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The daily catch: Flight altitude and diving behavior of northern gannets feeding on Atlantic mackerel

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ABSTRACT

Predators utilize a variety of behavioral techniques to capture elusive prey. Behavioral flexibility is essential among generalist predators that pursue a diversity of prey types, and capture efficiency is expected to be intense during the breeding season for parents that engage in self- and offspring-provisioning. We studied the foraging behavior of parental northern gannets in the northwestern Atlantic (Gulf of St. Lawrence) when they were feeding on Atlantic mackerel almost exclusively. Data-loggers recorded short (mean duration: 6.3 s), high speed (inferred vertical speeds of up to 54.0 m^*s^{-1}, equivalent to 194 km^*h^{-1}), and shallow dives (mean depth: 4.2 m; maximum: 9.2 m). Dives tended to occur in bouts, varying between 0.3 and 4.6 per hour (mean = 1.6). During foraging, overall flight heights ranged from 0 to 70 m, with no clear preferences for height. Most plunge-dives were initiated at flight altitudes of 11–60 m (mean ± SE = 37.1 ± 2.8 m; range 3–105 m except for 1 of 162 dives that was initiated at the sea surface). Dive depth and flight altitude at plunge-dive initiation were positively and significantly correlated, though it appears that low flight altitudes were sufficient to reach dive depths at which mackerel were present. Almost all dives were V-shaped indicating that a high acceleration attack is the most effective strategy for gannets feeding on large rapid-swimming prey such as mackerel that owing to thermal preferences does not occur below the thermocline and are thus well available and essentially trapped in the water depths exploited by northern gannets.

1. Introduction

To maximize success and efficiency, predators use a variety of foraging and prey capture tactics (Hixon, 1982). Predation efficiency is particularly critical for parents provisioning themselves and their offspring (Orians and Pearson, 1979). Many seabirds adjust their aerial diving behavior and underwater pursuit of prey (Elliott et al., 2008a,b). Generalist predators with a broad diet breadth make flexible decisions about the most effective behavioral interactions with prey (Hamer et al., 2007; Harding et al., 2007; Paiva et al., 2010).

Red-footed boobies (*Sula sula*), for example, exhibit a series of very specific flight and aerial adjustments in their pursuit of tropical fishes (Weimerskirch et al., 2005). The closely-related northern gannet (*Morus bassanus*) also modifies its aerial and underwater diving behavior when pursuing different prey (Garthe et al., 2000). Ropert-Coudert et al. (2009a) demonstrated that the maximum dive depths reached using the plunge-diving technique was 10–11 m. Using a biomechanical model they show that little additional depth can be obtained from momentum alone when initiating a plunge from heights higher than 40 m. Comparisons of dive angles by Australasian gannets (*Morus serrator*) similarly showed that dive patterns were adjusted before the bird entered the water (Machovsky Capuska et al., in press), confirming that dive depth is determined in the aerial phase of the plunge as suggested by Ropert-Coudert et al. (2009a). Machovsky Capuska et al. (2011a) also showed that Australasian gannets altered the height of their foraging flights to the depth of fish schools showing that in these circumstances dive profile is associated with prey location, as suggested by Elliott et al. (2008a, 2008b).

Northern gannets feed on a diverse array of pelagic fishes and squid that range in weights from grams to hundreds of grams and that are returned to chicks in loads consisting of from tens of prey items to single large individual prey (Montevecchi, 2007). Of the prey that northern gannets consume and deliver to chicks, Atlantic mackerel (*Scomber scombrus*) have the highest lipid contents and energy density (Montevecchi et al., 1984). Atlantic mackerel is one of the largest and fastest swimming pelagic fish consumed by an aerial diving seabird weighing many hundreds of grams and exhibits maximum burst speeds of up to 5 m^*s^{-1} (He, 1993).

We had hypothesized previously that rapid short duration V-shaped dives were aimed at large pelagic fishes and squids and that extended deep U-shaped dives by gannets were directed towards schools of

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small pelagic fishes such as capelin (*Mallotus villosus*) and sandlance (*Ammodytes* spp.; Garthe et al., 2000). This was broadly confirmed for gannets feeding on a mix of pelagic fish prey during another study (Garthe et al., 2011).

Here we report on a study at the largest colony of northern gannets in the northwestern Atlantic in the Gulf of St. Lawrence, where gannets were almost exclusively feeding on Atlantic mackerel during the 2007 breeding period. We analyze the foraging behavior of central-place foraging northern gannets preying on Atlantic mackerel, through the application of different data-logging units. We focus on the following questions:

(1) How deep and long do gannets dive when preying primarily on Atlantic Mackerel?
(2) Does a distinct diel rhythm exist?
(3) How high do gannets fly when they search for prey, and from which altitudes do they initiate their plunge-dives?
(4) Is the flight altitude before the start of the plunge-dive related to the dive depth?
(5) How can the flying and diving behavior of northern gannets observed in this study be explained by the biology of the Atlantic mackerel as their main prey?

2. Material and methods

2.1. Study site

This study was carried out between 1 and 11 July 2007 on Bonaventure Island (48°29′ N, 64°09′ W), a 5 km^2 island located 3 km off the Gaspé Peninsula in the boreal waters of the Gulf of St. Lawrence, Québec, Canada. Bonaventure Island is the site of the largest gannet colony in North America (ca. 59,600 pairs in 2009, JFR unpubl. data).

2.2. Diet sampling

Dietary data were collected by approaching gannets at the periphery of the colony such that some birds regurgitated food loads, and from observations of food scraps and feedings in the colony. Furthermore, some birds regurgitated food while being handled for attachment or removal of GPS devices. Dietary data are presented as the percentage of total prey loads identified. For mixed prey regurgitations the respective proportions of the prey categories were calculated. In addition to samples collected during the above mentioned study period, archived data from the Canadian Wildlife Service were analyzed to provide a broader picture of food consumption by northern gannets on Bonaventure Island.

2.3. Capture and handling of birds

Adult gannets incubating eggs or having small chicks (max. 2 weeks old) were captured and recaptured after 1–7 days with a telescoping noose-pole. To minimize disturbance, nests were chosen on the periphery of the colony. To reduce any potential bias due to unexperienced birds breeding at the periphery of the colony, birds were selected from the third or fourth row from the outer edge. Parental behavior and egg and chick survival appeared unaffected at nests where we attached data loggers to one parent. Capturing took usually 2–3 min, and attaching devices and marking a bird lasted 5–10 min at maximum. All birds were cared for in accordance with the guidelines of the Canadian Council on Animal Care.

2.4. Data loggers used

Birds were equipped with either an altimeter or a GPS logger.

Altimeters (15 g, 65 mm length, 16 mm diameter) specifically designed for this study by earth & OCEAN Technologies (Kiel, Germany) consisted of a pressure and a temperature sensor. The range of the pressure sensor was set to include altitudes from 2000 m high through dives to ca. 7 m deep; measurements were taken at a 1 s interval. Dives deeper than ca. 7 m were also recorded but the value remained at the deepest available option (we checked the raw values of the pressure channel for this purpose). The resolution was ca. 2 m in air with an estimated accuracy of ca. 8.5 m, and 0.0024 m in water with an estimated accuracy of 0.1 m (information provided by earth & OCEAN Technologies). Data collected were further calibrated; see section on flight altitude analysis below. Nine birds were equipped with these loggers all of which were recaptured, with seven data sets obtained for data analysis.

GPS TD logs (100 × 48 × 24 mm, 70 g; earth & OCEAN Technologies, Kiel, Germany) were attached to six birds of which five were recaptured with downloadable data. GPS loggers were taped to body feathers on the lower back just above the uropygial gland with Tesa® tape (Garthe et al., 2011). Devices included temperature/pressure sensors and comprised about 2% of adult body mass. Only data on pressure (i.e. dive depth) were used for this manuscript.

2.5. Diving analysis

Dives were analyzed using MultiTrace-Dive (Jensen Software Systems) and were defined as immersions deeper than 0.3 m; shallower measurements were attributed to bathing and preening movements. Two different dive types can be distinguished in recordings from northern gannets (Garthe et al., 2000): i) V-shaped dives, being usually relatively short and shallow, and with the ascent period following almost immediately the descent period; ii) U-shaped dives, being relatively long and often deep, with time spent at depth between descent and ascent periods. Dives were analyzed differently for the two devices. As dive depth was limited to ca. 7 m (varying slightly between the specific devices according to the calibration protocols) in altimeters, dive depth analysis for greater depth was limited to GPS TD loggers. It is important to note however that all dives deeper than ca. 7 m were also recorded by the altimeters (see above). Time of day was analyzed by relating each dive to the next full hour (i.e. 05 = 04:30–05:29), following Davoren et al. (2010). Inter-dive times were analyzed per foraging trip and day separately, measuring the time from the offset of one dive to the onset of the next.

2.6. Flight altitude analysis

All pressure values from the altimeters were first corrected for changing air pressure values by incorporating hourly measurements at the nearby weather station in Gaspé (data were downloaded from the Environment Canada website: http://www.climate.weatheroffice.gc.ca/climateData/canada_e.html). This was achieved by adding/subtracting air pressure measurements from the pressure values provided by the altimeter sensor to standardise air pressure in the atmosphere (to e.g. 1000 hPa). Altimeters were attached atop tail feathers, so that they remained above water when birds were swimming in order to determine 0 m altitude. This pressure calibration of the data sets was carried out frequently based on the periods when the birds were swimming. Data from lower pressure values were turned into flying height values (a difference of 1 hPa equates to a difference of ca. 8.4 m altitude in air).

Flight altitudes were determined separately for travel flight segments (periods of continuous flight after leaving the colony area and before reaching the foraging area; not further analyzed in this manuscript) and foraging bouts (periods with dives that are spaced less than 20 min apart). Flight altitudes were classified into 10 m classes separately for each individual.

Vertical speeds in the air were derived from differences in altitude between successive measurements (that are available in 1 s intervals, see above) after initiating the plunge-dive, resulting in speed values (m^*s^{-1}).

3. Results

3.1. Diet

Gannets from Bonaventure Island fed mostly on large pelagic fish species during late incubation and the entire chick-rearing periods (Fig. 1). Although varying from year to year, Atlantic mackerel was always the species consumed most frequently (49–91%), followed by Atlantic herring (*Clupea harengus*; 6–44%). Other fish species were of minor importance. There was a tendency for mackerel to slightly decrease from June–July to August–September while Atlantic herring increased in frequency as gannet prey.

During the period of logger deployment in 2007 (1–11 July), 94% of the 149 regurgitations contained mackerel, 3% capelin, 2% herring and 3% other species. Seven of the 14 birds retrieved with data loggers regurgitated mackerel, and none regurgitated any other fish species.

3.2. Diving behavior

Dives occurred between 03:48 and 20:52 local daylight savings time. Diving activity was only slightly elevated in the morning while there was a clear gap around mid-day (Fig. 2a). While some dives occurred during the first light and twilight periods, no dives occurred at night (sunrise: 04:20, sunset: 20:24, respectively).

The number of dives per hour at sea varied between 0.3 and 4.6, with a mean of 1.6 ($n = 10$ birds). Dives tended to occur in sequences of several dives rather than spread out equally over the foraging trips. In 33% of all dives another dive followed within 2 min, and in 73% of all dives another dive followed within 20 min (Fig. 2b). Only 17% of all dives were spaced by more than 1 h from the next dive. When dives occurred in bouts with little time in between, dives depths mostly remained at similar depths. In few cases, dive depths decreased and increased, respectively.

Most of the plunge-dives were initiated at flight altitudes of 11–60 m (Fig. 2c). Only 1 out of the 162 dives investigated was initiated at the sea surface (=0 m); all others were initiated at heights ranging from 3 to 105 m. Mean flight heights before diving ranged from 28.9 to 45.6 per individual, with an overall mean ± SE of 37.1 ± 2.8 m ($n = 7$ individuals).

Dives were usually shallow, with 91% of them less than 7 m deep with no clear evidence of any depth class preference (Fig. 2d). Mean dive depth was 4.2 m (GPS TD loggers only; $n = 288$), and the deepest dive was 9.2 m. Dives were mostly briefer than 11 s, with a mean of 6.3 s and a maximum of 23 s ($n = 731$). The proportion of U-shaped dives (dives that showed an extended horizontal phase after descent and before ascent) was 6%.

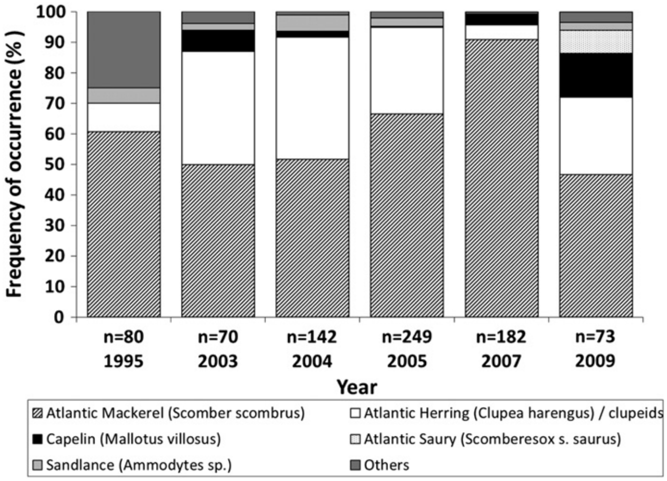

Fig. 1. Diet of northern gannets from Bonaventure Island from late June to mid-September during six years.

3.3. Flying behavior

Northern gannets used a wide range of altitudes when foraging. They often altered their flying heights, mainly because of plunge-dives (see examples in Fig. 3a) or attempts to plunge-dives, both of them involving an almost free fall and subsequent climbs. Most flights during foraging were conducted at altitudes of 0–70, with no clear preferences for heights of 10–60 m (Fig. 3b).

There was a positive significant relationship between dive depth and the flight altitude at which the plunge-dive was initiated ($t = 7.69$, $p < 0.001$, Linear Model) with higher onset altitudes generally resulting in deeper dives. There was, however, substantial variation in the data: dives of about 1 m depth were initiated at altitudes of 3–35 m, whereas those of about 5 m depth at altitudes of 16–85 m (Fig. 4). Similar to dive depth, there was a positive significant relationship between dive duration and the flight altitude at which the plunge-dive was initiated ($t = 7.04$, $p < 0.001$, Linear Model). We derived the speed of free-falling gannets from the vertical measurements. Differences in pressure from one measurement to the next (1 s interval) suggest vertical speeds of up to 54.0 m^*s^{-1}, equivalent to 194 km^*h^{-1}. Finer resolution of the pressure sensor would probably even better capture the fastest part of the vertical movement and may thus reveal even higher speeds.

4. Discussion

4.1. Mackerel as gannet prey in the Gulf of St Lawrence

Atlantic mackerel has the highest energy density of any prey of northern gannets (Montevecchi et al., 1984) and has been the principal prey of northern gannets in the Gulf of St. Lawrence (Nelson, 1978), seemingly a preferred choice. Other studies have also revealed Atlantic mackerel to be an important part of the diet of gannets, e.g. off Newfoundland (Montevecchi, 2007; Montevecchi and Myers, 1997), in the Celtic Sea (Votier et al., 2010) and in the North Sea (Hamer et al., 2007), with substantial variation between sites, years and season. Flight patterns, activity and diving behavior differed often remarkably as a consequence of the different prey choices (Garthe et al., 2011; Hamer et al., 2007).

The southern Gulf of St. Lawrence is the most important spawning ground for Atlantic mackerel on the east coast of Canada (e.g. Arnold, 1970; Mackay, 1979; Sette, 1943). The large mature fish begin their spring migration earliest entering the gulf followed by the juveniles (Mackay, 1967; Sette, 1950). Owing to varying swimming speeds, mackerel aggregates in size-associated schools (Sette, 1950). At 25 cm total length, 50% of this stock is mature (Grégoire et al., 2009). The slight decrease of mackerel in the gannets' diet in late summer can be well explained by their partial redistribution in the Gulf of St Lawrence, with individuals leaving for the Estuary as well as northern and eastern areas (FG unpubl. data).

Atlantic herrings are also abundant and have important spawning grounds in the southern Gulf of St. Lawrence in proximity to Bonaventure Island (LeBlanc et al., 2010). Both species are key prey for gannets with high energy density (10.3 kJ/g wet weight for mackerel and 9.2 kJ/g for herring; much higher than those for capelin (4.2 kJ/g wet weight; Montevecchi et al., 1984).

The thriving of the gannet population on Bonaventure Island is associated with good availability of high quality prey species such as mackerel and herring. The year-class strength of mackerel fluctuates profoundly, and a single strong year-class dominates (1999) the commercial catches for several years (Grégoire et al., 2009). Moreover, the mackerel's migration and distribution patterns as well as spawning grounds are undergoing profound changes (Grégoire

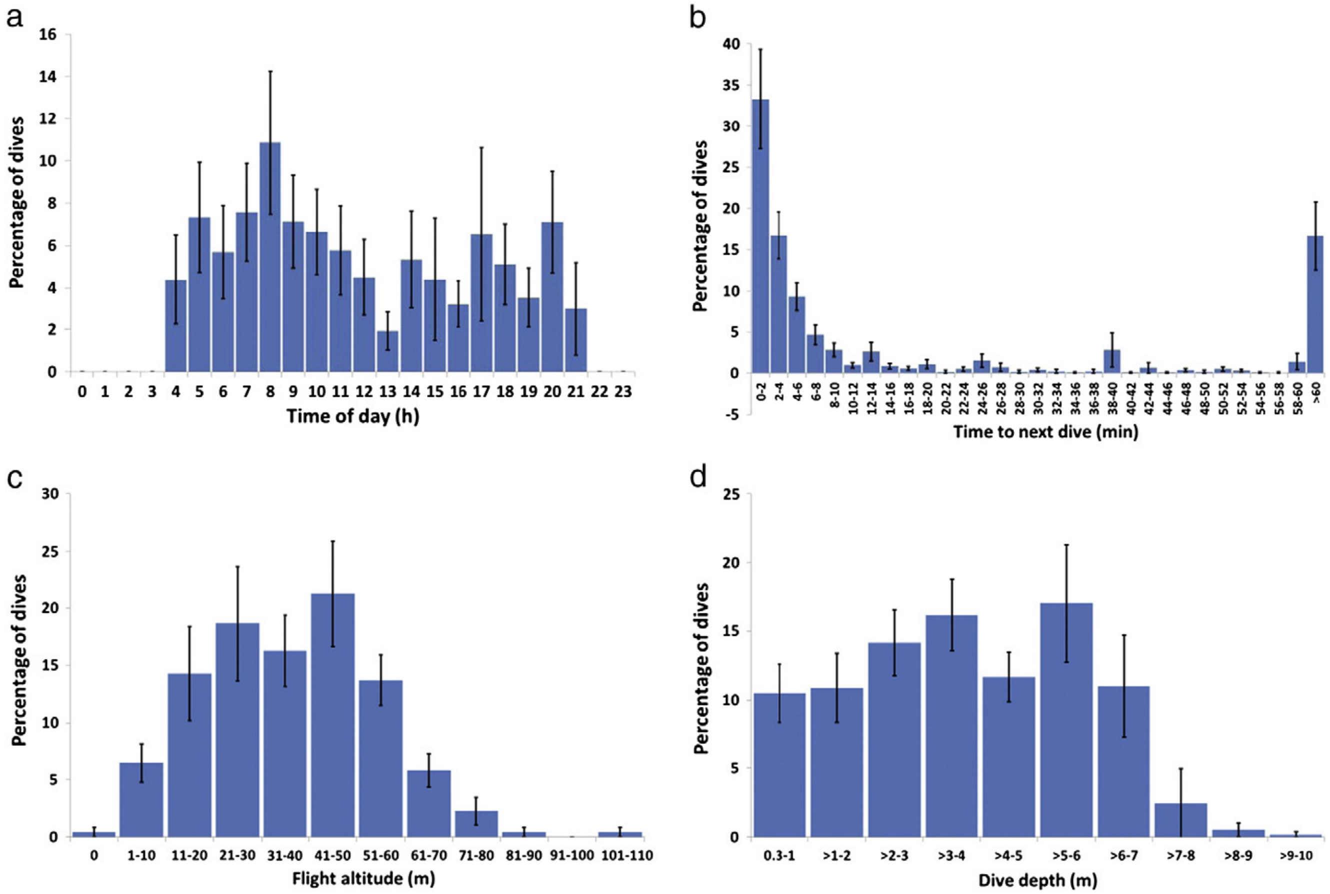

Fig. 2. Diving behavior of northern gannets from Bonaventure Island in July 2007. a) Diel rhythm of dives; n = 731 dives from 14 individuals. Vertical lines indicate standard errors. For details see text. b) Time from the offset of one dive to the onset of the next dive; n = 699 inter-dive times from 14 individuals. Vertical lines indicate standard errors. c) Flight altitudes before plunge-diving; n = 162 measurements from 7 individuals. For details see text. Vertical lines indicate standard errors. d) Dive depths from 731 dives from 14 individuals; both altimeters and GPS loggers. Vertical lines indicate standard errors.

et al., 2009). Recently, there has been a marked increase in fisheries landings of mackerel on the east coast of Newfoundland which has been accompanied by a drop in the catches in the southern Gulf of St. Lawrence (Grégoire et al., 2009). Thus, the availability and hence the importance of mackerel for northern gannets breeding on Bonaventure might alter in the future.

4.2. Foraging behavior in relation to mackerel as principal prey

We were fortunate to work in the colony on Bonaventure during a period when the gannets were almost exclusively preying on mackerel so that we can relate flight and dive patterns to this type of fish. GPS data were too few to make conclusive inferences, but the data from the five birds were within the spatial pattern described by Garthe et al. (2007a) for the same colony during summer 2003.

The flight altitude of northern gannets that forage on mackerel could be influenced by both the required acceleration for a sufficiently deep plunge dive and the search for a suitable prey school. We suggest that the latter factor may be more relevant as the relationship between flight altitude and dive depth is weak (Fig. 4) and low flight altitudes are obviously sufficient to reach dive depths at which mackerel were present and to provide the power and impact to stun and capture these large pelagic fishes. Time intervals between successive dives are short, in fact shorter than those previously reported for northern gannets (Garthe et al., 2011). This observation supports other findings which indicate that locating a suitable prey school is a key component for gannets when preying on mackerel and other pelagic shoaling fish species. Though viewed from a different perspective, Lewis et al. (2001) argued that density-dependent fish disturbance by gannets is sufficient to significantly reduce the profitability of fish shoals close to colonies, thereby generating suitable conditions for intra-specific competition. However, when preying predominantly on capelin in waters off northeast Newfoundland, gannets keyed in on spatially and temporally predictable prey shoals (Davoren et al., 2006) and concentrated foraging efforts in these areas (Garthe et al., 2007b; Montevecchi et al., 2009). In such circumstances involving intense diving activity, gannets also risk injury from plunging conspecifics (Machovsky Capuska et al., 2011b).

Once a suitable prey school has been located, frequent diving may enable rapid prey consumption. Unfortunately, success rates for dives could not be investigated in this study. Simultaneous and successive attacks by a predator presumably disrupt the attacked prey school (Camphuysen, 2011). Thus, we expected that mackerel would try to escape to deeper waters when attacked by plunge diving gannets. Hence, successive dives by an individual gannet should result in increasing dive depths. In a few cases we could observe this scenario but in many more cases the dive depth of successive dives remained the same or was even lower. We assume that this tendency towards shallower dives by the gannets was due to the mackerels' escape burst speeds which could only be maintained in the warmest surface water (i.e. that the mackerel tried to stay in the uppermost water level because of the water temperature), or because the school of fish were also being attacked from below, impeding escape to deeper water. During ship-based seabird surveys in the Gulf of St. Lawrence from 2007 to 2009, we observed that a high proportion of foraging northern gannets were indeed associated with marine mammals, particularly dolphins, such as the Atlantic White-sided Dolphin (*Lagenorhynchus acutus*, NG unpubl. data). Off Newfoundland, Davoren et al. (2010) found a closer

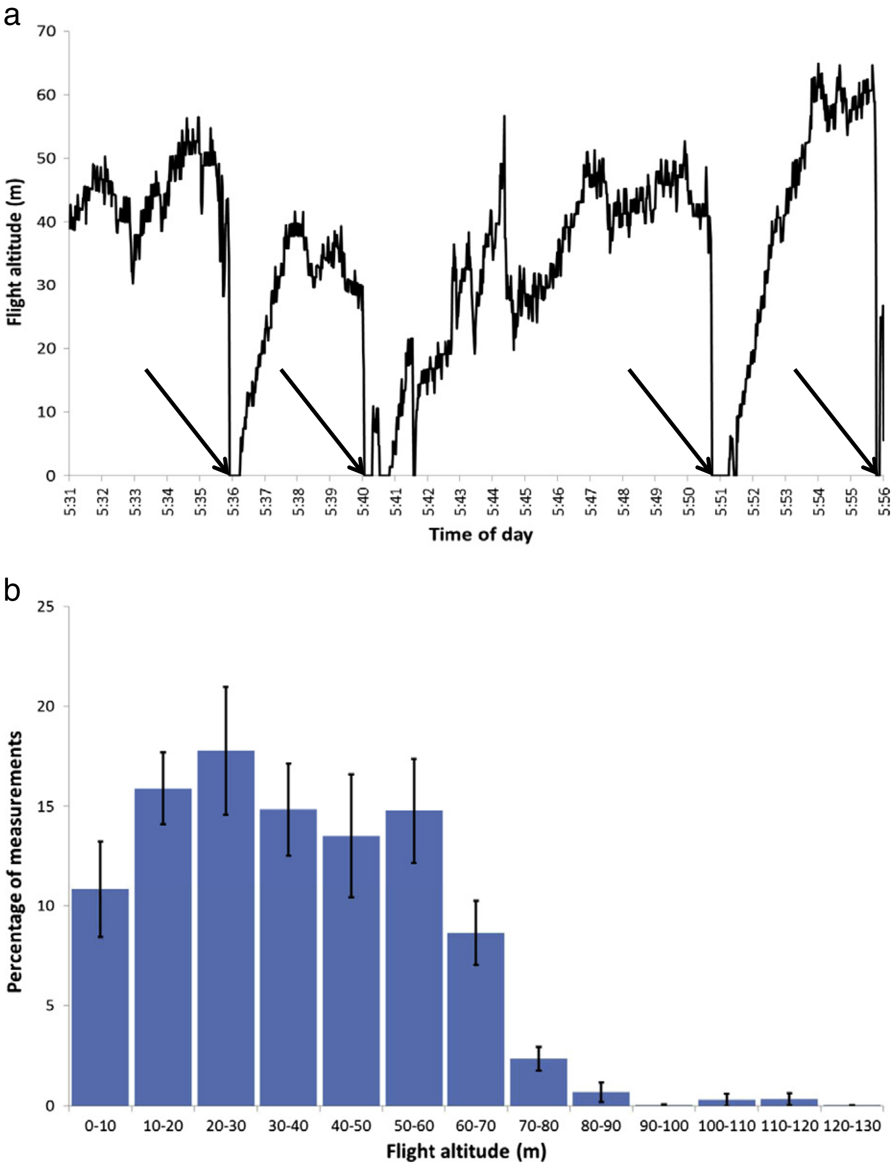

Fig. 3. Flying behavior of northern gannets from Bonaventure Island in July 2007. a) Flight altitude examples (25 min) for one individual. Dives are indicated by arrows; other approaches to (almost) 0 m were not related to dives. b) Flight altitudes during foraging; n = 36,389 measurements from 7 individuals. Vertical lines indicate standard errors.

spatial association between northern gannets and foraging marine mammals than with their primary prey (capelin).

Apart from the general abundance and the energy density of prey, its availability is a crucial feature for the predator. Mackerel is mostly distributed in the upper 10–15 m of the water column during summer in the southern Gulf of St. Lawrence as its thermal preferences do not allow it to go below the thermocline (Grégoire, 2006; Sette, 1950). In contrast, herring is associated with colder and deeper water. Thus, mackerel might be particularly available in the water depths which are exploited by plunge-diving northern gannets. Darbyson et al. (2003) sampled mackerel and herring with mid-water trawling in water depths of 3 to 24 m in the southern Gulf of St. Lawrence in June and found high catch rates for both herring and mackerel. Thus, herring is probably similarly available in water depths used by diving gannets, which is supported by its high level of importance in the diet of the breeding gannets from the Bonaventure colony over the years (Fig. 1). Yet herring schools may well have better escape options than mackerel by being able to move to depths below the thermocline. The thermocline may be an important foraging habitat for diving seabirds by concentrating prey at a specific depth (Kokubun et al., 2010; Ropert-Coudert et al., 2009b).

Besides its vertical distribution, prey swimming speed also influences availability for the predator. Mackerel and herring possess similar swimming capabilities (He and Wardle, 1988) being considerably faster than most other marine fish species. The probability of a successful attack is highly influenced by the burst speed of the prey. Atlantic mackerel has the highest recorded burst speed (Videler and Wardle, 1991) and reaches up to 5.50 m or 18 body lengths per second (He, 1993; Wardle and He, 1988). The high acceleration and powerful impact of the dives of the northern gannet likely enable it to exploit this large and powerful pelagic fish. Thus, mackerel represents a prototype of fast swimming and schooling pelagic prey. The foraging and particularly the diving behavior of gannets clearly respond to the characteristics of such a prey. In our study, we could show that the average dive depth was rather shallow and did not seem to require high flight altitudes to perform a successful dive. Strikingly, almost all recorded dives were V-shaped suggesting that a high acceleration attack at relatively low water depth is the most effective strategy for gannets preying on

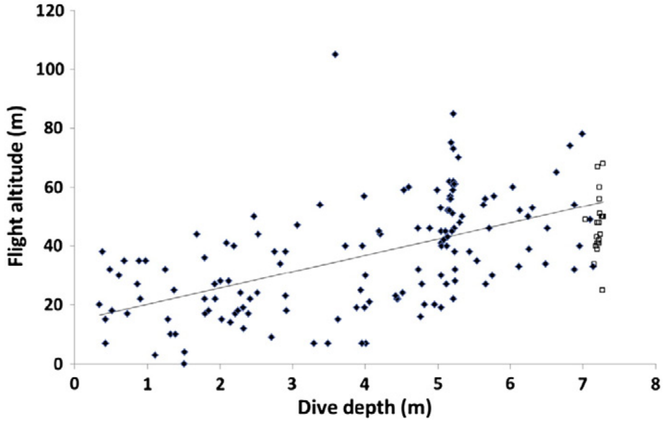

Fig. 4. Flight altitudes of northern gannets just before plunge-diving as a function of dive depth. Data originate from Bonaventure Island in July 2007; $n = 162$ measurements from 7 individuals; altimeters only. Open squares indicate measurements when the maximum values of the pressure sensor of the altimeters were reached; in these cases the effective dive depth remains unknown (for details see Materials and Methods); these data were not used for the regression line. Equation: $y = 5.545\times + 14.631$; $r^2 = 0.29$.

mackerel. If failure occurs, it seems to be more profitable for the gannets to invest in a new plunge dive compared to pursuing their prey underwater, despite the elevated cost associated with the take off following a plunge (Weimerskirch et al., 2000). This conclusion is also supported by the fact that the intervals between dives are short. The underwater pursuit of prey would result in U-shaped dives, which have proven to be a successful strategy applied by gannets when feeding on smaller and slower forage fish species, such as capelin (Garthe et al., 2000). It is also likely that at times gannets capture multiple similarly sized mackerel during a rapid succession of dives, as indicated in food loads sampled at the colony (WAM unpubl. Data).

4.3. Conclusions

Atlantic mackerel is both an attractive and also an elusive target, to which its predator, the northern gannet shapes its foraging behavior. This comprises adjustments regarding flight altitude as well as depth, frequency and specific shape of the dive. Mackerel is mostly distributed in the uppermost water column and thus in water depths that can be exploited by plunge-diving northern gannets. The high acceleration during the plunges and the apparent surprise attack from the air likely enables the gannets to capture this fast-swimming and large pelagic fish. (High) Flight altitudes are apparently mostly relevant for prey searching as low flight altitudes are obviously sufficient to reach dive depths at which mackerel were present. Dives often occurred frequently at short time intervals. These facts corroborate the idea that locating a suitable prey school is a key component for gannets when preying on mackerel and other pelagic shoaling fish species.

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