Diving Depths of Northern Gannets: Acoustic Observations of *Sula Bassana* from an Autonomous Underwater Vehicle

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ABSTRACT.—The Autonomous Underwater Vehicle (AUV) *Autosub-1* made observations of the sea surface with an upward-looking echosounder during fish surveys in the vicinity of Shetland and Orkney (North Sea) in July 1999. Echograms from the AUV contained vertical traces extending downwards from the sea surface that were caused by diving seabirds. Visual observations provided evidence that those seabirds were Northern Gannets *Sula bassana*. Analysis of trace extent suggests a mean dive depth of 19.7 m (n = 19, SD = 7.5). Data on gannet diving depths are sparse, but this value is somewhat deeper than that accepted for the related Cape Gannet (*Morus capensis*, mean 5.9 m) which has been used in foraging models for the Northern Gannet. These observations have implications for our understanding of the foraging capabilities of gannets, and the interactions of gannets with commercially targeted fish species.

One of the factors that limits availability of prey to seabirds at sea is the depth to which the birds can dive. Conversely, differing diving capabilities amongst taxonomically distinct groups of seabirds can result in the effective partitioning of commonly targeted resources. In the Southern Ocean, for example, penguins, prions, and albatrosses are all able to exploit Antarctic krill (*Euphausia superba*) in overlapping geographical areas by targeting them at different depths in the water column (Croxall et al. 1997). Knowledge of birds' diving capabilities is essential for understanding foraging strategies of individual species, for modeling food-web interactions in ecosystems containing multiple predatory species, and for identifying areas of potential competition between seabird diet and commercial fisheries.

The Northern Gannet (*Sula bassana*) is a plunge diver and its large size (it is the largest pelagic seabird in the North Atlantic) makes its foraging efforts spectacular and conspicuous. In the North Sea, the diet of the Northern Gannet includes herring (*Clupea harengus*), mackerel (*Scomber scombrus*) and sandeels

(*Ammodytes* spp.) (see Wanless 1984, Martin 1989), and they are also able to exploit discard from fishing vessels (Furness et al. 1992). Although their diet is well described, until very recently little was known of the depth range over which Northern Gannets are able to catch prey.

Data on foraging location and diving depths of predators at sea, including seabirds, have been obtained from a variety of mechanical and electronic telemetering devices attached directly to the animals under study (e.g. Burger and Wilson 1988, Wanless et al. 1997, Hull 1999, Waugh et al. 1999). Although satellite tags have been deployed on Northern Gannets breeding on the coast of the North Sea to investigate their foraging range (Hamer et al. 2000), there are no published data on the diving depths of gannets from that area, an area that is of major importance for the species as a whole. In summer 1999, Garthe et al. (2000) deployed time–depth recorders on Northern Gannets breeding off Canada's Atlantic coast. At the same time that their study was underway, we made independent observations of Northern Gannets diving in the North Sea. Our observations were obtained by an Autonomous Underwater Vehicle (AUV) engaged in a fishery survey around the islands of Shetland and Orkney (Fernandes and Brierley 1999). Our data indicate that Northern Gannets have diving capabilities in excess of those previously acknowledged, and suggest that the effective vertical foraging range of the species should be reconsidered.

Methods.—In July 1999, the AUV *Autosub-1* was deployed from the Fisheries Research Vessel *Scotia* during an acoustic survey for herring in the northern North Sea (Fernandes et al. 2000). *Autosub-1* is a 6.8 × 0.9 m, torpedo-shaped unmanned submersible vehicle: it is battery-powered and can conduct preprogrammed underwater missions at speeds of up to 3 knots, to depths of 500 m with a duration of over 24 h. During our study the AUV was deployed on missions that were on average 8 h long. For the vast majority of that time, the AUV was unattended, tens of kilometers away from *Scotia*, purposefully surveying transects geographically distinct from those that the ship was sampling.

For this study, *Autosub-1* was equipped with a Simrad EK500 scientific echosounder operating 38 and 120 kHz transducers generating conical 7° sampling

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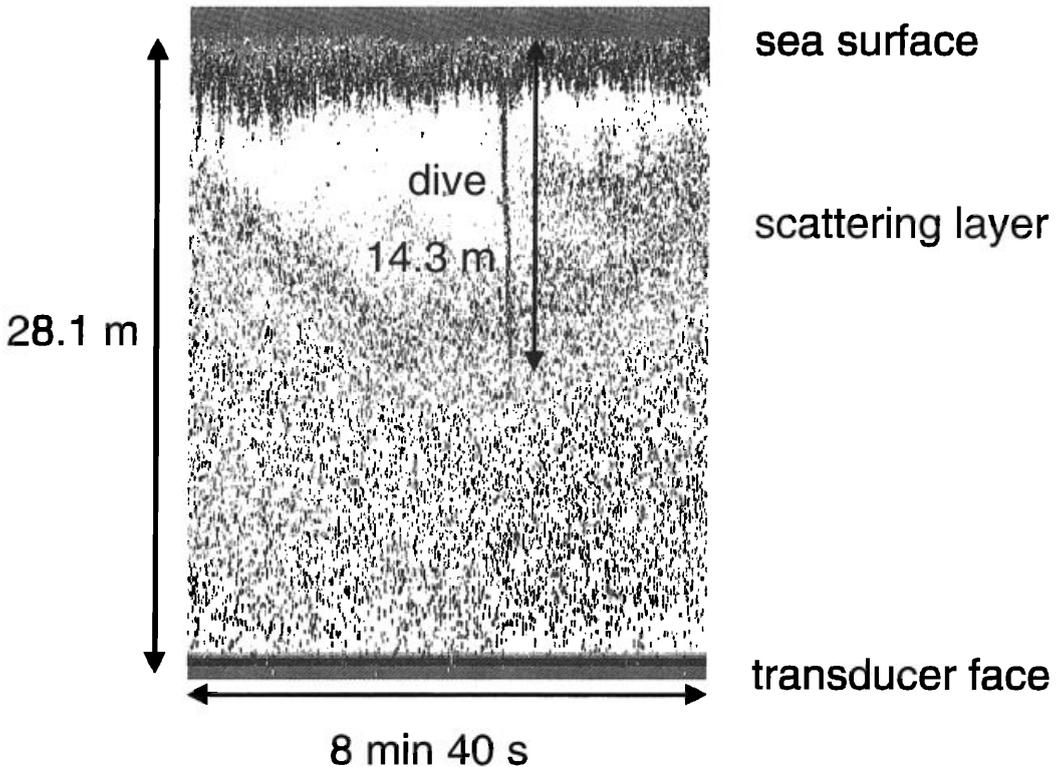
FIG. 1. Example echogram from the upward-facing 120 kHz transducer, showing the sea surface, a Northern Gannet dive trace, and an acoustic scattering layer composed possibly of the prey upon which the gannet was diving. At a nominal survey speed of 1.2 ms^{-1} (from left to right), 8 min 40 s equates to a distance of 624 m. See text for further explanation.

beams. Acoustic samples (pings) were collected every 1 s during each deployment and data were logged over an ethernet to a local personal computer using SonarData Echolog EK software. Echograms were downloaded at the end of each mission and viewed using the SonarData Echoview software package.

The echosounder transducers on *Autosub-1* could be arranged to be both downward looking, both upward looking, or one up and one down. The AUV was deployed on 12 missions with an upward looking transducer. The principal objective of the upward looking transducer was to obtain information on near-surface schools of herring *Clupea harengus* (Fernandes and Brierley 1999). On those deployments, the AUV was programmed to cruise at depths of either 20, 30, or 50 m, or to remain at a fixed depth above the seabed (effectively undulating between 35 and 50 m depth), and the sea surface was always "visible" acoustically.

Typically, an *Autosub-1* mission would begin with the vehicle "pottering" at the surface while waiting to obtain a GPS fix for navigation. During that time,

gannets were often attracted to the vehicle (it is bright yellow and equipped with strobe lights to aid relocation and recovery). Once a GPS fix had been obtained, the vehicle would be instructed by radio to dive and begin its mission. On many occasions when the AUV dive took place, gannets that had been circling above and in the vicinity of the vehicle dived at it. Some of those dives were visible clearly on the echograms and could be attributed directly to gannets: the insulating layer of air trapped amongst the birds' feathers makes the birds strong acoustic reflectors, and the bubble train trailing behind the diving birds leaves a conspicuous streak on the echogram (Fig. 1). Dives of exactly the same appearance were also evident in echograms recorded when the AUV was unattended; it is data from those dives that are considered in this paper. Dive depths were evaluated from the echograms as the difference between the range from *Autosub-1* to the sea surface and the closest approach of the dive trace to *Autosub-1* (see Fig. 1).

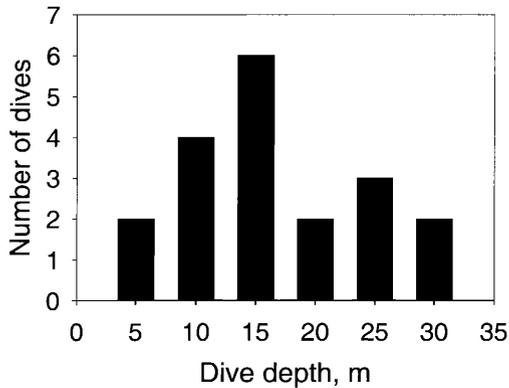*Results.*—Nine of the 12 *Autosub-1* missions when one or more echosounder transducers were facing

FIG. 2. Histogram of Northern Gannet dive depths ($n = 19$).

upwards towards the sea surface obtained good data (along a total survey track of over 330 km) and, during those, 19 gannet-like dive traces were evident on echograms recorded during the time the AUV was unattended. Those 19 dive traces were indistinguishable from those traces that coincided with the AUV dives, which we knew were caused by gannets: binocular observations made from the FRV *Scotia* (range < 200 m) of the diving AUV detected Fulmars (*Fulmarus glacialis*), but no auks (Alcidae), and so we are confident that the dives apparent on the echograms are due to gannets. The unattended missions were conducted mostly off shore, in areas where auks are known to be less prevalent and, furthermore, the dives we observed (Fig. 1) were of quite different appearance to dives by Common Murres (*Uria aalge*) observed in the Clyde Sea with a multibeam 3-dimensional sonar (P. G. Fernandes unpubl. data). We did not include gannet dives recorded by the AUV at the start of its missions in our analysis because those bird dives were, without doubt, triggered by the AUV dive and cannot therefore be considered as natural—their inclusion may have biased our conclusions.

Weather conditions deteriorated somewhat during the course of two missions, causing the sea surface to become increasingly disturbed. Air bubbles mixed downwards by wave action (Thorpe 1992) then partially obscured dive traces and, because we are less confident in our ability to distinguish dives at those times, we have not included data from those sections of cruise track.

The mean gannet dive depth from the 19 observations was 19.7 m (SD = 7.5, range 8.0 to 34.0 m). A histogram of dive depths is shown in Figure 2: the distribution did not differ significantly from normal (Anderson-Darling test, $P = 0.135$).

To investigate the possibility that the birds were diving on the AUV itself, we compared dive depth with AUV depth. The scatter of dive depths was quite large, but the relationship between dive depth and AUV depth was highly significant (ANOVA, $F = 16.45$, df = 17, $P = 0.001$).

Discussion.—There are few published observations of diving depths of gannet species, and we are aware of only one such data set for the Northern Gannet (Garthe et al. 2000), which was collected at the same time (but in a different location using a different technique) as the data reported here. The observations we report here are thus valuable both because they enhance understanding of the foraging capabilities of this species generally and, more specifically, provide the first data on foraging depths for Northern Gannets in the North Sea.

Observations by Adams and Walter (1993) on the Cape Gannets (*Morus capensis*) suggest that it can achieve a maximum dive depth of 12.6 m (mean 5.9 m, SD = 4.0 m). Garthe et al. (2000) reported a deeper maximum dive depth of 22 m for the Northen Gannet (mean 5.2 m, SD not reported). The Cape Gannet is a slightly smaller bird than the Northern Gannet and that between-species difference in previously reported maximum dive depths is in line with expectations that maximum dive depth is size dependent (see Burger 1991). Our observations suggest that Northern Gannets in fact have the potential to dive deeper still (mean 19.7 m, SD = 7.5 m).

Adams and Walter (1993) considered that it would only be possible for Cape Gannets to achieve their maximum observed dive depths by active swimming. During the course of the present fishery survey, Northern Gannets were often observed diving on the cod end of the trawl net during recovery, and were also seen swimming down to retrieve sinking, dead herring that had been discarded from the trawl deck. Those birds are clearly capable swimmers (see Nelson 1978). Garthe et al. (2000) report that the deeper gannet dives they recorded involved bent-winged underwater flight. Prince et al. (1994) have similarly suggested that some albatross species must regularly swim underwater to achieve recorded depths.

In addition to suggesting a new maximum diving capability for Northern Gannets, our observations differ from those of Garthe et al. (2000) in another key respect: they reported that the distribution of dive depths was Poisson-like, whereas the distribution of dive depths we observed did not differ significantly from normality. We believe that there are two possible explanations for this difference. Firstly, it is probable that the depths of prey species being sought by gannets in the North Sea (herring, mackerel, and sand eels) and the northeast Atlantic (predominantly capelin [*Mallotus villosus*]) differ. Secondly, we suggest that the loggers attached externally to the gannets studied by Garthe et al. (2000) may have either underestimated achieved

dive depths due to sampling limitations, or may have hampered the birds such that they were unable to reach their full potential depth. Garthe et al. (2000) suggest strongly that their recording devices had no negative effect on the birds. Concerns remain, however, that external recording devices may hamper performance by increasing drag (cf. Culik and Wilson 1991), and sampling-rate limitations of depth recorders may lead to a distorted representation of diving behavior (Wilson et al. 1995), a problem that may be particularly acute in animals that undertake dives where the time at maximum depth is short and where the rate of depth change is rapid. Direct observations of dives could overcome those potential limitations, and we suggest that our observations from the AUV are particularly valuable because they are of birds that were not encumbered by instruments. The use of time–depth recorders did however enable Garthe et al. (2000) to gather information on dive profiles, enabling them to distinguish between U and V shaped dives. Limitations inherent with our sampling technique do not enable those type of differences to be distinguished. The echo sounder transducers we were operating had 7° beam angles. At a range of 50 m, they provided a circular sampling window 6.1 m in diameter, but that window decreased in size as range from the AUV decreased (diameter = 2 × tan 3.5° × range), being 1.2 m at 10 m range (Fig. 3). Only dives that passed directly down the center of the echosounder beam would be observed in full and, unless the descent and ascent components of the dive were spatially very close, it is unlikely that bubble trails from both would be detected. The AUV traveled typically at a speed of 1.2 m s⁻¹ and, at a range of 50 m, would have been able to observe a fixed point in the water column above for only a little over 5 s. Another implication of the conical acoustic sampling window is that the deeper a dive was the more likely it was to pass out of the sampling beam (see Fig. 3): our reported dive depths are therefore likely to be conservative estimates. The acoustic records do however reveal something of the prey field upon which the gannets were diving. Figure 2, for example, shows a scattering layer that deviates around the maximum depth of the gannet dive. The deviation may be due to prey actively attempting to avoid the diving gannet. Different sampling techniques clearly reveal different aspects of foraging behaviour, and our data and those collected at the same time, albeit in a different location, by Garthe et al. (2000) should be viewed together to provide the most comprehensive information so far available on diving behavior of Northern Gannets.

It is possible that the AUV itself was the cue for the gannet dives observed here. If that is so, then how often gannets would naturally dive to the depths we have recorded is questionable. We believe though that gannet dive-depths and AUV operating depths appeared to be related significantly because the con-
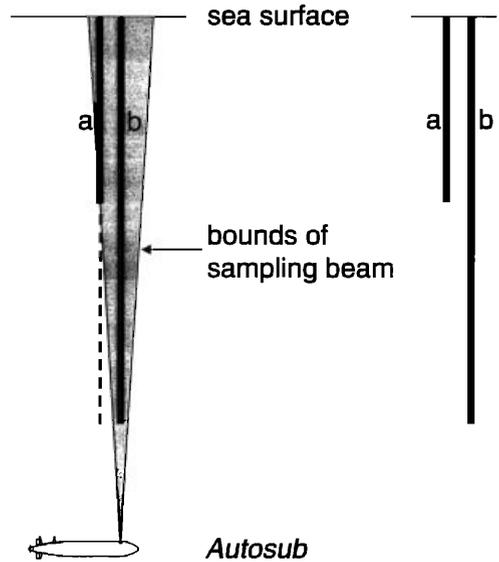

FIG. 3. Schematic representation of the acoustic sampling window above the AUV (left) showing the echogram traces (right) of two dives that descended to the same depth either partially (a) or entirely (b) within the 7° echo sounder beam (shaded). The deeper part of dive (a) is undetected (dashed line) because it passes outside the beam. The figure is to scale with the AUV at 33 m; the echo sounder beam diameter at the sea surface is 4 m.

ical shape of our sampling window made it more likely that deep gannet dives would be detected when the AUV was deeper. Whether naturally cued or not, however, the fact that gannets were recorded diving to depths >25 m at least demonstrates a potential to do so for natural foraging. Other species of sea birds have been recorded at considerable depths, depths that are often much beyond those generally believed to be possible (Harrison 1996). Light-mantled Sooty Albatross (*Phoebetria palpebrata*), for example, have been recorded diving to 12.4 m (Prince et al. 1994) and Sooty Shearwaters (*Puffinus griseus*) have reached depths of 65.4 m (Weimerskirch and Sagar 1996).

The potential for Northern Gannets to dive in excess of 25 m enables them to exploit considerably more than "the upper few meters" of the water column in the North Sea (Garthe et al. 1999) previously thought possible. Previous fishery surveys around Shetland have concluded that herring are only found near the surface in the northern reaches of the fishery survey area (E. J. Simmonds pers. comm.). Interestingly, that is close to a large breeding colony of gannets at Hermaness at the extreme north of Shetland. Mackerel and sandeels—another important food for gannets—are more pelagic in

distribution. Although herring are otherwise pre-dominantly associated with the bottom during day-light, they do form midwater schools (Fernandes et al. 2000), and the extended diving range of gannets reported here may make these fish accessible fur-ther afield. The possibility that gannets are exploit-ing herring over a wide geographic area (see Hamer et al. 2000 for data on foraging ranges of Northern Gannets in the North Sea) has implications for the effects of fishing activities on gannets. Although Northern Gannet populations are presently on the increase (del Hoyo et al. 1992, Murray and Wanless 1997), and North Sea herring stocks do not appear to be in decline, the potential for future conflict be-tween fisheries and gannets remains.

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Factors Affecting Reed Warbler Risk of Brood Parasitism by the Common Cuckoo

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ABSTRACT.—In this study we conducted a multiple
logistic regression analysis of factors hypothesized
to influence the risk of Reed Warbler (*Acrocephalus
scirpaceus*) brood parasitism by the Common Cuckoo
(*Cuculus canorus*) on study sites in the south-eastern
part of the Czech Republic. We collected data from
Common Cuckoo nesting sites surrounding two fish-
ponds. Our logistic regression models were based on
the dichotomous dependent variable, parasitism of
the Reed Warbler nest, and seven independent vari-
ables. Our first model used all data available across
sites and years and resulted in a final model in which
the only significant contributor was the independent
variable "cuckoo view," the view of host nests from
the cuckoo's vantage point in a tree. A second model
was developed using data limited to sites and years
with the largest sample sizes and expected to yield
the most reliable results. That model resulted in
three significant contributors: site, cuckoo view, and
neighborhood view. In both data sets, the odds of
nest parasitism were shown to increase as the view
of the host nest became more direct. However, a di-
rect view of the focal nest raised the risk of parasit-
ism to a much greater degree than did a direct view
of the neighborhood of nests. Our results provide
support for a nest-exposure hypothesis of brood par-
asitism risk. Although our models have identified
nest exposure to be the best predictor of nest para-
sitism in this system, work remains to unravel the
potentially complex relationship among Common
Cuckoos, habitat structure, and Reed Warbler hosts.

In recent decades, scientists have focused partic-
ular attention on the process by which avian brood
parasites search for host nests. In fact, as early as the
1920s, the ornithologist E. Chance (1922, 1940) de-
scribed female Common Cuckoos (*Cuculus canorus*)
using visual vantage points in trees to observe their
host's nest building activity. From such vantage
points, the cuckoo would later fly secretively down
to the host nest and, usually within seconds, lay its
egg. Subsequently published observations by Gärt-
ner (1981, 1982) and Wyllie (1981) have supported
Chance's original observations. Despite the fact that
watching the activity of the hosts is frequently re-
ferred to as the only nest-finding cue employed by
the cuckoo, systematic studies of its nest-searching
behavior are more or less lacking (Øien 2000). Re-
cently, Alvarez (1993), Øien et al. (1996), and Moskát
and Honza (2000) have observed that hosts breeding
close to trees suffered a higher risk of being parasit-
ized by cuckoos than those breeding farther away
from trees. That higher risk is hypothesized to occur
because it is easier for cuckoos to spot host-nesting
activity when the nests are built near trees. Further-
more, Øien et al. (1996) and Moskát and Honza
(2000) recorded the degree of concealment of host
nests (referred to as "cuckoo view") and found a
strong, negative relationship between the degree of
nest concealment and risk of parasitism.

Clotfelter (1998) recently reviewed the literature
on the nest searching behavior of the North Ameri-
can generalist brood parasite, the Brown-headed
Cowbird (*Molothrus ater*), and suggested four differ-
ent hypotheses that might explain how this parasite
searches for and localizes nests. He found little sup-

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