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Review
Shags in Antarctica: their feeding behaviour and ecological role in the marine food web

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Abstract: Feeding behaviour, ecological role in the marine food web and population trends of the Antarctic shag *Phalacrocorax bransfieldensis* and the South Georgia shag *P. georgianus* in Antarctica are analysed. The diving depths and duration recorded for these shags are the deepest and longest among all flying birds in Antarctica and match deep dives performed by small Antarctic penguins. Individual shags of both sexes partition foraging depths and food resources, which might diminish intra-specific competition. Like other sub-Antarctic shags, *P. bransfieldensis* and *P. georgianus* are bottom feeders that prey predominantly on demersal fish. In the southern Scotia Arc and west Antarctic Peninsula, nototheniids, mainly *Notothenia coriiceps*, constitute their main prey. Shag partners alternate the time at sea and, as the energy requirements at the nest increase, they increase the number but reduce the duration of the feeding trips. A steady declining trend in the number of breeding pairs of both species has been observed in the last decade at several Antarctic localities; this phenomenon at the South Shetland Islands might be at least partially explained by the effect of the commercial fishery on their prey. In inshore shallow waters shags occupy the trophic niche of main predators of demersal fish and play an important ecological role as regulators of populations of particular fish prey that have marked site fidelity. The potential use of shags as biomonitors in Antarctica is discussed.

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Introduction

The phalacrocoraciids (shags and cormorants) are cosmopolitan medium to large sized diving waterbirds that occur inland or along marine coasts and exploit both fresh waters and marine habitats.

Two phalacrocoraciid species are found in Antarctica: the Antarctic shag *Phalacrocorax bransfieldensis* Murphy (formerly the blue-eyed shag *P. atriceps bransfieldensis*), which inhabits the Antarctic Peninsula and the South Shetland Islands and the South Georgia shag *P. georgianus* Lonnberg (formerly the blue-eyed shag *P. a. georgianus*), which inhabits the South Orkney Islands and the sub-Antarctic South Sandwich Islands, South Georgia and Shag Rock (Orta 1992). In both species the breeding period is from October to February, the maximum clutch size is three eggs, chicks hatch after an incubation period of 30 days, and fledge at an approximate age of 50–65 days (see Shaw 1986, Casaux 1998a).

In the Southern Ocean, most of the studies on diet of shags have been carried out on species from sub-Antarctic areas (see below), whereas up to the mid 1980s only two studies had focused on shags from the Antarctic area. These were on *P. georgianus* at Signy Island (Shaw 1986), and on *P. bransfieldensis* at Green Island, West Antarctic Peninsula (Schlatter & Moreno 1976). Since 1990, the feeding ecology and other biological aspects of breeding shags in localities of the southern Scotia Arc and the Antarctic Peninsula have been studied with special interest within the shore-based biological research program developed by Argentina. These studies started at Duthoit Point, Nelson Island (Casaux & Barrera-Oro 1993a, Coria *et al*. 1995a, Casaux *et al*. 1997a) and were extended to other localities in the South Shetland Islands such as Roca Baja (Casaux *et al*. 1995), Half Moon Island (Casaux & Barrera-Oro 1995, Barrera-Oro & Casaux 1996a) and Harmony Point (Casaux 1998a, Casaux *et al*. 2001), in the South Orkneys such as Pirie Peninsula (Casaux *et al*. 1997b, Casaux & Ramón 2002) and in the Peninsula such as Danco Coast (Casaux *et al*. 2002).

In the Southern Ocean, fish are by far the main prey of breeding shags, whereas benthic organisms such as polychaetes, gastropods, bivalves, cephalopods and crustaceans are known to be secondary diet components. While the fish prey of most seabird species are pelagic or

Table I. Summary of published information on maximum diving depths (MDD in m) of Antarctic and sub-Antarctic *Phalacrocorax* species, with indication of the geographical area and the methodology used.

Species	Locality	MDD	Mean MDD	Method	Source
P. bransfieldensis	South Shetland Islands	113	37.8	Capillary depth gauges	Casaux *et al*. 2001
P. bransfieldensis	South Shetland Islands	73	15.6	Time Depth Recorders	Casaux & Coria in press
P. georgianus	South Georgia	116	---	Time Depth Recorders	Croxall *et al*. 1991
P. georgianus	South Georgia	107	63–84	Time Depth Recorders	Kato *et al*. 1992
P. georgianus	South Georgia	125	56–91	Capillary depth gauges	Wanless & Harris 1993
P. georgianus	South Georgia	73	38.2	Time Depth Recorders	Wanless *et al*. 1999
P. georgianus	South Orkney Islands	25	---	Entangled individual	Conroy & Twelves 1973
P. nivalis	Heard Island	60	---	Time Depth Recorders	Green & Williams 1997
P. purpurascens	Macquarie Island	66	27.1–29.3	Time Depth Recorders	Kato *et al*. 1996

pelagic stages of demersal-benthic fish caught close to the surface (Furness 1978, Croxall *et al*. 1984, Montevecchi & Berruti 1991, Barrera-Oro 2002), the Antarctic and South Georgia shags are the only flying birds in Antarctica that feed chiefly on benthic demersal fish. In agreement with data from cormorants feeding in other nearshore marine communities (Duffy & Laurenson 1983, Duffy *et al*. 1987, Wanless *et al*. 1992) we found that the fish species represented in pellets of *P. bransfieldensis* agreed qualitatively and in relative numbers with those regularly sampled by means of bottom gears such as hook and lines and trammel/gill nets in the same area (Casaux & Barrera-Oro 1993a, Casaux *et al*. 2002). It was suggested that an appropriate long-term project monitoring diet and breeding performance of shags could provide very useful data on changes in coastal fish populations which are not accessible by trawl surveys (Casaux & Barrera-Oro 1993a). A method was proposed to CCAMLR (Commission for the Conservation of Antarctic Marine Living Resources) (Casaux & Barrera-Oro 1993b) and it was finally approved in 1998 for a five year test period (Casaux & Barrera-Oro 1998, CCAMLR 1998, Annex 4, para 9.30; CCAMLR 2001).

After a decade of studies on the biology of shags from the southern Scotia Arc and the Peninsula, the aims of this review are:

1) to provide some insight into the ecological role of shags in the food web in the South Atlantic region of Antarctica, and
2) to consider the feasibility of using shags as monitors of coastal demersal fish populations, including species of commercial importance.

Diving behaviour

Diving capacity

The first data on diving behaviour of shags in Antarctica indicated a foraging depth down to 25 m (Conroy & Twelves 1973). However, this information is limited, since it came from a single South Georgia shag found entangled in a net set on the bottom at a known depth. Later, the diving behaviour of the Antarctic shag was analysed by the use of capillary-tube depth gauges (Casaux 1998a) and Time and Depth Recorders (Casaux & Coria in press). The maximum diving depth (MDD) and duration recorded for the Antarctic shag is 112.6 m (Casaux *et al*. 2001) and 5.35 minutes (Casaux & Coria in press) respectively, and is the deepest and longest duration record for any flying bird in Antarctica. The diving ability of the South Georgia shag in the Antarctic area of its occurrence, the South Orkneys, was not methodically investigated, but it has been reported that around South Georgia is similar to that reported for the Antarctic shag (see Croxall *et al*. 1991, Wanless *et al*. 1992, Wanless & Harris 1993).

The comparison of our data (Casaux *et al*. 2001, Casaux & Coria in press) with those from sub-Antarctic shags shows that the MDD recorded for the Antarctic shag is similar to that reported for *P. georgianus* at South Georgia (Croxall *et al*. 1991, Kato *et al*. 1992, Wanless & Harris 1993), but deeper than those reported for *P. nivalis* Falla at Heard Island (Green & Williams 1997) and for *P. purpurascens* Brandt at Macquarie Island (Kato *et al*. 1998) (Table I). The mean MDD registered for the Antarctic shag are similar or slightly shallower to that reported for *P. purpurascens* but markedly shallower than the values registered for the South Georgia shag at South Georgia. The differences in mass among these shag species (see Cooper 1986) and the different technologies used to measure dive behaviours did not explain the differences in diving depths. The diving depths may reflect the food availability and/or the characteristics of the foraging areas rather than the diving abilities of the species (see also Wilson & Wilson 1988, Casaux 1998a, Wanless *et al*. 1998). In this sense, the food availability inshore in shallow waters around South Georgia seems to be lower than around the South Shetland Islands. This conclusion is consistent with the shag reproductive output observed at both archipelagos (see Croxall *et al*. 1991, Wanless *et al*. 1995, Casaux 1998a). Green & Williams (1997) reached a similar conclusion when comparing the dive performance of *P. nivalis* at Heard Island and *P. georgianus* at South Georgia.

Diving strategy

The diving behaviour of *P. bransfieldensis* was studied by

direct observation on individuals foraging at Harmony Cove (maximum depth = 40 m), during 1995 and 1996 breeding seasons (Casaux 2004). These shags foraged in shallow waters (seasonal means = 6.7 and 9.2 m, respectively) and, according to the duration of the dives (mean = 39.6 and 67.4 sec; maximum 171 sec) and the diving efficiencies (*sensu* Dewar 1924), presumably they dived predominantly aerobically (the aerobic dive limit estimated by Wanless *et al*. 1992, for the South Georgia shag is 174 sec). They displayed relatively short diving bouts (mean = 9.2 and 8.7 min) composed of few dives (mean = 9.0 and 5.2). In 1995 the duration of the dives decreased with the number of dives per bout and increased with the diving depth; these relationships were not statistically significant in 1996. The duration of the bouts increased with the number of dives per bout in 1995 but not in 1996, and was not significantly correlated with the mean diving depth of the bout in both seasons.

The mean diving efficiencies of the bouts observed at Harmony Cove fall within the range reported by Cooper (1986) for phalacrocoraciids. They were not significantly affected by the mean duration of the dives, the number of dives per bout or the mean diving depth. In both seasons, the duration of the dives was positively correlated with both the surface resting time preceding and succeeding the dive. This suggests that these birds display anticipatory or reactive dives (*sensu* Lea *et al.* 1996) possibly according to the foraging conditions (Casaux 2004). Evidence indicating that birds modify the diving strategy according to prey availability was also provided by Ydenberg & Forbes (1988) and Ydenberg & Clark (1989). In this sense, the diving strategy seems to be an indicator of the foraging conditions rather than being a feature of the species.

Sexual differences in diving depths

Casaux *et al*. (2001) investigated sexual differences in MDD and in diet composition of the Antarctic shag at Harmony Point, during the 1995 and 1996 breeding seasons. The mean MDD estimated by the capillary-tube depth gauge technique was 37.8 m. Females dived significantly deeper than males and reached the MDD registered (112.6 m). This information differs from that reported for other shags species (Kato *et al*. 1996, Watanuki *et al*. 1996, Green & Williams 1997).

The analysis of the stomach contents recovered when the individuals with capillary-tubes returned to the nest from foraging trips indicated that males ingested almost exclusively large *Notothenia coriiceps* Richardson specimens, whereas females preyed more intensively on smaller fish specimens and species (*N. coriiceps*, *Harpagifer antarcticus* Nybelin and *Lepidonotothen nudifrons* Lonnberg). The relative importance by mass of *H. antarcticus* in the diet increased and that of *N. coriiceps* decreased with the increase of the MDD. Our observation that shallower-diving males caught larger fish also disagrees with earlier studies (Wanless *et al*. 1992, Kato *et al*. 1996, Favero *et al*. 1998).

Shallower dives and the capture of larger fish by males may be related to the fact that males deliver more food to the chicks and visit the nest more often than females (see Casaux 1998a, Favero *et al*. 1998). Casaux & Barrera-Oro (2002) observed that the structure of the population of a fish with marked site fidelity like *N. coriiceps* (Everson 1970, Barrera-Oro & Casaux 1996b, North 1996) may be affected by a constant catch rate. Based on that finding and on the high amount of fish consumed by shags during the breeding season (see below), Casaux *et al.* (2001) and Casaux (2003) suggested that these birds can deplete fish stocks in waters close to their colonies (see also Birt *et al*. 1987, Leopold *et al*. 1998). Thus, the differences observed suggest that individuals of both sexes partitioned foraging depths and food resources, which may diminish the intra-specific competition during the breeding season and probably allows males to undertake a higher breeding effort and/or the population prevent the depletion of the fish stocks around the colony (Casaux *et al*. 2001).

Feeding

Methodological background

The method of pellet analysis has been extensively used in shags (for example Green *et al*. 1990a, 1990b, Barrett 1991, Harris & Wanless 1991, Wanless *et al*. 1992) since it provides diet information with little effort in a short time, without disturbance to the colony. Otoliths within the pellets show a high level of species specificity, and from their measurements the size and mass of the ingested fish can be calculated (see Jobling & Breiby 1986, Casaux & Barrera-Oro 1993a). However, the technique may give biased results due to the erosion of the otoliths during digestion, or their loss throughout the gastrointestinal tract (Jobling & Breiby 1986). These biases were demonstrated experimentally in feeding trials on other species such as the cape cormorant *P. capensis* Sparrman (Duffy & Laurenson 1983) and the European shag *P. aristotelis* L. (Johnstone *et al*. 1990), the cormorant *P. carbo sinensis* L. (Zijlstra & Van Eerden 1995) and also on *P. bransfieldensis* (Casaux *et al*. 1995). In these studies it was concluded that the analysis of pellets underestimates the number and mass of fish ingested. Thus, it was suggested that the pellet analysis should not be used to estimate the daily food intake of shags (Carss *et al*. 1997).

It was thought that the estimation of correction factors could serve to diminish the errors caused by digestive processes (see Casaux *et al*. 1995, Dirksen *et al*. 1995). A feeding experiment with a captive Antarctic shag allowed us to estimate correction factors for four fish species (Casaux *et al*. 1995). These factors were applied to data from pellet analysis and the results were compared to those obtained

Table II. Summary of published information on diet composition of breeding Antarctic and sub-Antarctic *Phalacrocorax* species, with indication of the geographical area, the methodology used and the number of samples analysed (in parenthesis). Asterisks indicates those papers where strict identification of fish represented in shags diet is not provided, but it is assumed that fish prey were mainly demersal species.

Species	Locality	Main prey	Secondary prey	Method of analysis	Source
P. bransfieldensis	Green Is, AP	demersal fish	octopods, crustaceans	pellets (64)	Schlatter & Moreno 1976*
P. bransfieldensis	Danco Coast, AP	demersal fish	octopods, gastropods, polychaetes	pellets (616)	Casaux *et al*. 2002
P. bransfieldensis	Nelson Is, SS	demersal fish	octopods, gastropods	pellets (50)	Casaux & Barrera-Oro 1993a
P. bransfieldensis	Nelson Is, SS	demersal fish	octopods, polychaetes, gammarideans	stomach contents (40)	Coria *et al*. 1995a
P. bransfieldensis	Half Moon Is, SS	demersal fish	gastropods, octopods, bivalves	pellets (38)	Barrera-Oro & Casaux 1996a
P. bransfieldensis	Nelson Is, SS	demersal fish	octopods, polychaetes	pellets (45), stomach contents (40)	Casaux *et al*. 1997a
P. bransfieldensis	Nelson Is, SS	demersal fish	octopods, gammarideans, euphausiids	stomach contents (139)	Favero *et al*. 1998
P. bransfieldensis	Nelson Is, SS	demersal fish	octopods, gammarideans, polychaetes	pellets (112), stomach contents (139)	Casaux *et al*. 1998a
P. bransfieldensis	Nelson I., SS	demersal fish	gammarideans	stomach contents (84)	Casaux *et al*. 2001
P. bransfieldensis	Nelson I., SS	demersal fish	polychaetes, gastropods, octopods	pellets (862)	Casaux 2003
P. georgianus	South Georgia	demersal fish	octopods, polychaetes, crustaceans	pellets (87)	Wanless & Harris 1993*
P. georgianus	South Georgia	demersal fish	octopods, polychaetes, crustaceans	pellets (48)	Wanless *et al*. 1992*
P. georgianus	Signy Is, SO	demersal fish	octopods, polychaetes, crustaceans	regurgitated samples (84)	Shaw 1986
P. georgianus	Laurie Is, SO	demersal fish	octopods, gammarideans, decapods	stomach contents (29)	Casaux *et al*. 1997b
P. georgianus	Laurie Is, SO	demersal fish	octopods, bivalves, polychaetes	pellets (420)	Casaux & Ramón 2002
P. melanogenis	Marion Is	demersal fish	crustaceans, polychaetes, salps	pellets (2), stomach contents (1)	Blankley 1981
P. melanogenis	Marion Is	demersal fish	crustaceans, octopods, polychaetes	pellets (50), stomach contents (47)	Espitalier Noel *et al*. 1988
P. melanogenis	Iles Crozet	demersal fish	crustaceans	stomach contents (19)	Derenne *et al*. 1976*
P. melanogenis	Iles Crozet	demersal fish	bivalves, crustaceans, polychaetes	stomach contents (129)	Ridoux 1994
P. nivalis	Heard Is	demersal fish	polychaetes, gastropods, octopods	pellets (430)	Green *et al*. 1990a
P. nivalis	Heard Is	demersal fish	polychaetes	pellets (210)	Green & Williams 1997
P. purpurascens	Macquarie Is	demersal fish	---	stomach contents (47)	Brothers 1985
P. purpurascens	Macquarie Is	demersal fish	crustaceans, gastropods, polychaetes	pellets (64)	Green *et al*. 1990b
P. purpurascens	Macquarie Is	demersal fish	crustaceans, gastropods, bivalves	regurgitated samples (77), pellets (42)	Kato *et al*. 1996

Locality: AP = Antarctic Peninsula, SO = South Orkney Islands, SS = South Shetland Islands

from the analysis of stomach contents collected simultaneously at Duthoit Point (Casaux *et al*. 1997a). The correction factors appeared to be somewhat high, probably due to some experimental deficiencies: the feeding trial was carried out on one bird only, some of the fish species were scarcely used as food and wild conditions were not appropriately reproduced (Casaux *et al*. 1998a). On the other hand, the length and mass of fish ingested were better approached by the analysis of stomach contents, but this method demands more time in the field and disturbs the colony (Coria *et al*. 1995a). It was also suggested that by the comparison of pellets and stomach contents collected simultaneously, a better fit of correction factors could be obtained (Coria *et al*. 1995a).

The analysis of pellets collected at Half Moon Island from incubation to post-fledging during the 1993/94 breeding season showed that the diet varied in close relation to chicks' energetic demands (Casaux & Barrera-Oro 1995). This was also observed by the analysis of stomach contents (Casaux *et al*. 1997b), in conjunction with observations on foraging behaviour (Favero *et al*. 1998). The examination of a similar number of pellets and stomach contents collected simultaneously at Duthoit Point from incubation to late rearing, allowed Casaux *et al*. (1998a) to calculate new correction factors for specific periods of the breeding season. Between both methods, we found slight qualitative (the trophic spectrum represented in pellets was wider than the observed in stomach contents) but important quantitative differences. These are explained by the problem of erosion and loss of otoliths associated with pellet analysis and also by a greater number of food loads represented in pellets (see Casaux *et al*. 1995). However, as suggested by Wanless *et al*. (1993) for *P. aristotelis* L. and by Favero *et al*. (1998) for *P. bransfieldensis*, the stomach contents might reflect mainly the chicks' diet, the adult food being completely or partially digested before returning to the nest. Pellets seem to reflect more appropriately both adult and chick diet (see also Harris & Wanless 1993), which also would explain the differences observed. If confirmed for the Antarctic shag, this finding suggests that biases could be also associated with the estimation of correction factors by this method. It is obvious that during pre-laying, laying and incubation the food represented in stomach contents reflects the adult diet. On the other hand, Casaux (2003) observed for the Antarctic shag that the food carried to the nest by parents during early- and mid-rearing seem to exceed the energy requirements of the chicks and that the duration of the foraging trips were shorter than the

time required by cormorants to digest their own food (see Bowmaker 1963). From this information, it could be inferred that the stomach contents collected from birds arriving from foraging trips during these periods of the breeding season represent not only the chicks' diet but also, at least partially, the adults' diet.

As also occur with discriminant functions, when the correction factors are tested with the sample used to generate them, their precision is overestimated. Thus, Casaux (2003) tested these last correction factors at two localities in the South Shetlands during the 1995 and 1996 breeding seasons and obtained estimates of food consumption similar to those reported in the literature for *P. bransfieldensis* (Bernstein & Maxson 1982) and *P. georgianus* (Wanless *et al*. 1992). These findings suggest that the analysis of pellets, applying correction factors to compensate the digestion and loss of the otoliths throughout the gastrointestinal tract, is an acceptable method to quantify the diet of the Antarctic shag, that demands little time in the field without disturbing the birds (see also Dirksen *et al*. 1995). Moreover, one of the main goals of this method is to allow the daily consumption of different prey species or different components of their populations to be estimated.

Diet

Since the early nineties, after two pilot studies carried out in the South Orkneys (Shaw 1986), and the Peninsula (Schlatter & Moreno 1976), the predator–prey interaction between shags and fish have been studied regularly at several localities in these areas and also in the South Shetlands.

As observed in shags breeding in sub-Antarctic areas (Table II), the analysis of stomach contents and pellets indicated that the diet of the Antarctic and the South Georgia shags in Antarctica is diverse, demersal fish being largely the main prey, followed by octopods, gammarid amphipods and polychaetes (e.g. Casaux *et al*. 1998b, 2002, Casaux & Ramón 2002). Among fish, *N. coriiceps* is the most important prey, whereas *H. antarcticus, Gobionotothen gibberifrons* Lonnberg and/or *L. nudifrons*, depending on the area studied, follow in importance.

The analysis of shags' diet throughout the breeding season in the Antarctic zone indicated that in order to respond to chicks' increasing energetic requirements, during the main rearing period the parents forage on larger fish specimens/species (such as *N. coriiceps*) more intensively than in periods of chicks' lower demands (Casaux & Barrera-Oro 1995, Casaux *et al*. 1997b, Favero *et al*. 1998). The Antarctic shag at Duthoit Point increased the number and decreased the duration of the foraging trips during the breeding season, although the extension of the daily foraging activity and the mass of the loads carried to the nest did not vary significantly (Favero *et al*. 1998). In contrast, at Harmony Point, these shags also increased the extension of the daily foraging activity as well as the mass of the food loads (Casaux 1998a). The increase in the mass of the food loads and predation on larger fish in periods of higher energy demands at the nest was also observed in the South Georgia shag (Casaux *et al*. 1997b). As observed in seabirds from the Northern Hemisphere (e.g. Burger & Piatt 1990), these findings demonstrate the existence of different mechanisms which led both species to buffer variable food abundance or energy requirements (see Casaux 1998a).

Sexual differences in diet composition

By the analysis of stomach contents obtained from birds recently arrived from foraging trips Favero *et al*. (1998) and Casaux *et al*. (2001) investigated sexual differences in the diet composition of the Antarctic shag. Overall, the stomach contents of males were heavier and contained a lower number of fish, but of larger sizes than those of females.

Although fish constituted the bulk of the diet in both sexes, females foraged more intensively on invertebrates than males. *Notothenia coriiceps* was the most important fish prey for both sexes, but whereas males preyed almost exclusively on this species females did mainly on smaller species and on smaller specimens.

Favero *et al*. (1998) suggested that sexual differences in the diet could be related to:

1) temporal differences in prey availability and activity of sexes, and

2) differences in prey handling abilities related to sexual dimorphism.

Casaux *et al*. (1990) observed at Potter Cove (a locality close to Harmony Point and Duthoit Point) that the activity of *N. coriiceps* was low during the morning and night, and increased from midday to the afternoon/evening. In this sense, hypothesis 1 would explain differences from incubating to mid-rearing, when females forage mainly during the morning and males during the afternoon/evening. However, from mid-rearing to fledging males and females perform several foraging trips alternating the time at sea, thus increasing the possibility that a female encounter a *N. coriiceps* specimen but still forage more frequently on *H. antarcticus*. Taking into account the sexual differences in the bill size (Casaux & Baroni 2000), males may present better handling performance for more powerful fish than females (see also Koffijberg & Van Eerden 1995) but although females were able to catch *N. coriiceps* specimens of a size slightly smaller than the largest ingested by males, they preyed more intensively on specimens of species smaller than *N. coriiceps*. Thus, these two hypotheses do not fully explain the sexual differences in the composition of the diet. Sexual differences in the breeding effort (Casaux 1998a, Favero *et al*. 1998) and/or mechanism tending to diminish the intra-specific competition such as sexually

partitioning the use of foraging depths and areas, also contribute to the explanation of the differences in diet composition (Casaux *et al*. 2001).

Foraging strategy

As observed in shags inhabiting the Northern Hemisphere (e.g. Platteeuw & Van Eerden 1995), during pre-laying, incubation and early chick rearing, Antarctic (Bernstein & Maxson 1984, Casaux 1998a, Favero *et al*. 1998) and South Georgia (Shaw 1986) shags forage once a day, usually females early in the morning and males when their partners return to the nest. As chicks grow older and the energy requirements at the nest increase, the parents increase the number of foraging trips, usually alternating the time at sea.

Antarctic and South Georgia shags forage during daylight hours (Williams *et al*. 1991, Wanless *et al*. 1999, Casaux 1998a) and the extension of this activity varies throughout the season, mainly in relation to the energy requirements at the nest. The starting time of foraging activities in females is positively correlated with sunrise (Bernstein & Maxson 1984, Wanless *et al*. 1995, Casaux 1998a).

Bernstein & Maxson (1985) and Favero *et al*. (1998) reported that, although breeding Antarctic shags of both sexes display a similar number of daily foraging trips, females spent more time foraging. In contrast, male and female South Georgia shags at South Georgia invest a similar time in foraging activities (Wanless *et al*. 1995).

In the Peninsula *P. bransfieldensis* frequently forage in groups of up to 200 individuals (Bernstein & Maxson 1985), whilst at Harmony Cove, breeding individuals usually forage solitarily but occasionally in groups of 2–8 individuals (Casaux 2004). It is thought that foraging in group is advantageous when shags forage in the water column and/or in turbid waters (Van Eerden & Voslamber 1995) or when the prey is patchy distributed (Orians & Pearson 1979). *Notothenia coriiceps*, the main prey of *P. bransfieldensis* around the South Shetlands (Casaux *et al*. 1998b), is a demersal-benthic fish with a strong site fidelity (Barrera-Oro & Casaux 1996) and is uniformly distributed in rocky bottoms with algal beds. This would explain why solitary foraging is the most common strategy at Harmony Cove, an area with clear waters. However, foraging in large groups might be more frequent when fish availability is scarce (see Casaux 2004) or during the post-breeding period. The foraging strategy of *P. georgianus* in Antarctic areas has not been documented yet.

Antarctic shags have seen swallowing fish at the surface in only 12% and 4.3% of the dives observed by Casaux (2004) in the 1995 (n = 225) and 1996 (n = 211) breeding seasons at Harmony Cove. The fish swallowed at the surface were larger than 15 cm; smaller fish as well as invertebrates may have been ingested underwater. Shags were seen swallowing at the surface up to three fish within a diving bout. At the surface, fish were manipulated in order to be swallowed head-first. It was occasionally observed that during such manipulations the fish caught by shags were kleptoparasited by kelp gulls *Larus dominicanus* Lichtenstein, southern giant petrels *Macronectes giganteus* Gmelin and brown skuas *Catharacta antarctica* Lesson.

Agreement between diet and conventional gear

A good agreement was found both qualitatively and in

Table III. Variation in the number of breeding pairs of the Antarctic shag *Phalacrocorax bransfieldensis* at several localities of the Antarctic Peninsula and the South Shetland Islands indicated by the total count of nests at the colonies.

	South Shetland Islands					Antarctic Peninsula					
	Harmony Point	Duthoit Point	Half-moon Island	Bajas Rock	Hannah Point	Primavera Island	Paulet Island	Orne Island	Jougla Point	Paradise Bay	Petermann Island
1988	112[1]	---	---	---	---	---	---	---	---	---	---
1989	110[2]	---	---	---	---	---	---	---	60[14]	---	---
1990	---	163[5]	41[8]	---	---	---	---	---	---	---	---
1991	---	---	---	8[4]	---	100[11]	---	---	---	---	---
1992	---	140[4]	50[9]	7[4]	---	---	---	---	---	---	---
1993	---	133[6]	49[9]	8[4]	---	---	---	---	43[13]	90[13]	---
1994	---	120[7]	38[10]	---	10[13]	33 [11]	---	15[13]	31[13]	100[13]	34[13]
1995	45[3]	104[3]	27[3]	---	6[13]	---	432[13]	9[13]	23[13]	73[13]	30[13]
1996	68[3]	79[3]	---	---	5[13]	---	343[13]	5[13]	---	66[13]	29[13]
1997	---	73[4]	---	---	7[13]	9[12]	---	3[13]	20[13]	53[13]	29[13]
1998	---	77[4]	---	5[4]	5[13]	---	---	1[13]	22[13]	49[13]	---
1999	---	64[4]	24[4]	3[4]	7[13]	---	---	---	25[13]	---	---
2000	55[4]	66[4]	---	1[4]	5[13]	---	---	---	---	---	---
2001	49[4]	48[4]	---	---	---	---	---	---	---	---	---
2002	44[4]	42[4]	---	---	---	---	---	---	---	---	---
2003	31[4]	36[4]	---	---	---	---	---	---	---	---	---
2004	30[4]	32[4]	---	---	---	---	---	---	---	---	---

[1]Favero *et al.* 1991, [2]M. Favero, personal communication 1995, [3]Casaux 1998b, [4] R. Casaux, unpublished data, [5]Casaux & Barrera-Oro 1993a, [6]Coria *et al*. 1995b, [7]Casaux *et al.* 1998a, [8]Favero & Silva 1991, [9]McDermott & Vázquez, personal communication 1994, [10]C. Esponda, personal communication 1995, [11]Quintana *et al.* 2000, [12]Casaux *et al.* 2002, [13]Naveen *et al*. 2000, [14]Parmelee 1992, quoted in Naveen *et al.* 2000.

relative numbers between the fish species sampled by means of conventional fishing equipment and those represented in pellets of the Antarctic shag in the same site. This finding has been reported in two separate areas, the South Shetlands (Casaux & Barrera-Oro 1993a, Barrera-Oro & Casaux 1996a) and the Danco Coast (Casaux *et al*. 2002, 2003a). Interestingly, among the species caught with nets inshore at the South Shetlands (reviewed in Barrera-Oro 2002), only *Notothenia rossii* Richardson and *G*. *gibberifrons* were absent or scarcely represented in the pellets. For that area this is not surprising, since these species have decreased markedly in trammel-net catches over the last 19 years, presumably due to the offshore commercial exploitation at the end of the 1970s (Barrera-Oro *et al*. 2000). This contrasts with the high incidence of *G. gibberifrons* in the diet of shags and in trammel-net catches both at the Danco Coast, reflecting higher availability of this fish in an area remote from the main historical fishing grounds (Elephant Island and north of Livingston/King George Islands) and the Antarctic Peninsula (Joinville Island) (Kock 1992) The geographical distribution of *N. rossii* barely reaches the Danco Coast area (DeWitt *et al*. 1990) supporting the low frequency in the diet.

All this information indicates that in fish distributed from littoral to deep shelf waters, changes in the abundance of the offshore part of the population might be reflected inshore (Barrera-Oro & Marschoff 1991).

Shag populations: status and trends

The population size for the Antarctic and South Georgia shags in Antarctica has been estimated at 10 900 (Orta 1992) and 2600 breeding pairs (Casaux & Ramón 2002, N. Coria personal communication 2001) respectively. Although these figures might be underestimates, a steady declining trend in the number of breeding pairs of both species has been reported for the last twelve years at several colonies in the South Shetlands and Peninsula (Table III) and the South Orkneys (Casaux & Barrera-Oro 1996, Woehler *et al*. 2001, Naveen *et al*. 2000).

Four causes are generally proposed as major perturbations in seabird populations in the Southern Ocean:

1) human disturbance,

2) introduced predators,

3) climatic changes, and

4) changes in availability of prey (Green *et al*. 1998).

At the colonies in the South Shetlands there was no evidence that causes 1 to 3 could explain the decline observed in breeding populations. With reference to point 4, Casaux & Barrera-Oro (1996) suggested that the decline in the inshore populations of *G gibberifrons* and *N. rossii* over the last two decades in shallow waters of the South Shetlands (Barrera-Oro *et al*. 2000), may be one factor influencing the trend. Given that the monitoring of the status of the Antarctic shag population at the South Shetlands started after the population decrease of those two fish species, more conclusive data cannot be provided.

At the Danco Coast, Casaux *et al*. (2002) observed that the fish prey consumed at Py Point differed markedly from those consumed in the other colonies. Among colonies there were marked differences in the size of the fish consumed, the smaller specimens being eaten by shags from Py Point. This was mainly influenced by the number of specimens of the smallest fish prey species, *H*. *antarcticus*, consumed at that colony. Interestingly, the diet of shags from Py Point was broadly similar to that of shags breeding at the South Shetlands (see Casaux *et al*. 1998b for review). Compared to Midas Island and Primavera Island, the shags from Py Point displayed longer foraging trips and invested more time in foraging activities (Casaux & Baroni 2002). Although at the beginning of the study the number of chicks per nest observed at the three colonies was similar, the breeding output at Py Point was markedly lower, possibly due to the differences in fish prey consumption between these shags and those from Midas Island and Primavera Island (Casaux & Baroni 2002). The facts that *H. antarcticus* lives sheltered under rocks and that larger fish provide proportionately more energy than smaller ones (Hislop *et al*. 1991) support this view.

In the Antarctic shag low breeding output and high foraging effort might result in low recruitment and high adult mortality respectively, both factors adversely affecting the population trend of this species. Considering the information from the Danco Coast reported above, the present low availability of the former abundant prey *G. gibberifrons* and *N. rossii* in inshore waters of the South Shetlands may be at least partially responsible for the decrease in the number of breeding Antarctic shags in that archipelago.

A similar decrease in colony size reported for the sub-Antarctic Crozet shags *Phalacrocorax melanogenis* Blyth at Marion Island is also suggested, as being caused by an altered availability of food, which was reflected by a changed dominance in nototheniid prey in the diet (Crawford *et al*. 2003).

Discussion

Ecological role of shags in the food web

The main pathway of energy flow through shags and other high predators in the food web in the study area is shown in Fig. 1. In Antarctica, most of the seafood dependent flying birds take their prey at or just below (less than 1 m depth) sea surface. Some albatrosses and petrels in sub-Antarctic areas also have limited diving capabilities. The albatrosses *Diomedea chrysostoma* Forster (grey-headed), *D. melanophris* Temminck (black-browed) and *Phoebetria*

palpebrata Forster (light mantled sooty) forage regularly down to 3–5 m and occasionally to 6–12 m depth (Prince *et al*. 1994, Huin & Prince 1997), whereas the diving petrels *Pelecanoides georgicus* Murphy & Harper and *P. urinatrix* Gmelin reach on average depths of 26 and 33 m respectively, maximum 40–50 m (Bocher *et al*. 2000). In the Southern Ocean, seabirds in general feed on pelagic organisms, mainly euphausiids, squid and fish. Among flying birds only shags have the capacity to dive deeper than 100 m to feed almost exclusively on demersal-benthic prey, close to the bottom. These deep dives match those performed regularly around 100 m (MDD 121–212 m) for periods of 3–6.2 min by small Antarctic penguins such as the gentoo (*Pygoscelis papua* Forster) (Boyd & Croxall 1996, Robinson & Hindell 1996, Wilson *et al*. 1996), Adélie (*P. adeliae* Hombron & Jacquinot) (Watanuki *et al*. 1997, Wienecke *et al*. 2000, Ropert-Coudert 2001) and chinstrap (*P. antarctica* Shiino) (Bengston *et al*. 1993, Mori 1997).

Information from Antarctic research over the last 20 years indicates that many predators feed on species other than krill (Barrera-Oro 2002). Shags constitute a good example of this, occupying in inshore-shallow waters the trophic niche of main predators of demersal fish. The fish eaten by Antarctic penguins are mostly pelagic, only the gentoo feeds inshore on pelagic and demersal species (Brown *et al*. 1990, Bost *et al*. 1994, Coria *et al*. 2000). Although demersal notothenioids constituted the main prey of the gentoo penguin in some areas in some years (Croxall & Prince 1980, Croxall *et al*. 1988, Williams 1991, Coria *et al*. 2000), it has been reported that myctophids are also a dominant prey (e.g. Hindell 1989, Green & Wong 1992, Robinson & Hindell 1996). The fish taken by Antarctic pinnipeds are mostly pelagic and the information on species identity and proportion of demersal fish in seal diets is scarce (Barrera Oro 2002). Nevertheless, it is known that Antarctic fur seals (*Arctocephalus gazella* Peters), Weddell seals (*Leptonychotes weddellii* Lesson), southern elephant seals (*Mirounga leonina* L.) and leopard seals (*Hydrurga leptonyx* Blainville) prey on demersal fish inshore (see Everson 1970, Green & Williams 1986, Plötz *et al*. 1991, Casaux *et al*. 1997c, 1998c, 2003b, Burns *et al*. 1998, Daneri & Carlini 2002) (Fig. 1). However, it seems in general that in inshore shallow waters, shags have little competition in their ecological role as main predators of demersal fish.

In their turn, demersal fish are major consumers of benthos and also feed on zooplankton (mainly krill in summer). Shags are therefore links between benthic and pelagic levels of the food web; through them and other high predators energy is transferred to land in the form of pellets (birds), fish remains, regurgitations and faeces (birds and seals). In the entire Antarctic ecosystem, however, the ecological role of shags as demersal fish consumers in biomass terms must be less important than that of other predators, in view of the limited shag population.

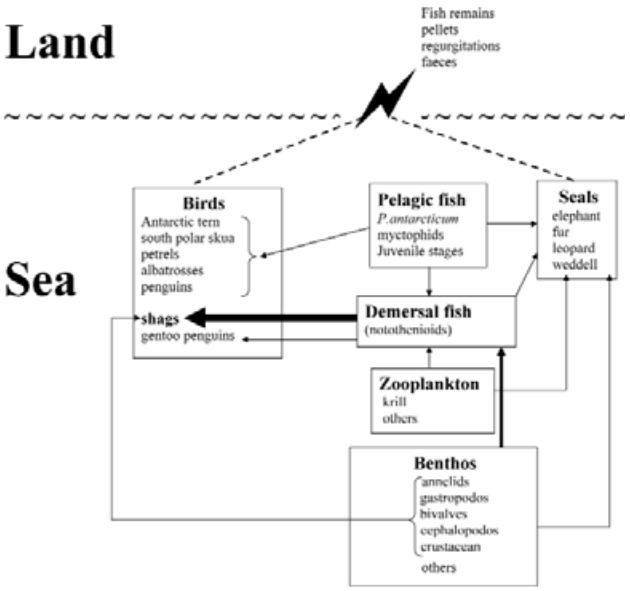

Fig. 1. Diagram indicating the position of shags and other high predators in the Antarctic marine food web

Casaux (2003) estimated that *N. coriiceps* provide, depending on the period of the breeding season, 60 to 93% of the energy ingested by the Antarctic shag at Harmony Point and Duthoit Point. The estimated consumption of fish by shags in the 1995 and 1996 breeding seasons (November–February) were respectively 13 and 21.5 tonnes at Harmony Point (45 and 67 active nests) and 28.5 and 25.9 tonnes at Duthoit Point (104 and 79 active nests) (Casaux 2003). Given that shags forage close to the colonies (up to 5 km at Harmony Point, Casaux *et al*. in press), it is likely that *P. bransfieldensis* plays an important ecological role as regulator of populations of its main fish prey that have a marked site fidelity, such as *N. coriiceps*. This role contrasts with the contrary effect, i.e. the steady decline of shag breeding populations due to the decrease in the availability of some fish prey due to the commercial fishery.

The role of shags as prey in the Antarctic marine ecosystem is very minor and has been scarcely documented. Although occasional predation on shags by leopard seals at sea has been indicated (Hamilton 1946, Pitman 1957), most of shag predation episodes are carried out by other seabirds. Predation on adult specimens of Antarctic or South Georgia shags by seabirds has not been reported, but we observed a pair of brown skuas killing a female Antarctic shag when it returned to the shore after a diving bout (R. Casaux, personal observation 2002). In other areas, gulls (Harris 1965, Jarvis & Cram 1971, Derenne *et al*. 1976, Cooper *et al*. 1982) and skuas (Bayes *et al*. 1964, Brothers 1985) prey frequently on cormorants' eggs and chicks. After 3000 bird-hours of observation Bernstein & Maxson (1984) did not detect attacks on Antarctic shag chicks at the Antarctic Peninsula, whereas Casaux (1998a), after 11 400 bird-hours of observation at the South Shetlands, did not detect

predation on eggs and only witnessed two unsuccessful attempts of predation on chicks by skuas. Perhaps due to the abundance of alternative food resources and the limited space between neighbour nests (see Brothers 1985), the predation pressure of gulls and skuas on shags' colonies seems to be negligible.

The South Polar skua *Catharacta maccormicki* Saunders was observed kleptoparasiting the South Georgia shag at the South Orkneys (Burton 1968) and on the Antarctic shag at the Peninsula (Holdgate 1963, Maxson & Bernstein 1982) and the South Shetlands (Casaux 1998a). The efficiency of kleptoparasitism was low (0 to 12.5% of effectiveness, Maxson & Bernstein 1982, Casaux 1998a) and the strategy observed is energetically expensive. This would explain why South Polar skuas display this behaviour more intensively in years of food shortage (Maxson & Bernstein 1982).

Kleptoparasitism by the brown skua, the kelp gull, and the southern giant petrel on Antarctic shags was observed occasionally when shags emerged at the sea surface carrying a fish (Casaux 1998a). Pale-faced sheathbills *Chionis alba* Gmelin were observed kleptoparasiting adult Antarctic shags when shags regurgitated food for their chicks (Favero 1995). These two strategies were infrequent or scarcely effective.

In conclusion, predation and kleptoparasitism on shags in Antarctica imply a low transfer of energy to other levels of the food web.

Advantages of the potential use of Antarctic shags as biomonitors

The good agreement between the fish species represented in the diet of shags in Antarctica and those regularly sampled by means of conventional fishing gears suggests that these birds could be used as proxy monitors for inshore populations of demersal fish species. Points in support of this are:

1. demersal fish contribute roughly 99% of the diet of shags by mass (Casaux *et al*. 1997b, 2001).
2. shags are able to dive to 125 m (Croxall *et al*. 1991, Kato *et al*. 1992, Wanless & Harris 1993, Casaux *et al*. 2001), thus covering the depth distribution range of inshore demersal fish.
3. shags show a strong breeding site fidelity over years (Bernstein & Maxson 1982, Shaw 1985, Casaux 1998a) and forage relatively close to the colonies (usually up to 10 km from the colony; Bernstein & Maxson 1985, Casaux 1998a, Casaux *et al*. in press), thus reflecting local conditions.
4. the analysis of pellets is an adequate method to estimate qualitatively and quantitatively the diet of shags (Casaux 2003) and can reflect differences in fish availability between seasons and areas (Casaux *et al*. 2002, Casaux & Ramón 2002).

After six years of testing of the Standard Method implemented in CCAMLR, it was recognized that it had the potential to provide information on ecological relationships and changes in populations of certain fish species (CCAMLR 2003, paragraph 3.57). These species are adult (e.g. *Trematomus* spp., *Lepidonotothen* spp.) and juvenile/early adult stages (e.g. *N. rossii*, *G. gibberifrons*, *N. coriiceps*) of demersal inshore fish populations, including commercially important species (CCAMLR 2003). Considering the similarities in foraging strategies and reproductive behaviour between Antarctic and sub-Antarctic shags, the methodology proposed may well be readily used with other sub-Antarctic shag species. At the present time, the development of this methodology is a continuing task in support of CCAMLR.

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