activities was assessed through the classification of prey fish within three categories depending on their local economic importance, i.e. high, medium and minor importance. Moreover the size range of fish eaten by shag is compared to the size-frequency distribution of 4 fish species sampled by experimental censuses on *Posidonia oceanica* beds (Harmelin-Vivien, 1982), recreational (Bernard *et al.*, 1998) and professional fishing (Daniel *et al.*, 1998). The experimental censuses were performed using a small beam-trawl as this fishing gear is well suited to this non-rocky biotope in the area studied (Harmelin-Vivien, 1982; Harmelin-Vivien *et al.*, 2000; Letourneur *et al.*, 2001; Vacquier *et al.*, 2008). The opening of the beam-trawl used was 1.5 × 0.5 m, with a 8 mm net mesh size (Harmelin-Vivien, 1981). Data from recreational and professional fishing were obtained by investigations with fishermen (Bernard *et al.*, 1998; Bonhomme *et al.*, 1999, Daniel *et al.*, 1998; Goñi *et al.*, 2008; Soler *et al.*, 2008).

Fish length and otolith length are correlated (Morat *et al.*, 2008). Linear regressions between total fish length (TL) and otolith length (OL) were determined for all species eaten by shag. Digital pictures of a sub-sampling of otoliths among three categories (small, medium and large) were made for all species, and their length measured digitally using the software Visilog 6.3 (Neosis, Orsay, France). Total length of all fish individuals and otolith categories were then back-calculated. Fish biomass was computed using available length-weight relationships (Froese et Pauly, 2007). The majority of otoliths found in pellets belonged to small and medium-sized categories. So only the daily minimum and medium biomass were determined for assess a range of daily biomass consumed for each month sampled.

A comparison test for proportion (z test) was used to test for differences between the proportions of fish families eaten during

the four years of this study, and  $z$  was then compared with a normal distribution with  $\alpha = 0.05$ .

$$z = \frac{f_1 - f_2}{\sqrt{\hat{p}^*(1-\hat{p})^*\left(\frac{1}{n_1} + \frac{1}{n_2}\right)}}$$

With  $\hat{p} = \frac{n_1 f_1 + n_2 f_2}{n_1 + n_2}$ ,  $n_1$  and  $n_2$  lengths and  $f_1$  and  $f_2$  numerical frequencies of two samples.

## Results

### Overall diet composition

A total of 2 462 pairs of fish otoliths was found in the 109 regurgitation pellets of *Phalacrocorax aristotelis desmarestii*. Fragments of *Posidonia oceanica* leaves were found in numerous pellets (around 40%). The mean number of ingested fish per pellet was  $22.6 \pm 12.5$  (min.-max.: 4 - 78). They belonged to 25 species from 12 fish families, plus 4 unidentified species (Table I). The six most frequently fish families occurring in pellets were Sparidae (71% of pellets), Pomacentridae (70%), Labridae (61%), Centracanthidae (49%), Atherinidae (42%) and Serranidae (40%). These families represented 92% of the total number of prey ingested, with only two families alone (Atherinidae and Pomacentridae) accounting for 47% of prey abundance (Fig. 2).

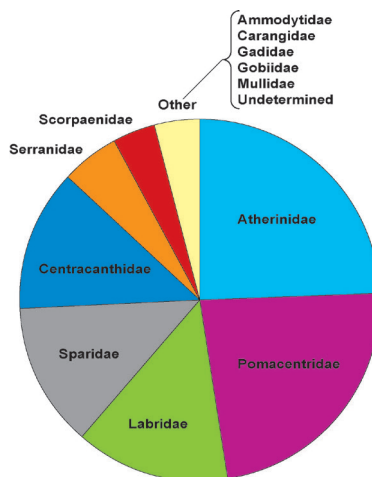
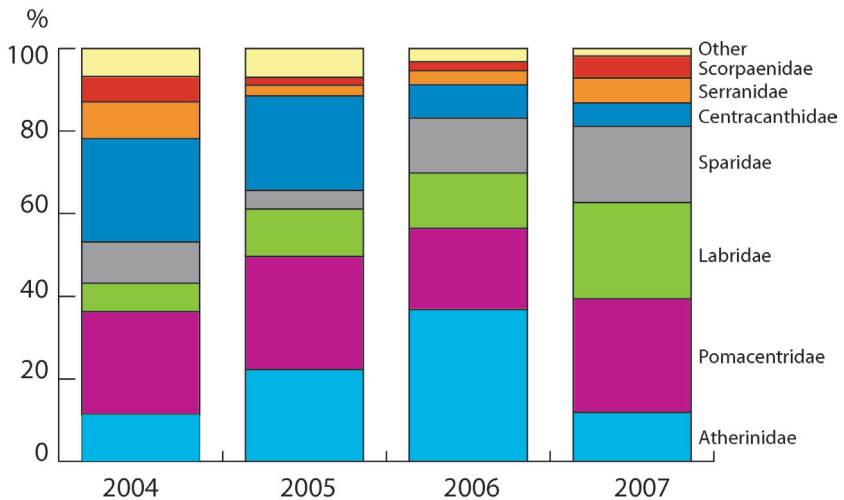


Figure 2. Proportion in abundance percentage of the most important fish families in the diet of *Phalacrocorax aristotelis desmarestii* in the Riou Archipelago, NW Mediterranean.

### Temporal variations

Inter-annual variations of diet during the non-breeding period from 2004 to 2007 were low overall (Fig. 3), and only two families displayed significant differences, i.e. Atherinidae between 2006 and 2004/2007 ( $z = -2.28$  and  $2.27$  respectively,  $p < 0.05$ ) and Centranchthidae between 2006 and 2004 ( $z = 1.99$ ,  $p < 0.05$ ). However, these differences could be due to the fact that sampling was not performed in April and May 2004 and 2007, while Atherinidae were numerous in shag pellets during these months in 2005 and 2006.



**Figure 3.** Comparison of the abundance percentage of the fish families ingested by shag between the 4-year studied in the Riou Archipelago, NW Mediterranean. Other see Fig. 2.

On a monthly basis Atherinidae were generally the main prey in April and May (respectively  $17.6$  and  $8.2$  fish-pellet<sup>-1</sup>, representing 53% and 40% of prey abundance) and became a minor part of the diet in August and September ( $0.4$  and  $0.7$  fish pellet<sup>-1</sup>, representing only 2% and 3% in prey abundance) (Fig. 4). Pomacentridae were poorly represented in April and May ( $2.1$  and  $2.4$  fish pellet<sup>-1</sup>, 6% and 7%). They became the main prey eaten in June and July ( $6.8$  and  $7.8$  fish pellet<sup>-1</sup>, 33% and 37%) and also represented 23% and 27% of the diet in August and September. A high proportion of Centranchthidae was also observed these latter months (27% and 20% in abundance,

respectively). So, the diet composition of shags displayed clear monthly variations in proportions for a few fish families during the non breeding periods studied, although most families displayed non-significant fluctuations over months (Fig. 4).

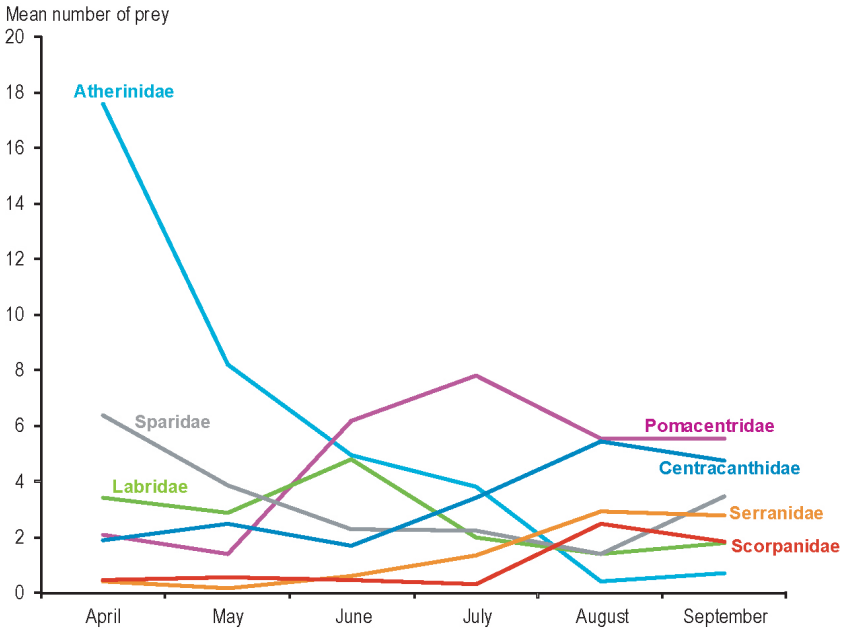


Figure 4. Mean number of fishes from the 7 most important families eaten by shag each month, in the Riou Archipelago, NW Mediterranean.

### Fishing depths range and commercial importance of prey

Each fish species occurs in a given part of the water column in relation to its ecological characteristics. The bulk of the diet was composed of pelagic fishes (surface and mid-water column) which represented 64.6% of prey abundance (Fig. 5). Seagrass meadow and rocky demersal fishes constituted 29.8% of the diet, and benthic fishes only 5.6%. The occurrence of fragments of *Posidonia oceanica* leaves was noticed in numerous pellets, indicating that shag fishing areas were mainly located in and above seagrass meadows.



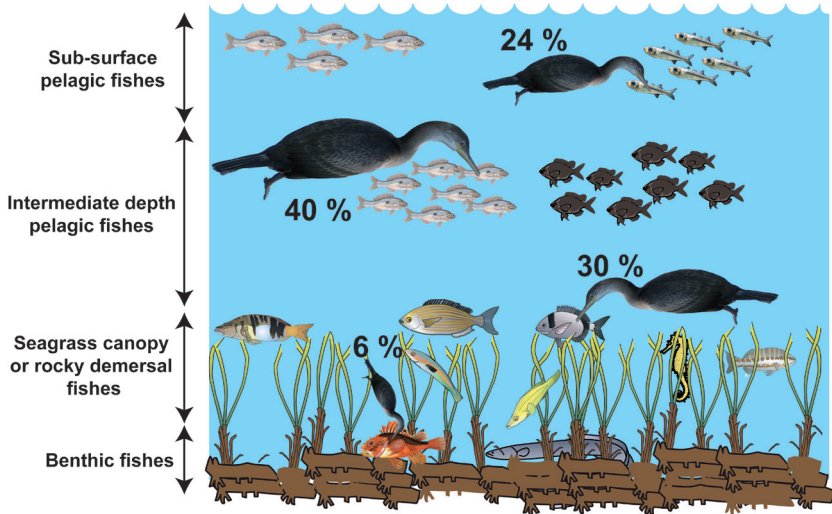


Figure 5. Depth distribution of shags feeding above *Posidonia oceanica* seagrass meadows according to the ecology of fish prey: benthic, demersal, medium-column or surface pelagic species. Silhouettes of Pomacentridae, Centracanthidae adult, Centracanthidae juvenile, Serranidae, Syngnathidae, Sparidae, Labridae, Scorpaenidae, Congridae are presented in this figure (modified from Harmelin-Vivien 1982 and Pergent et al. 2012). Organism silhouettes came from the integration and application network website <http://ian.umces.edu/>.

The analysis of the local economic importance of fish (Table I) caught by shags around Riou Archipelago revealed that 49% of prey (*Chromis chromis* and *Atherina* spp.) were of minor economical value, 31% of fish a medium value (*Sarpa salpa*, *Coris julis* and *Trachurus* sp.) and only 20% a high value, such as Sparidae of the genus *Diplodus* and the two species of Scorpaenidae. Moreover, the size-frequency distribution patterns of two medium value (*Coris julis*, *Symphodus* spp.) and two major value (*Serranus scriba*, *Scorpaena* spp.) commercial species caught by shag was compared with those from experimental censuses, professional and recreational fishing (Fig. 6). This revealed that shag's and fishermen's activities do not target the same size range although a slight overlap could be observed for some species. In fact, fishes eaten by shag were < 14 cm (TL), with a median size < 10 cm for these 4 species, whereas fishermen targeted fish larger than those caught by shag (at least 12 to 16 cm TL depending of species).

**Table I.** Diet composition of *Phalacrocorax aristotelis desmarestii* in the Riou Archipelago (France) between April and September 2004 to 2007. Contribution was expressed as frequency of occurrence (FO), number of individuals (N) and family numerical frequency (% N). For each fish species, the level of local economic importance is expressed: minor (1), medium (2) and high (3).

Fish taxa	Year Number of pellets Local economic importance	2004 25		2005 10		2006 48		2007 26		Total 109	
		FO	N	FO	N	FO	N	FO	N	FO	N
<b>Ammodytidae</b>										11	22
<i>Gymnammodytes cicirellus</i>	1	16	9			17	13				
<b>Atherinidae</b>										42	600
<i>Atherina boyeri</i>	1	28	69	30	35	56	358	31	56		
<i>Atherina hepsetus</i>	1					25	75	12	7		
<b>Carangidae</b>										12	45
<i>Trachurus sp.</i>	2	12	24	20	10	13	8	8	3		
<b>Centracanthidae</b>										49	311
<i>Spicara smaris</i>	2	76	148	60	36	44	95	27	30		
<i>Spicara maena</i>	2	4	2								
<b>Gadidae</b>										8	15
<i>Trisopterus minutus capelanus</i>	2	12	8	10	1	8	5	5	1		
<b>Gobiidae</b>										6	7
<i>Gobiidae sp.</i>	1					6	4	12	3		
<b>Labridae</b>										61	340
<i>Coris julis</i>	2	40	29	30	11	46	64	46	86		
<i>Symphodus mediterraneus</i>	2	16	5	30	7	60	94	50	37		
<i>Symphodus ocellatus</i>	2	12	4								
<i>Xyrichthys novacula</i>	2	8	3								
<b>Mullidae</b>										2	2
<i>Mullus barbatus</i>	3					2	1	4	1		
<b>Pomacentridae</b>										70	568
<i>Chromis chromis</i>	1	84	149	80	43	67	231	58	145		
<b>Scorpaenidae</b>										28	94
<i>Scorpaena notata</i>	3	40	34	20	3	19	23	35	28		
<i>Scorpaena porcus</i>	3	12	3			2	3				
<b>Serranidae</b>										40	129
<i>Serranus scriba</i>	3	60	53	20	4	29	40	50	32		
<b>Sparidae</b>										71	320
<i>Boops boops</i>	2	4	1	10	1	19	20	19	15		
<i>Diplodus annularis</i>	3					13	8	12	7		
<i>Diplodus cervinus</i>	3	20	14			2	1				
<i>Diplodus sargus</i>	3	8	2								
<i>Diplodus vulgaris</i>	3	64	40	40	5	52	110	69	60		
<i>Lithognathus mormyrus</i>	3					10	6	15	5		
<i>Pagellus erythrinus</i>	3					2	5				
<i>Sarpa salpa</i>	2	8	3	10	1	10	6	19	10		
<b>Undetermined</b>										8	9
<i>Und. sp1</i>						6	4	8	2		
<i>Und. sp2</i>						2	1				
<i>Und. sp3</i>						2	1				
<i>Und. sp4</i>						2	1				
<b>Total</b>		<b>600</b>		<b>157</b>		<b>1177</b>		<b>528</b>		<b>2462</b>	

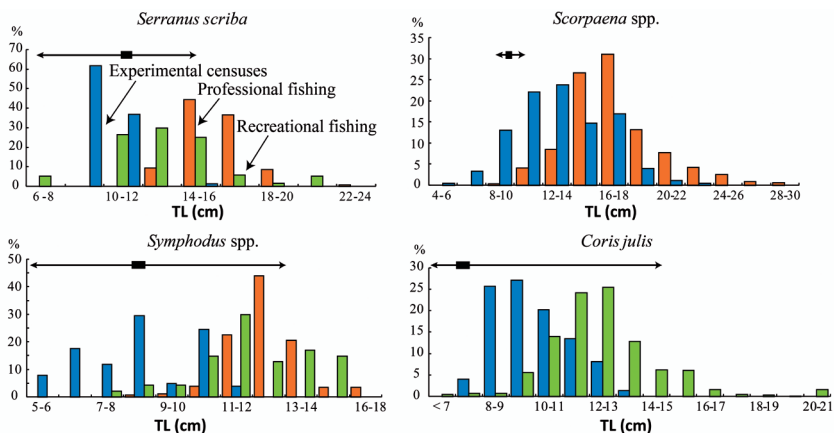


Figure 6. Size-frequency distribution of 4 fish species sampled by experimental censuses, recreational fishing and professional fishing. Among these fishes, two have a high commercial value (*Serranus scriba* and *Scorpaena porcus*) and two have a medium commercial value (*Symphodus* spp. and *Coris julis*). Arrows indicate the range of fish size eaten by shags for each species, the mark on the arrows indicate the median size eaten.

### Biomass consumed

The relationships between otolith length (OL) and total fish length (TL) (Table II) were used to further assess fish size and biomass.

Table II. Relationships between fish size (TL, mm) and otolith size (OL, mm) for the species studied.

Species	Relationships	n	r <sup>2</sup>	p
<i>Atherina</i> sp.	TL = 34.67 OL - 10.51	11	0.97	***
<i>Boops boops</i>	TL = 28.11 OL + 35.65	10	0.84	***
<i>Chromis chromis</i>	TL = 24.53 OL - 14.57	4	0.95	*
<i>Coris julis</i>	TL = 77.03 OL - 58.55	10	0.96	***
<i>Diplodus annularis</i>	TL = 35.67 OL - 32.21	9	0.98	***
<i>Diplodus vulgaris</i>	TL = 43.67 OL - 69.54	12	0.91	***
<i>Lithognathus mormyrus</i>	TL = 44.44 OL - 69.44	7	0.96	***
<i>Scorpaena</i> sp.	TL = 19.76 OL - 8.14	9	0.97	***
<i>Serranus scriba</i>	TL = 37.43 OL - 42.38	5	0.99	***
<i>Spicara</i> sp.	TL = 27.59 OL - 9.56	8	0.87	***
<i>Symphodus mediterraneus</i>	TL = 41.12 OL + 7.97	6	0.96	***

Shags eat fish varying in length from 2.3 to 21.9 cm (TL). Prey presented a mean size between 7.4 and 18.4 cm (TL) depending of species. However, most prey caught was smaller than this mean size. For this reason, only minimum and mean sizes of fish were used to assess the daily biomass consumed per bird each month. These results

displayed a clear seasonal trend, characterized by minimal values of biomass eaten in June-July (both for minimum and average estimates), and reached a peak in April (Table III). During the non breeding period, the highest consumption ranged between a maximum of 128 g and 383 g in April, and a minimum of 77 g and 213 g in June. During the 6 month studied, each shag ingested daily a mean biomass ranging between  $103 \pm 19$  g and  $278 \pm 54$  g.

**Table III.** Minimum and mean daily biomass (BM) (g) individually consumed by shags at during the non-breeding period studied.

Month	Biomass min.	Biomass mean
April	127	383
May	116	297
June	77	213
July	79	237
August	104	260
September	115	279
<b>Average</b>	103	278

## Discussion

### A diversified diet

The diet of the European shag (*Phalacrocorax aristotelis*) was studied at several sites within its distribution range and is mainly composed of Gadidae (23% to 70%) in Norway (Barrett et Furness, 1990; Barrett, 1991), or Ammodytidae (71% to 86%) in Galicia, Spain (Velando et Freire, 1999; Velando *et al.*, 2005). Our study showed that the Mediterranean subspecies, *P. aristotelis desmarestii*, displayed a more diversified diet in Riou Archipelago, composed of at least 25 fish species belonging to 12 families during the studied periods. However, 92% of the abundance of prey was accounted by 6 fish families and, among these, in particular 24% by Atherinidae and 23% of Pomacentridae. These results strongly contrasted with those of other studies in which most of the diet was composed by only one fish family (Barrett *et al.*, 1990; Velando et Freire, 1999; Lilliendahl et Solmundsson, 2006). The proportion of Atherinidae found in the present study was lower than that found in Corsica where they represent 72% of prey (Guyot, 1985c; 1988). The European shag thus presents a variable diet depending on the geographic area considered and the local environmental characteristics, as suggested by Velando et Freire (1999). Our results reinforce the idea that shag may be considered as an opportunistic predator (Barrett, 1991) able to change its food preferences following an unusual event occurring in its environment (Velando *et al.*, 2005).

The marine environment near the Riou archipelago is characterised by three principal types of habitats: rocky areas, *Posidonia oceanica* seagrass meadows and sandy bottoms. Rocky areas are localised mainly in the South of the archipelago, associated with high depths (> 80 m) thus favouring fish communities dominated by small pelagic fishes such as *Atherina* spp. Around the archipelago, few sandy bottoms are observed and the fish communities are dominated by *Mullus barbatus* and *Xyrichtys novacula* which are poorly represented in the shag's diet. *Posidonia oceanica* seagrass meadows, associated with lower depth (< 50 m), are more extensive in the North of the archipelago, and presented a high diversity and abundance of fish species (Bell et Harmelin-Vivien, 1982; Harmelin-Vivien *et al.*, 2000). The fish community is dominated there by Labridae (*Coris julis*, *Symphodus* spp.), Pomacentridae (*Chromis chromis*), Centranchthidae (*Spicara* spp.) and Serranidae (*Serranus scriba*) (Harmelin-Vivien *et al.*, 2000). These species were among the predominant prey consumed by shags in the Archipelago.

The preferential consumption of prey by shags could also partly be influenced by parasitism and particularly digeneans. They are able to manipulate the host behaviour to increase the risk of predation by top predators such as seabirds (Bartoli *et al.*, 2005; Bartoli et Boudouresque, 2007). *P. aristotelis desmarestii* is the definitive host of some digeneans like *Galactosomum lacteum* (Bartoli Pierre, Pers. Comm.). The first intermediate host of this digenean is the mollusc *Cerithium mediterraneum* and the second host is always a *Symphodus* spp. (Bartoli Pierre, Pers. Comm.). In infected fish, parasites encyst near brachial nerves. This infection decreases the mobility of the pectoral fins (Bartoli Pierre, Pers. Comm.) and the swimming ability of fishes (Maillard, 1976; Faliex, 1991; Faliex et Morand, 1994), increasing their probability of predation by the final host, i.e. shag. Few parasitic cycles with shags as the definitive host are known, but many fish species eaten by this seabird, such as *Spicara* spp. or *Atherina* spp. are highly infected by parasites (Bartoli *et al.*, 2005). So, it is possible that the consumption of fish species by shags partly results from behavioural manipulation of fish by parasites, as found for the Yellow-legged gull (*Larus michahellis*) (Bartoli et Bianconi, 1988).

The Riou Island is an insular terrestrial ecosystem and like other island is a nutrient-limited environment. Croll *et al.* (2005) show that seabird colonies deliver in insular ecosystem nutrient rich guano from marine ocean waters to nutrient-limited plant communities. Moreover these plant communities are dependent on guano abundance. So seabird colonies could be a bond between marine and terrestrial ecosystems. In Riou Island, the shag colony could play this role and enriched the terrestrial ecosystems.

## Temporal variations

The inter-annual diet study revealed significant differences in the proportions of only two fish families. These differences could partly be the result of sampling problems as suggested above. However, temporal modifications of shag diet are observed in other areas, such as in Norwegian waters for Ammodytidae and Gadidae (Barrett *et al.*, 1990) and may reflect fish stock variations or alteration in prey availability.

Variations in proportions of each fish family were also observed on a monthly basis in Riou Archipelago. This could be linked to temporal fluctuations of the predominant prey according to months, with higher proportions of Atherinidae in April and May, Pomacentridae in June and July, and Centranchidae in August and September. Seasonal variations in family proportions are also observed in the diet of Galician shag populations with an increase in Ammodytidae between February and June (Velando and Freire, 1999). In our study, two explanations could be proposed. First, April and May coincided with the end of the feeding period of shag chicks in the Mediterranean Sea (Guyot, 1985c, b; 1990). Atherinidae are small thin fishes more adapted than other fish families (Pomacentridae or Centranchidae) to the feeding of young birds, which have a small bill. Secondly, these changes may be explained by natural variations of atherinid populations. Atherinidae and Pomacentridae occur near the coasts of Marseilles during the whole year, but their relative proportions and biomass vary with seasons (Bell et Harmelin-Vivien, 1982; Ruitton, 1999; Harmelin-Vivien *et al.*, 2000). For example, *Chromis chromis* presents high abundance between June and September with a peak of 4-8 cm sized-individuals in June and July (Ruitton, 1999). The highest proportions of this species in shag pellets were also observed during these two months. So, variations in natural fish populations could explain some of variations observed in shag diet.

## Fishing depths and biomass consumed

Several studies have demonstrated that shag consume high proportions of mid-water column fishes which represent 56% - 73% of the diet in Galicia (Velando et Freire, 1999) and 72% in Corsica (Guyot, 1985a). However, the proportion of these preys in the diet of the Riou shag population was much lower, reaching only 40%. The rest of the diet was composed of surface fishes (25%) or seagrass meadows and rocky demersal fishes (30%). These differences in prey types caught by shag suggest that the preferential fishing depths depended on water depth and habitat characteristics near the seabird colony. Shag fisheries areas are usually located within a short distance around the colonies, between 4 and 17 km (Wanless *et al.*, 1991; Velando *et al.*,

2005). Large *Posidonia oceanica* seagrass meadows are found within this “circular” distance near Riou Archipelago. These meadows have a diversified and relatively abundant ichthyofauna, whereas pelagic fishes constitute a more variable resource over time and space (Bell et Harmelin-Vivien, 1982).

In our study, the length of prey eaten by shags was estimated between 7.4 cm and 14.0 cm depending on species. The modal length was estimated at 10 cm in Spain (Velando et Freire, 1999), and the mean length at 6-8.0 cm on the Isle of May (Scotland) (Wanless *et al.*, 1993). In Norway, the mean prey length varies according to species: 9.0 cm for Ammodytidae and 6.0-14.0 cm for Gadidae (Barrett *et al.*, 1990). All these results confirm that the European shag has a preferred range of prey size as suggested by Velando et Freire (1999). The shag’s bill (culmen) length is a conservative trait on the distribution range (Martinez-Abraín *et al.*, 2006), and could be responsible for this narrow size range of prey consumed. The mean daily fish biomass eaten by shags during our study was estimated at ~280 g per pellet. However, monthly differences were observed with a higher biomass consumed in April and May. For Mediterranean shag populations, these two months correspond to the end of the feeding period of young individuals (Guyot, 1985c, b; 1990). Nevertheless, our estimates were much lower than the 430 g and 671 g of biomass consumed daily by Norwegian (Barrett *et al.*, 1990) and Icelandic shag populations (Lilliendahl Kristjan, Pers. Comm.) respectively. These two latter biomass values represent respectively 24% and 34% of the shag body mass in these two populations, and only 15% for the Riou population. Such a difference of biomass consumed could result likely to a higher consumption of prey in cold waters than in temperate waters due to higher energy requirements in energy for the basic metabolism (Birt-Friesen *et al.*, 1989).

### Overlap with fishermen activities

In average, shags regurgitate one pellet per day (Barrett *et al.*, 1990). Our results showed that, in Riou Archipelago, shags consumed ~280 g of fish biomass per day, resulting in a total of  $3.5 \pm 0.7$  tonnes of fish for the 70 individuals of the colony during the non breeding period. Most prey had a mean length of 10 cm (TL) and only 20% of them had a high local commercial value. Recreational fishing near the archipelago is estimated to remove a total biomass ranging between 9.4 and 12.8 tonnes from July to September, and professional fishermen have caught 11.2 tonnes in that area in 1996 during these three months (Bernard *et al.*, 1998; Daniel *et al.*, 1998). The shag colony consumed during these three months only 1.8 tonnes of fish, which represented 7.4% of the total biomass fished around the archipelago. The predominant fish species eaten by shags were *Atherina* spp.



and *Chromis chromis*. Fishermen (both professional and recreational) mostly targeted *Dicentrarchus labrax*, *Sparus aurata*, *Scorpaena* spp. and *Diplodus* spp. (Bernard *et al.*, 1998) which indicate that shags and fishermen are not in major competition for resources in the area studied.

In conclusion, the results of our study revealed that this top-predator had a diversified diet which depended of its environment and the associated fish communities. This Mediterranean shag subspecies population utilised mainly a fishery area located around and above *Posidonia oceanica* seagrass meadows and consumed mainly small fish (~10 cm TL), particularly *Chromis chromis* and *Atherina* spp. and thus did not strongly interact with local fishermen. Finally, this subspecies consumed daily a lower biomass of fish than the sub-species found in northern Europe.

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