

Microhabitat use and prey capture of a bottom-feeding top predator, the European shag, shown by camera loggers

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ABSTRACT: Studies of the fine-scale use of foraging habitat are essential for understanding the role of seabirds in marine ecosystems. However, until recently, relationships between foraging and habitat usage were only possible at a coarse scale. We used miniaturized bird-borne digital still-picture camera loggers to obtain high-quality images of the foraging habitat used by 9 European shags *Phalacrocorax aristotelis*. Underwater images revealed that shags are almost exclusively benthic feeders, but used 2 very distinct foraging habitats: sandy areas and rocky areas with brittlestars, soft corals and kelp. We found no evidence that individuals specialize on a particular habitat. Birds were recorded in rocky and sandy areas over the course of a day and in some cases within a trip. Foraging behaviour differed markedly between habitats. In rocky areas birds foraged solitarily, over a wide range of depths (10 to 40 m) and travelled along the bottom while searching for bottom-living fish such as butterfish *Pholis gunnellus*. In contrast, shags using sandy habitat frequently fed with conspecifics, foraged mainly at 2 depths (24 or 32 m) and spent the bottom phase of the dive probing into the sand with their bill, presumably to catch lesser sandeels *Ammodytes marinus*, the major prey item in the diet. This study highlights the flexible foraging strategy of European shags and illustrates how image and dive data can be combined to improve our understanding of the factors influencing the foraging success of benthic feeders.

KEY WORDS: Microhabitat · Image data · Prey capture · Shag

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INTRODUCTION

To understand better the interactions between marine resources and top predators, it is essential to study how predators use their foraging environment. In coastal marine ecosystems, fine-scale (<1 km) heterogeneity in topology and physical and chemical conditions is often associated with a complex benthic community structure (Broitman & Kinlan 2006), and such features may be critical for the foraging of top predators (Estes et al. 1978, Coyle et al. 1992, Seitz et al. 2006). However, until recently, analyses of relation-

ships between predator foraging behaviour or habitat usage (determined by land-based or satellite-linked radio tracking and geolocating archival tags) and habitat structure (determined by ship-based surveys and satellite imagery) has only been possible at a relatively coarse scale (>1 km) (Pinaud & Weimerskirch 2005, Shaffer et al. 2006). Global positioning system data loggers provide data on fine-scale movement of animals (Ryan et al. 2004), but accompanying information on benthic microhabitat remains problematic to collect.

Digital still-picture loggers (DSL) and video recorders mounted on seals and large seabirds have provided

direct qualitative information on biotic and abiotic features of the foraging environment and detailed descriptions of prey capture and interactions with conspecifics and other species (Ponganis et al. 2000, Bowen et al. 2002, Takahashi et al. 2004, Grémillet et al. 2006). However, because of the large size of the devices, these techniques have been restricted to mammals and flightless and/or captive birds. The recent development of a small DSL that gives high-quality image data provides the opportunity to study microhabitat use in medium-sized, volant, free-living seabirds.

Cormorants and shags are important predators in many coastal ecosystems (Wiens & Scott 1975, Birt et al. 1987, Schreiber & Clapp 1987). Typically they are generalist feeders, exploiting both bottom-living fish and epipelagic schooling fish (Grémillet et al. 1998, Kato et al. 1998). For example, Japanese cormorants *Phalacrocorax filamentosus* feeding on bottom-living fish in one year showed individual feeding habitat specialization, but in another year, when they fed on epipelagic fish individuals, foraged in a variety of habitats and in association with other diving seabird species (Watanuki et al. 2004). Such changes in foraging behaviour may reflect changes in the distribution and/or abundance of prey, since spatio-temporal variability in abundance is usually less for bottom-living fish than epipelagic fish at a coarse scale (Litzow et al. 2004). However, changes in foraging behaviour between different habitats at a fine scale have seldom been recorded because of logistical difficulties.

European shags *Phalacrocorax aristotelis* breeding on the Isle of May, 6 km off the east coast of Scotland, are known to forage in sandy and rocky areas around the island (Wanless et al. 1991a). Birds use a range of foraging depths, mainly between 15 and 40 m, and typically feed benthically (Wanless et al. 1991b, Watanuki

et al. 2005, but see Grémillet et al. 1998, Wanless et al. 1998) on lesser sandeels *Ammodytes marinus* (Harris & Wanless 1991). Breeding success tends to be lower in years when the abundance of sandeels (as measured by catch per unit effort of the local sandeel fishery in June) is low (Rindorf et al. 2000). However, shags also feed on other bottom-living species, particularly butterfish *Pholis gunnellus* (Watanuki et al. 2007). In 2005 and 2006 we deployed small DSL on European shags to collect detailed data on microhabitat use and prey capture. Here, we describe fine-scale patterns of habitat use for individual dives and diving bouts and highlight marked differences in prey species and foraging behaviour between the 2 main foraging habitats.

MATERIALS AND METHODS

Deployment of data-loggers. Fieldwork was carried out on the Isle of May ($56^{\circ} 11' N$, $02^{\circ} 33' W$) between 17 and 20 June 2005 and 27 June and 5 July 2006. Two males, each with 2 recently hatched chicks, in 2005 and 7 males, each with 2 or 3 medium-sized chicks, in 2006 were captured on the nest using a crook, usually in the evening (20:00 to 22:00 h local time) (Table 1). A DSL was attached to the back feathers with Tesa tape, with the longitudinal axis of the logger along the body axis of the bird. The attachment process took <5 min. After release, each bird went back on its nest within 10 min and resumed brooding. Birds were recaptured approximately 1 d later, and the logger was removed (Table 1).

The DSL (DSL-380DTV, Little Leonardo) had a mass of 72 g in the air, measured 21 mm in diameter and 122 mm in length and was fitted with a depth sensor (1 m accuracy, Fujikura). On average, the device mass was 3.9% of the body mass of birds used in deploy-

Table 1. Summary data for deployments of digital still-picture camera loggers on 9 male European shags *Phalacrocorax aristotelis*. Habitat of 1 bout from Bird 1 and 1 bout from Bird 9 could not be determined because images were not clear. Birds 3 and 6 each made 1 bout in the evening of the first day of logger deployment. See Fig. 2 for habitat definitions

Bird ID (yr)	Body mass (g)	Period of deployment (h)	No. of dives to depths >5 m	No. of images	Mean dive depth (m) in dives to depths >5 m	Mean dive duration (s)	No. of bouts in ROCKY habitat	No. of bouts in SANDY habitat
Bird 1 (2005)	2190	16.4	51	265	28 ± 9	76 ± 23	3	0
Bird 2 (2005)	1790	20.9	131	448	15 ± 5	52 ± 16	3	0
Bird 3 (2006)	1820	26.6	104	544	26 ± 5	73 ± 12	0	6
Bird 4 (2006)	1700	22.6	69	322	25 ± 4	66 ± 13	1	2
Bird 5 (2006)	1830	23.6	46	278	36 ± 5	86 ± 16	3	1
Bird 6 (2006)	1840	26.9	159	614	19 ± 8	57 ± 20	5	1
Bird 7 (2006)	1750	22.3	74	377	28 ± 7	76 ± 19	2	2
Bird 8 (2006)	1740	22.3	109	495	25 ± 5	67 ± 12	1	2
Bird 9 (2006)	1930	16.8	141	650	27 ± 7	70 ± 14	2	2
Mean \pm SD	1843 \pm 138				25 ± 6	69 ± 10		

ments (range 3.3 to 4.2%; Table 1). The cross-sectional area of the devices was 3% that of shags (calculated from girth measurements collected during the present study; K. Sato pers. obs.). Depth data were recorded every second, and image data (370×296 pixels) were recorded every 15 s during the time a bird dived below 2 m. Since it took time to write the previous image data on the logger memory, images were taken 7 to 8 s after the time programmed. Data were downloaded with a PC using Logger Tool Ver. 5 (MMT).

Analyses of dives. Because of the accuracy of the depth sensor (± 1 m) only dives deeper than 1 m were recorded. Images indicated that dives shallower than 5 m (5% of 929 dives; Table 1) were associated with washing and/or surface swimming, and such dives were excluded from analyses of foraging behaviour. Visual inspection of dive profiles confirmed the previous findings of Watanuki et al. (2005) that birds predominantly made U-shaped dives. Thus, different phases of a dive were readily defined from the rate of change in depth (descent, less than -0.6 m s^{-1} ; bottom, -0.3 to $+0.3 \text{ m s}^{-1}$; ascent, $>1 \text{ m s}^{-1}$), enabling descent duration, bottom duration, ascent duration and post-dive surface duration to be estimated using the Macro Program of Igor Pro Ver. 4 (Wave Metrics). Rates of descent and ascent were obtained by dividing depth at the start and the end of the bottom phase by descent and ascent duration, respectively. Dive duration was the sum of descent, bottom and ascent durations. As bottom depth showed very little variation within a dive (Watanuki et al. 2005), the maximum depth and average depth recorded during the bottom phase were very similar and the maximum depth was defined as dive depth in the present paper.

Shags usually dived in bouts, and bout-ending criteria were identified using a log-survivor curve of all post-dive surface durations (including those for dives <5 m) (Gentry & Kooyman 1986). The inflection point of the curve was around 340 s, and accordingly this value was used to define discrete bouts. Single dives were not designated as bouts.

Images taken during 5 of the inter-bout intervals showed that the birds were on land, probably at or near the nest site. The durations of all these inter-bout intervals exceeded 1.5 h. This threshold accorded well with extensive visual records of brooding shifts on the Isle of May (F. Daunt pers. obs.) Inter-bout intervals >2 h were therefore assumed to indicate that the bird had returned to the colony, allowing identification of individual foraging trips from DSL output.

Analyses of images. A total of 3993 images were taken (265 to 650 images for each bird; Table 1). By comparing the time when each picture was taken to the time-depth profile, after adjusting for time lags (ca. 7 to 8 s), images were assigned to the descent, bottom,

ascent and surface phases of the dive. Images taken during the bottom phase of a dive provided information about microhabitat at the foraging location, while those at the surface gave information on the prey caught when prey were large enough to discern. Microhabitats associated with each dive were characterized according to sediment type and any organisms present. If a bird had prey in its bill either at the surface or underwater, the dive was assumed to be successful. In some cases the image at the surface did not include the bill, and such dives were categorized as unknown and excluded from the analyses involving dive success. Prey items were identified to as low a taxon level as possible. The number and species of any other birds appearing in any images were also recorded.

Diet. The diet of shags on the Isle of May during the periods of DSL deployment was assessed from food voluntarily regurgitated by birds and pellets containing prey remains (Harris & Wanless 1993). For the regurgitated loads (available in 2006 only), an initial visual assessment of prey species present was made. Samples were then placed in a saturated solution of biological washing powder at 40°C , to dissolve away flesh and soft tissue. After 48 h, fish otoliths and any other hard remains were extracted and identified under a dissecting microscope to as low a taxon level as possible, using keys in Harkönen (1986). Prey remains were extracted from pellets (available in both years) using the above method. Diet in each year was expressed as the frequency of occurrence of a particular prey item in the total sample of regurgitates or pellets.

Statistics. Statistical tests were carried out using SPSS Ver. 14 (SPSS). Habitat used during each dive bout was defined using cluster analyses (hierarchical cluster using Ward's method) of the proportion of microhabitats in that bout. Where data consisted of multiple observations per individual, we used the linear mixed models with the restricted maximum-likelihood method. To test the effect of habitat type on dive depth, we included individual as a random effect and habitat as a fixed effect. Significance of the effect of habitat was determined with a Type III test. To test the effect of habitat type on bottom duration, we included individual as a random effect, habitat as a fixed effect and dive depth as a covariate. We also used a linear mixed model to test the effect of habitat type on bout start time, bout duration, body angle (i.e. proportion of images during the bottom phase, indicating that the bird was orientated upwards, horizontally, or downwards relative to the surface), the proportion of images in which birds were probing the substrate during the bottom phase, and the proportion of descent, bottom and ascent durations spent in association with

other shags, using each dive bout as the sample unit. All proportional data were arcsine transformed prior to analyses. To test the effect of the success of prey capture on bottom time with dive depth as a covariate, we repeated the above models. Sequential Bonferroni adjustment was applied if necessary.

RESULTS

DSLs were retrieved from all 9 birds *Phalacrocorax aristotelis* and provided depth and image data for between 16.4 and 26.9 h (Table 1). Birds started diving in the morning (05:31 to 09:10 h local time) and made the last dive of a day in the late afternoon/early evening (15:53 to 20:04 h). They never dived before sunrise or after sunset. All except 5 dives (<1% of the total of 884 dives deeper than 5 m) were U-shaped and showed a clear bottom phase. Mean dive depth, dive duration, descent and ascent rates for the 9 individuals varied between 15 and 36 m, 52 and 86 s, 1.4 and 1.7 m s⁻¹, and 1.7 and 2.0 m s⁻¹, respectively (Table 1).

Microhabitat usage

Of the dives deeper than 5 m, 28 (3.2%) lacked bottom images because they were shallow (<10 m) and the bird did not reach the sea bed, while 94 (11.1%) had bottom images that were too dark to distinguish habitat features, mainly because of poor light conditions associated with deep (>40 m) water. The remaining 762 (86.2%) dives included 1 to 6 bottom images, and microhabitats were classified into 5 categories: 'kelp' (43 dives: apparently rocky sediment mostly covered with seaweed, particularly large kelp; see Watanuki et al. 2007), 'rock' (181 dives: bare rock), 'soft coral' (128 dives: apparently rocky sediments with >50% coverage of deadman's fingers *Alcyonium digitantium*; see Watanuki et al. 2007), 'brittlestar' (93 dives: apparently rocky sediments with brittlestar *Ophiothrix* sp. present in >50% the area; Fig. 1a), and 'sand' (317 dives: sediment composed of fine to coarse sand, often with pebbles and shells, and apart from a few brittlestar lacking any other detectable organisms; Fig. 1b).

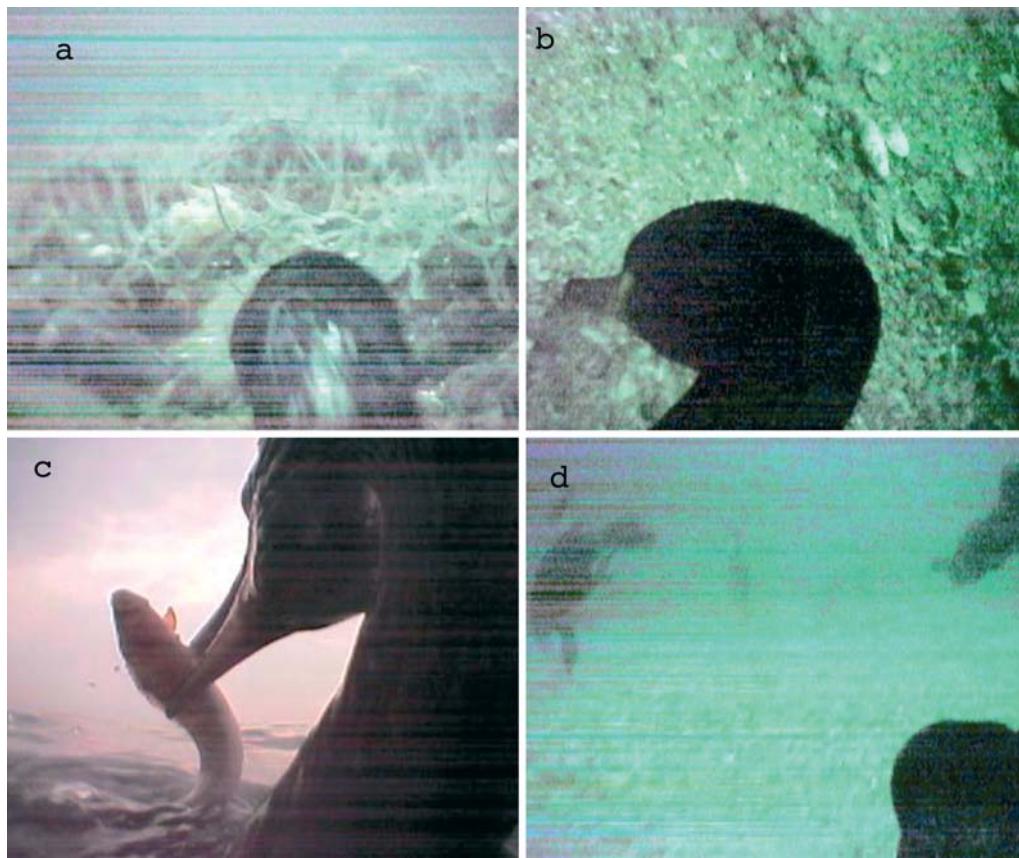


Fig. 1. *Phalacrocorax aristotelis*. Typical images from digital still-picture loggers deployed on European shags showing (a) a bird searching for prey in ROCKY habitat, (b) a bird probably searching for lesser sandeels *Ammodytes marinus* by probing into the sand with its bill, (c) a bird at the surface holding a butterfish *Pholis gunnellus*, and (d) a bird foraging with conspecifics, showing the typical vertical body orientation associated with SANDY habitat

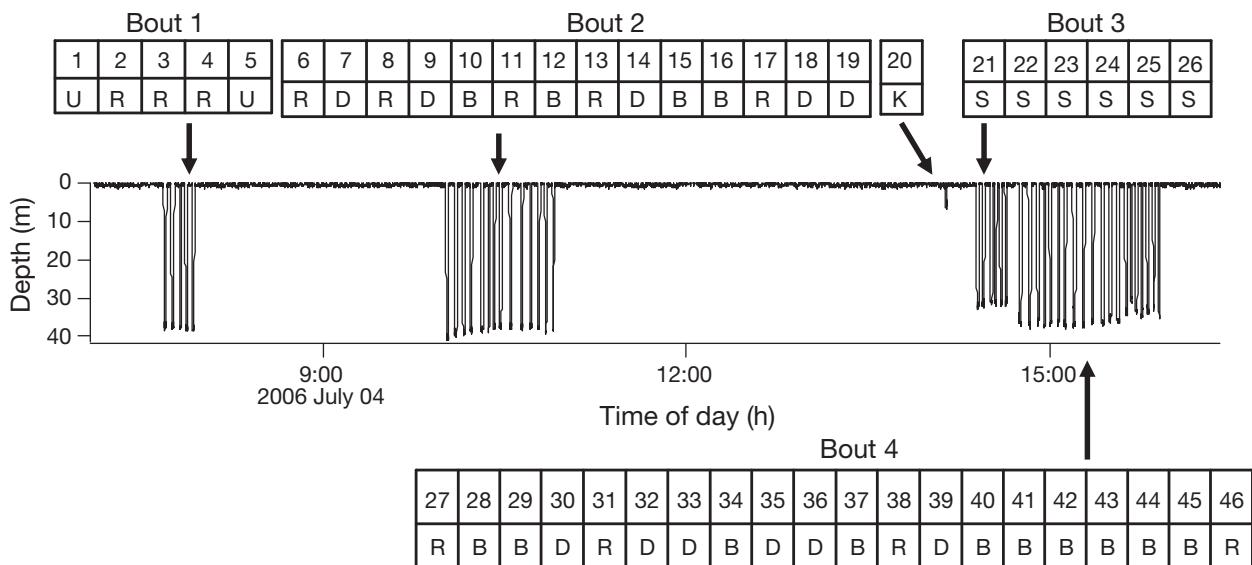


Fig. 2. *Phalacrocorax aristotelis*. An example of dive activity over a single day. Assuming that the bird returned to the colony during inter-bout intervals >2 h, the bird made 3 foraging trips—2 containing single dive bouts and the third trip comprising 2 dive bouts. Accompanying boxes indicate dive number and microhabitat used (R: rock; D: soft coral; B: brittlestar; K: kelp; S: sand; U: unidentified) for each dive. A single dive (No. 20) made at the start of the third trip was not assigned to a dive bout. The bird used ROCKY habitats (R, D, B or K) in Bouts 1 and 2 during the first and the second trips, respectively, but both SANDY (Bout 3) and ROCKY (Bout 4) habitats during the third trip

All but 4 solitary dives occurred within bouts, with birds making 2 to 78 dives bout^{-1} and 3 to 5 bouts d^{-1} (Fig. 2). Within a dive bout, shags remained in either sandy or rocky microhabitats, although, within the latter, they frequently moved between kelp, brittlestar and soft coral areas on consecutive dives (an example of the fine-scale habitat usage for 1 bird over the course of a day is shown in Fig. 2). The bouts were clustered into 2 types of habitat according to the proportion of microhabitat recorded: SANDY (96 to 100% of dives in 'sand' microhabitat) and ROCKY (mixture of 'kelp', 'rock', 'soft coral' and 'brittlestar' in variable proportions). Microhabitat could not be determined for 2 bouts because of low light levels, and these bouts were excluded from the following analyses.

The 2 shags sampled in 2005 were only recorded in ROCKY habitat, but 6 of the 7 birds followed in 2006 used both SANDY and ROCKY habitats within a day (Table 1). Nine trips contained >2 bouts, and, on 4 of these, birds used both habitats (Fig. 2). All analyses of the effect of habitat type that follow entail a comparison of these 2 types (SANDY and ROCKY).

Habitat and diving behaviour

Birds dived mostly either to 24 or 32 m in SANDY habitat, but dive depth was more variable in ROCKY habitat (Fig. 3). The effect of habitat on dive depth

was significant ($F_{(1,756.978)} = 119.089$, $p < 0.001$, Type III ANOVA test, SPSS).

Both bottom duration (Fig. 4a) and dive duration increased with increasing dive depth, although effects of habitat and the interaction were not significant (Table 2). Post-dive surface duration increased with

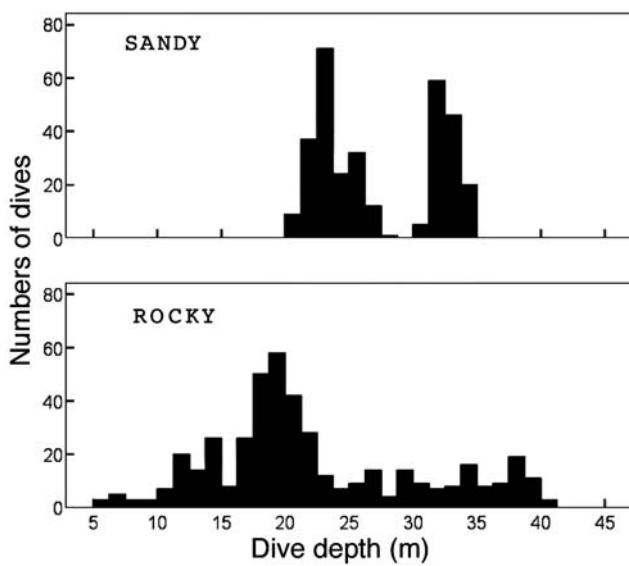


Fig. 3. *Phalacrocorax aristotelis*. Frequency distribution of dive depths of European shags in SANDY and ROCKY habitats. See Fig. 2 for habitat definitions

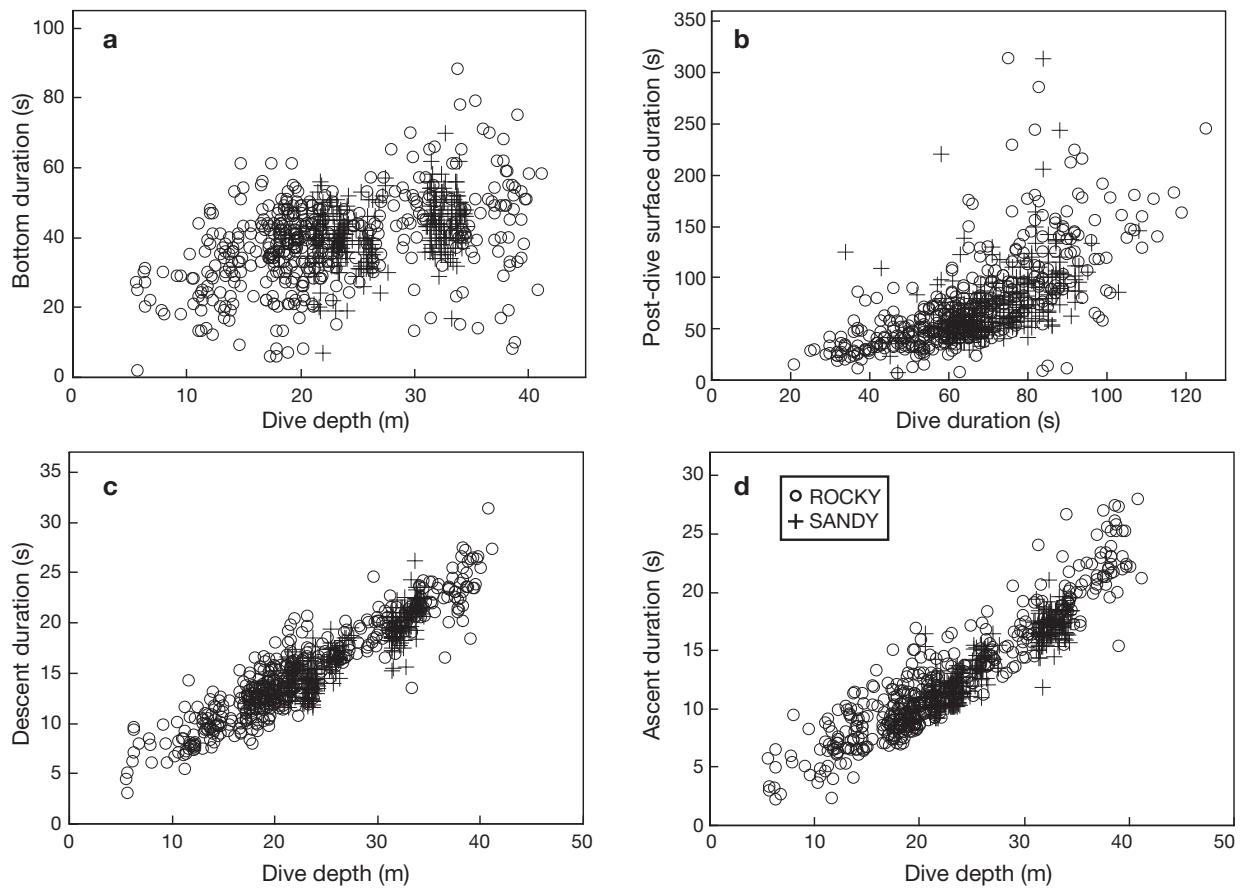


Fig. 4. *Phalacrocorax aristotelis*. Effects of foraging habitat (ROCKY and SANDY; see Fig. 2 for habitat definitions) on the relationships between (a) bottom duration and dive depth, (b) post-dive surface duration and dive duration, (c) descent duration and dive depth, and (d) ascent duration and dive depth, in dives >5 m made by European shags

increasing dive duration (Fig. 4b, Table 2), and, in this case, there was a significant interaction with habitat type such that post-dive surface duration was more positively related to dive duration in rocky habitats than in sandy habitats. Descent duration and ascent duration were both significantly longer with increasing depth, but these relationships did not differ between ROCKY and SANDY habitats (Fig. 4c,d, Table 2).

Bout duration and start time did not differ between SANDY and ROCKY habitats (Table 3). The coefficient of variation (CV) of the depth of dives within a dive bout varied between 0.29 and 50.38. The distribution of CVs was bimodal, with a break at a value of ca. 10. Thus, we designated bouts with a CV < 10 as those in which dive behaviour was relatively stable and uniform. Such stability was more frequent in SANDY habitat (16/16 bouts) than ROCKY habitat (8/20). For 12 bouts with a CV > 10 in ROCKY habitat, trends of dive depth with dive order were examined with regression analyses for each bout and were categorized into 'depth increase type' (0.5 to 5.4 m dive^{-1} , $p < 0.05$; 4 bouts), 'depth decrease type' (-0.1 to -0.4 m

Table 2. *Phalacrocorax aristotelis*. Effects of habitat (ROCKY vs. SANDY) and dive depth on dive, bottom, descent and ascent duration, and the effects of habitat and dive duration on post-dive surface duration. Results of the linear mixed-effects model using 759 dives by 9 birds in which birds were treated as random factors are shown

Dependent factors	Independent factors	Type III F	p
Dive duration	Depth	688.062	0.000
	Habitat	0.861	0.354
	Depth × Habitat	0.010	0.921
Bottom duration	Depth	85.158	0.000
	Habitat	0.160	0.690
	Depth × Habitat	0.036	0.849
Post-dive surface duration	Dive duration	174.157	0.000
	Habitat	3.470	0.063
	Duration × Habitat	6.214	0.013
Descent duration	Depth	2692.838	0.000
	Habitat	1.367	0.243
	Depth × Habitat	0.190	0.663
Ascent duration	Depth	1657.300	0.000
	Habitat	0.001	0.980
	Depth × Habitat	1.319	0.251

Table 3. *Phalacrocorax aristotelis*. Comparison of characteristics of dive bouts of European shags foraging in ROCKY and SANDY habitats (see Fig. 2 for habitat definitions). The effects of habitats (ROCKY vs. SANDY) were tested with linear mixed-effects models with Type III tests using 36 dive bouts from 9 birds in which birds were tested as random factors. n: number of bouts

	ROCKY (n = 20)	SANDY (n = 16)	Effect of habitat Type III F	p
Time at start (h)	11.4 ± 4.7	12.7 ± 3.9	0.783	0.382
Bout duration (h)	0.9 ± 0.7	0.8 ± 0.7	0.167	0.686
Orientation of head in bottom phase of dive^a				
%Downwards	51.2 ± 21.7	84.7 ± 15.4	23.624	0.000
%Horizontal	45.5 ± 20.3	14.6 ± 16	22.367	0.000
%Upwards	3.4 ± 5.2	0.7 ± 1.6	1.353	0.253
Feeding behaviour during the bottom phase of dive				
%Probing	0.2 ± 0.5	17.1 ± 18.2	15.902	0.000
% Images with other birds	0.1 ± 0.3	7.1 ± 9.0	16.83	0.000

^aStatistically significant results were retained after sequential Bonferroni adjustment

dive⁻¹, p < 0.05; 4 bouts) and 'variable type' (p > 0.05; 4 bouts). Among bouts with a CV < 10 in ROCKY, trends were significant for 4 bouts (-0.1 to -0.3 m dive⁻¹, p < 0.01) and not significant for others. Among 16 bouts in SANDY habitat, trends were significant for 3 bouts, but the effects of the dive order were small (-0.04 to 0.05 m dive⁻¹).

Behaviour during the bottom phase of the dive

In 1948 images taken during the bottom phase of the dive, the approximate angle of the bird's body could be determined. Orientation was classified as 'downwards' if the image showed bottom features only (Fig. 1b), 'horizontal' if the image was about 50% water and 50% seabed (Fig. 1a), and 'upwards' if only water was visible. The percentage of images in which birds kept their body horizontal was significantly greater for bouts in ROCKY than in SANDY habitat, while the percentage in which birds were pointing downwards was significantly greater for bouts in SANDY habitat (Table 3).

A shag's head was frequently visible in the images. Birds sometimes probed into the sediment with their bills (Fig. 1b), and this activity was recorded frequently in SANDY but rarely in ROCKY habitat (Table 3).

Habitat and group foraging

None of the images showed other birds in the field of view during the descent phase of the dive. However, during the bottom, ascent and surface phases, other shags were observed in 7 % of the images from SANDY

habitat (Fig. 1d, Table 3). On average, 3.4 ± 3.2 (range: 1 to 12, n = 10 images) shags were present in images taken at the surface; 2.0 ± 1.7 (1 to 5, n = 8 images), during the bottom phase; and 1.0 ± 0.0 (n = 13 images), during the ascent phase. In images taken during the bottom phase of a dive, 15 of 16 shags present were clearly probing into the sand with their bills (see Fig. 1d also). One image taken during ascent showed a single common guillemot *Uria aalge*. In contrast, other shags were never recorded in the images from ROCKY habitat. The only evidence of feeding associations in ROCKY habitat was a single image at the surface showing 2 gulls *Larus* sp.

Habitat and prey

Analyses of the pellets and regurgitations collected concurrently with the period of logger deployment showed that in both years shags were feeding on a wide variety of prey, including sandeels (mainly lesser sandeels *Ammodytes marinus*), butterfish *Pholis gunnellus*, bullheads (bull rout *Myoxocephalus scorpius*), several species in the cod family and a range of other fish species and small invertebrates (Table 4).

In 2005, all images of fish showed only butterfish, and, in 2006, most images were also of butterfish (Table 4, Fig. 1c). Sandeels were never seen in any of the images despite their prevalence in the diet data (cf. Table 4). Butterfish were recorded in 31 images in ROCKY habitat, but in a single image in SANDY habitat. Among 139 dives in which a clear image of a bird's head was obtained at the surface and foraging habitat was also determined, 50 (36 %) cases showed the bird holding a fish and 89 (64 %) cases showed the bird had nothing in its bill. The percentage of dives in which a bird returned to the surface with a prey item was markedly lower in SANDY habitat (14 % of 36 dives) than in ROCKY habitat (44 % of 103 dives).

In ROCKY habitat, bottom duration was unrelated to whether the birds had fish at the surface, but there was a significant interaction between dive depth and success, with bottom time independent of dive depth among successful dives (Fig. 5) (dive depth: $F_{(1,97)} = 20.253$, p = 0.01; success: $F_{(1,97)} = 3.371$, p = 0.069; interaction term: $F_{(1,97)} = 10.003$, p = 0.002). Post-dive surface duration was dependent on dive duration, but there was no effect of success and no significant interaction (dive duration: $F_{(1,97)} = 50.794$, p < 0.01; success: $F_{(1,97)} = 0.030$, p = 0.862; interaction term: $F_{(1,97)} = 0.407$, p = 0.525). We did not examine

Table 4. *Phalacrocorax aristotelis*. Frequency (%) of prey types taken by European shags in 2005 and 2006, based on samples derived from regurgitations and pellets and images from bird-borne digital still-picture camera loggers. Numbers in brackets indicate cases where identification was problematic

	2005		2006		
	13–20 Jun (31 pellets)	17–19 Jun (13 images)	26 Jun–7 Jul (29 pellets)	24 Jun–13 Jul (36 regurgitations)	29 Jun–3 Jul (38 images)
Sandeels, Ammodytidae	74	0	45	58	0
Bullheads, Cottidae	65	0	48	0	11(5)
Cod-like species, Gadidae	74	0	79	31	0
Gobies, Gobiidae	32	0	14	0	0
Butterfish, Pholididae	58	100	45	19	50
Blennies, Blenniidae	0	0	0	3	5(3)
Eelpouts, Zoarcidae	13	0	14	0	5(3)
Flatfish, Pleuronectidae	23	0	45	0	3
Dragonets, Callionymidae	0	0	3	6	0
Pipefish, Syngnathidae	0	0	0	11	0
Wrasse, Labridae	3	0	0	0	0
Eels, unknown family	0	0	0	0	5(5)
Crustacea	10	0	24	3	0
Mollusca	0	0	41	0	0
Unknown	0	0	21	11	21

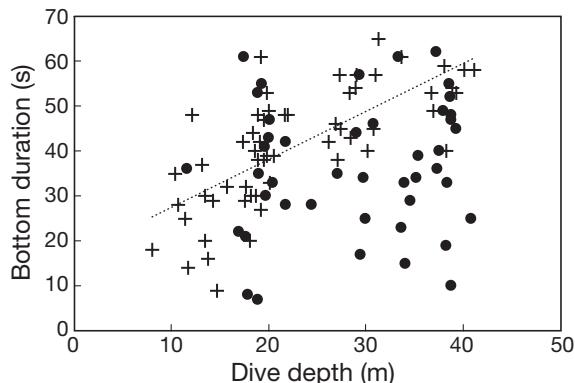


Fig. 5. *Phalacrocorax aristotelis*. Effects of dive depth on bottom duration in successful dives (those after which a bird returned to the surface with a fish; ●) and apparently unsuccessful dives (+) of European shags foraging in ROCKY habitat (see Fig. 2 for habitat definitions). Linear regression for unsuccessful dives (dotted line) was significant with the relationship described by the equation: bottom time (s) = $1.06 \times$ dive depth (m) + 16.84 ($r^2 = 0.50$, $p < 0.001$)

the effects of the success on bottom duration for SANDY habitat because of the small sample size (36 dives).

DISCUSSION

Device effects

Although the DSL used in this study represented a major technological advance in terms of miniaturization, we were aware that the devices were still large relative to our study species and thus could potentially impact on their foraging performance. Therefore, to

minimise the severity of any effects we restricted data collection to males (which in European shags *Phalacrocorax aristotelis* are significantly larger and heavier than females; Daunt et al. 2001) and only deployed loggers for very short periods (<27 h). Dive parameters (Table 1) obtained using DSL (346 mm² in cross-sectional area and 72 g in mass) all fell within the range of previously published values for birds at this colony fitted with smaller devices (200 mm² in cross-sectional area and 16 g in mass; Watanuki et al. 2005). Moreover, the foraging habitats used were also broadly similar to those previously identified using small VHF radio transmitters (177 mm², 19 g; Wanless et al. 1991a). While we cannot discount the possibility that the DSL increased energy costs, we are confident that the locational and behavioural data collected were representative of the Isle of May shag population and thus that our results do substantially increase our understanding of habitat usage and prey capture in this species.

Limitation of DSL data

To keep the mass of the DSL as low as possible, we did not incorporate any artificial lighting to compensate for low natural light levels. We were therefore unable to identify the microhabitats used by shags on some dives deeper than 40 m. More generally, water clarity and sunlight conditions will compromise DSL performance for animals associated with turbid waters or those that forage nocturnally.

The sampling rate used to take images in the current study was relatively slow (15 s). This almost certainly biased detection of prey in favour of large items that

take longer to handle and swallow, particularly those that need to be taken to the surface. Double-crested cormorants *Phalacrocorax auritus* feeding on relatively large fish invariably brought them to the surface, where the average handling time was 3.8 s (Enstipp et al. 2007). In our study, it was therefore possible that some items brought to the surface had already been swallowed before the image was taken, thus underestimating the frequency of successful dives. Cormorant species are also known to swallow small fish underwater (Cooper 1985, Wanless et al. 1993, Enstipp et al. 2007), and handling times in such cases may be extremely short. The sampling frequency currently used for the DSL is probably too slow to record such rapid events, but future technical developments will hopefully overcome this limitation.

Habitat and prey

Despite these constraints, images from the DSL undoubtedly represent the most comprehensive data thusfar collected on microhabitat use by European shags during individual dives and dive bouts. Shags, including those on the Isle of May, do sometimes forage in the water column using V-shaped epipelagic dives (Grémillet et al. 1998, Wanless et al. 1998). However, the majority (97 %) of images recorded by the DSL during the bottom phase showed the sea bed, indicating benthic foraging during U-shaped dives (Wanless et al. 1991b, Watanuki et al. 1996, Grémillet et al. 1998). Our study also confirms that shags use both ROCKY and SANDY areas, as suggested previously from radio-tracking (Wanless et al. 1991a). Image data showed that within a dive bout, birds remained within either rocky or sandy habitats, but sometimes changed habitats between consecutive bouts on the same trip.

Images from DSL also provided information on prey taken in each habitat, although, as discussed above, with some inevitable biases due to the low sampling frequency. In ROCKY habitat, shags fed predominantly on butterfish, a territorial, bottom-living species associated with rocky and/or weedy habitats providing cover (Wheeler 1978). Bottom duration during dives that were definitely successful in ROCKY habitat and in which the main prey was butterfish was highly variable and unrelated to dive depth (Fig. 5). In contrast, in dives that were recorded as unsuccessful, although they could have included instances in which small prey were ingested rapidly during the bottom phase or at the surface, duration was strongly related to depth. These behavioural differences suggest that shags foraging in a ROCKY habitat were mainly targeting solitary prey, whereby the chances of encountering and capturing another prey item were small and unpre-

dictable. Thus, a bird might be either terminating a dive if a large prey item that was difficult to handle was caught early on, or extending bottom time to ensure prey capture. Similar differences in dive parameters in relation to foraging success have also been recorded in captive Great cormorants *Phalacrocorax carbo* (Ross 1976).

Images showing birds with prey were extremely rare in SANDY habitat. Diet data collected concurrently with the logger data indicated that sandeels were a major prey in both study years (Table 4). The SANDY habitat used by shags (Fig. 1b) appeared highly suitable for lesser sandeels in terms of depth (ca. 30 m) and particle size (fine to coarse grains between 0.25 and 2 mm; Holland et al. 2005). During early summer lesser sandeels typically feed in the water column in the morning and spend the afternoon and night buried in the sand (Winslade 1974). However, by mid- to late June, when the present study was carried out, some fish could have stopped feeding and thus been present in the sand throughout the day (Greenstreet et al. 2006). Data from the DSL indicated that shags fed in sandy areas throughout the day and appeared to be catching the fish in the sand rather than in the water column, confirming earlier suggestions of Wanless et al. (1993). Sandeels eaten by shags on the Isle of May during the chick rearing period are typically <12 cm in length (Wanless et al. 1993). Hence, with a sampling interval of 15 s, the probability of recording the actual moment of capture and ingestion of small prey in a DSL image was likely to be very low.

Habitat and foraging behaviour

We found marked differences in foraging behaviour between the 2 foraging habitats. In ROCKY habitat, birds typically maintained a horizontal body angle and frequently changed dive depth over the course of a bout. This suggests that individuals were travelling horizontally over irregular bottom topography as they searched for prey. In contrast, in SANDY habitat, body orientation during the bottom phase was mainly vertical, and there was no evidence that birds travelled horizontally over the bottom. Secondly, the incidence of foraging with conspecifics differed, with shags often foraging with other shags in SANDY habitat but feed solitarily in ROCKY habitat. Sampling of sandy sediments around the Isle of May indicates that sandeel density is highly variable, but can reach 60 to 80 fish m⁻² (Holland et al. 2005), representing high-quality localised feeding patches for shags. Limited foraging sites in SANDY habitat might induce group foraging. We are not aware of any published estimates of densities of bottom-dwelling fish, such as butterfish, in the vicinity of the Isle

of May, but consider it highly unlikely that they would be as high as those of sandeels. Solitary feeding might therefore be favoured by birds feeding on sparse and/or cryptic prey in ROCKY habitat.

Individual specializations in prey, habitat and foraging site have been previously reported in coastal-feeding, diving birds (e.g. pigeon guillemots *Cephus columba*, Golet et al. 2000; South Georgian shags *Phalacrocorax georgianus*, Bearhop et al. 2006; Japanese cormorant *P. filamentosus*, Watanuki et al. 2004; rock shags *P. magellanicus*, Quintana 2001). Spatial distribution of different foraging habitats is thought to be an important factor influencing individual feeding specializations (Partridge & Green 1985). The seabed around the Isle of May is extremely varied including rocky, sandy, gravelly and muddy sediments within a 12 km radius encompassing the main foraging range of shags (Wanless et al. 1991a). Given the relatively short periods over which DSL were deployed, our finding that 6 of 9 shags foraged in both SANDY and ROCKY habitats within a single day (in some cases within a single trip) suggests that individuals were not habitat specialists, despite markedly different feeding techniques being used in the 2 habitats.

Although sandeels—that are associated with sandy areas and have high energy value—have been regarded as the main prey of shags on the Isle of May (Harris & Wanless 1991), recent studies (Harris et al. 2005, Watanuki et al. 2007, present study) indicate an increase in predation on bottom-living fish, such as butterfish, that are associated with rocky areas and have less energy value (Litzow et al. 2004). This diet change might be in response to decreases in sandeel availability driven by climate change and fisheries (Frederiksen et al. 2004, Wanless et al. 2005). The ability of individual shags to exploit prey in both ROCKY and SANDY habitats over a short time period may thus buffer the population against short-term decreases in prey. Ongoing studies using DSL and other bird-borne devices are providing opportunities to investigate this further.

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