Flexible foraging tactics by a large opportunistic seabird preying on forage and large pelagic fishes

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ASTRACT: Generalist and opportunistic marine predators use flexible foraging behaviour to exploit prey bases that change in diversity and spatial and temporal distributions. Behavioural flexibility is constrained by individual cognitive and physical capabilities, age, reproductive condition, central place foraging, etc. To assess flexibility in the foraging tactics of a marine bird, we investigated the diets and foraging behaviour of the largest seabird predator in the North Atlantic Ocean. Northern gannets *Sula bassana* exploit a broad spectrum of pelagic prey that range in mass by more than two orders of magnitude. We investigated their foraging activity at their largest offshore colony in the western Atlantic during 1998-2002, when they preyed primarily on shoals of spawning and post-spawning capelin *Mallotus villosus*, a small forage fish (~15 grams), and also on a much larger pelagic fish, post-smolt Atlantic salmon *Salmo salar* (~200 grams). Inter-annual dietary variation is associated with gannet and prey fish distributions. Landings of capelin at the colony by gannets were correlated with returns of larger foraging flocks from inshore, whereas landings of Atlantic salmon were associated with smaller flocks returning from offshore. Maximum foraging trip distances ranged from 20 – 200 km and averaged 57 ± 12 (SE) km, consistent with distances to inshore capelin aggregations. When capelin abundance was low (2002), more gannets foraged offshore, preyed on large pelagic fishes (mostly Atlantic salmon), and exhibited greatest dietary diversity. Though the outbound portions of foraging trips were more sinuous than inbound routes, individual gannets exhibited general fidelity to foraging sites. These large avian predators used flexible foraging tactics to adjust to changing prey conditions and to generate longer-term strategies to take advantage of diverse trophic interactions over a range of ocean ecosystems.

41 KEY WORDS: Foraging tactics · seabirds · forage fishes · diets · capelin · gannet · salmon ·

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46   INTRODUCTION

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48   Predators behave opportunistically to take advantage of changing prey and environmental

49 conditions. Many apex marine predators exhibit flexible foraging behaviour to exploit shifting prey

50 diversity and their changing spatial and temporal distributions (Croxall 1987, Bowen et al. 2006,

51 Watanuki et al. 2008). This behavioural flexibility is mediated by the decision-making of individual

52 predators each being constrained by its own cognitive and physical capabilities. Individuals bring

53 both transient and steady-state behavior to navigate their daily lives in dynamic marine

54 environments (Ollason et al. 2006). Breeding seabirds are further constrained by working to meet

55 the increasing energy demands of offspring while foraging from a fixed colony-site (Orians &

56 Pearson 1979)

57   Among large seabird predators, gannets employ flexible tactics to capture a variety of ephemeral

58 pelagic prey that can vary in mass from tens to many hundreds of grams (Montevecchi & Berruti

59 1991, Bunce 2000, Hamer et al. 2001). They also scavenge discards and offal from fishing vessels

60 (Burger & Cooper 1984, Garthe et al.1996). The largest gannet and the largest North Atlantic

61 seabird, the northern gannet (*Sula bassana*) delivers loads of from one to tens of prey (numbers

62 inversely related to prey mass that range from < 10 to > 500 grams) to rapidly growing, lipid-

63 loading chicks during a 13-week nestling period (Montevecchi et al. 1984). Chicks are fed primarily

64 large oily pelagic fish (e.g. mackerel *Scomber scombrus*, herring *Clupea harengus*) and at times

65 small forage fishes (e.g. capelin *Mallotus villosus*, sandeels *Ammodytes* spp.; Nelson 1982,

66 Montevecchi & Myers 1995, Garthe et al. 2007b).

67   Associated with a centennially anomalous cold water perturbation in the northwest Atlantic

68   during 1991 (Drinkwater 1996), gannets switched from preying on large migratory, warm-water

69   species (mackerel, Atlantic saury *Scomberesox saurus*, short-fined squid *Illex illecebrosus*; their

70   dominant prey during the late 1970s and 1980s) to cold-water fishes, primarily capelin, for longer

71   than a decade (Montevecchi 2007). Throughout this period, gannets have successfully provisioned

72   offspring, and their populations in the Northwest Atlantic have grown substantially (Chardine

73   2000).

74   In this paper, we integrate different levels of dietary and behavioural analyses to highlight the

75   foraging tactics of gannets, when preying on small forage fishes (capelin) and large pelagic fishes

76   (Atlantic salmon *Salmo salar*) during 1998-2002. Inter-annual variation in diets is compared with

77   concurrent avian and capelin distributions and densities obtained from vessel surveys during 1998-

78   2002. Off the northeast Newfoundland coast, capelin shoals exploited by avian and mammalian

79   predators often persist in fixed locations (Davoren et al. 2003b), and we assessed the gannets'

80   fidelity to foraging areas (e.g. Hamer et al. 2001, Watanuki et al. 2003) by comparing the directions

81   and distances of successive trips by the same individuals equipped with compass loggers. The

82   returning directions and sizes of foraging flocks were related to landings of capelin and of large

83   pelagic fish, mostly Atlantic salmon, and foraging trip patterning was explored by comparing the

84   fractal dimensions of outbound and inbound routes. Because seabirds often use different foraging

85   strategies when provisioning themselves *versus* when gathering food for offspring (Weimerskirch et

86   al. 1994, Davoren & Burger 1999), we compared the distances from the colony of terminal diving

87   bouts on a foraging trip (chick provisioning dives) with the distances of previous diving bouts

88   (presumably those for self-provisioning). We use this information to assess the flexible foraging

89   tactics used by the largest seabird predator in the North Atlantic.

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91   METHODS

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93   **Study site and period**. Research was carried out on Funk Island (49° 45' N, 53° 11' W), a small

94   (800 x 400 m) flat granite rock in the northwest Atlantic (Montevecchi & Tuck 1987), about 50 km

95   off the northeast coast of Newfoundland (Fig. 1), Canada. The island has an estimated population of

96   9,800 pairs of northern gannets (Chardine 2000) and is the fourth largest and most oceanic of the six

97   gannet colonies in North America. Researchers were on the island.from 4 - 17 August 1998, 26 July

98   - 5 August 1999, 5 - 13 August 2000, 30 July - 7 August 2001, and 6 - 13 August 2002.

99   **Diet sampling**. Food samples were obtained by approaching roosting gannets that often

100   regurgitated as they moved away from researchers (Montevecchi & Myers 1995). Samples were

101   also obtained from birds captured for data logger attachments and removals and from discarded

102   regurgitations and scraps in the colony. While there are likely differences between samples

103   collected in roosts and in the colony, samples from these sources are comparable (WAM unpub

104   data), and we opted to minimize disturbance to breeders by collecting regurgitations at roosts well

105   outside the colony. Regurgitated prey were identified to species, fresh fish samples were measured

106   for total length, and very fresh fish were weighed with spring scales. Prey landings are presented as

107   percentages of total regurgitations during each year.

108   **360° scans for flocks returning to colony**. From the island's highest point near the northeast

109   end, using compass-directional binoculars, the numbers of gannets in incoming flocks were

110   recorded within each 45° sector during 360° scans at various times of day. Binoculars were held

111   with the horizon at mid-diameter as the observer slowly scanned the sector for 1-min. Three full

112   rotations (24 min) comprised a scan session. Wind speed and direction were recorded with a hand-

113   held anemometer and the directional binoculars at the outset of scans and if conditions changed also

114   at the end. Two or three observers counted each year, usually working in pairs with one person

115   counting and the other recording; counts were recorded on a portable tape recorder when a single

116   observer counted. Because observers worked in multiple years most often in pairs of the same

117   observers, and because data were analyzed in 90° quadrants, influences of individual differences

118   were minimized. Frequencies of returning foragers within 90° quadrants were compared on daily

119 and annual bases with chi square tests, and numbers were plotted as percentages of total counts.

120 Comparisons of the percentages of gannets returning from inshore (135° to 315°) and offshore (315°

121 to 135°) directions were correlated with the numbers of regurgitations of the four most common

122 prey (capelin, Atlantic salmon, Atlantic saury, herring) landed in the colony on the same day. The

123 average sizes of flocks returning from inshore and offshore were compared with one-way analysis

124 of variance.

125 **Vessel surveys and spatial distribution calculations.** A meso-scale (1 – 800 km) survey

126 aboard the 23 m Canadian Coast Guard research vessel *Shamook* was run over 5 days within avian

127 foraging ranges and prime capelin spawning and staging areas to the south and west of the Funk

128 Island during July and August 2000 – 2002 (Fig. 1). Nine east-west cross-shelf transects 9 km apart

129 on north-south axis were run during the 12 h d^{-1} that the *Shamook* operated. Surveys were

130 periodically interrupted to identify the species composition of acoustic signals using a modified

131 shrimp trawl. The majority of fish sampled by mass were capelin in each year (2000: 96%; 2001:

132 71%; 2002: 55%).

133 During transects, vessel speed (11 - 16 km/h) was held constant and signals of prey species were

134 recorded continuously using two hydroacoustic systems. For the 2000 survey, a Simrad EQ100

135 system was operated through a hull-mounted single 38 kHz beam transducer that operated at 1 ping

136 per sec over a range of 250 m with a bandwidth of 0.4 – 0.6 ms. The transducer was at a depth of 3

137 m and acoustic signals were reliable at 8 m and deeper. The sample depth of the acoustic system (8

138 - 250 m) and vessel speed (14 - 16 km/h) were held constant throughout all surveys. Echograms

139 were continuously printed and the relative abundance of fish was quantified by estimating the

140 percent cover of the prey image in each 250 m by 10 m vertical bin (Piatt 1990). An index of

141 percent cover of prey in each bin was estimated from 0 (no prey) to 9 (near-saturation). Values were

142 squared before analysis (0 - 81) to account for the non-linear change in sounder intensity relative to

143 fish school density (Piatt 1990), giving a relative measure of acoustic prey abundance.

144   During 2001 and 2002, a BioSonics DT 6000 hydroacoustic operated through a 38 kHz split-

145   beam transducer in a towed body. The transducer had a 2-way beam angle of 22.671 dB and the

146   echo sounder was operated at 1 ping per sec, a bandwidth of 5.1 kHz and a pulse duration of 0.4 ms.

147   The transducer was at a depth of 5 m and the upper resolution of the acoustic signals (8-10 m) was

148   well within the diving range of northern gannets to 20 m (Garthe et al. 2001). Vessel speed was

149   maintained between 11 - 14 km/h. Raw high-resolution acoustic data (volume backscattering

150   coefficients, s_v) were recorded continuously and used to derive a capelin biomass estimates (g m^{-2};

151   see Davoren et al. 2006). Variability in the quality of hydroacoustic systems used and data

152   processing techniques precluded comparing capelin abundance among years but allowed inter-

153   annual comparisons of distributional patterns.

154   During acoustic transects, seabirds were counted continuously by a single observer in a 90° arc

155   out to 300 m from the bow to the port side of the ship using standard strip methods (Tasker et al.

156   1984). Counts with behavioural descriptions (on water, flying, feeding) were entered on a laptop

157   computer with counting software (D. Senciall, Birds & Beasty Counter, 1998, Fisheries and Oceans

158   Canada, version 1.0) connected to the vessel's navigational system. A latitude-longitude position

159   was appended to each sighting.

160   **Capture of birds**. Adult gannets with 4– 6 week old chicks in their nests were captured with a

161   telescoping noose pole from a small portable blind to minimize disturbance to neighbouring birds.

162   We avoided capturing pairs with younger poikilothermic chicks as this was more disturbing to

163   parents, and because parents with older chick had greater energetic demands. Pairs on the colony

164   periphery were used to avoid disruption to the interior colony; to reduce possible sampling bias in

165   potential differences between peripheral and interior nesting pairs, we captured birds in the third or

166   fourth rows from the colony edge. Breeding success was high at the sites where we worked (WAM,

167   SG per obs). Birds were captured, marked on the head and neck with colored markers for

168   identification from a distance, equipped and banded with USFWS bands issued by the Canadian

169   Wildlife Service usually within 5 – 10 min. We held the necessary university, provincial and federal

170 permits, and birds were treated in accordance with the guidelines of the Canadian Council on

171 Animal Care.

172   **Data loggers.** Four types of data loggers were used on 24 breeding adults for a total of 49 foraging

173 trips. Durations of attachments varied from 27 to 75 h. Lotek LTD_100 tags were attached to seven

174 gannets that made 9 foraging trip in 1999. Dall'Antonia (DA) activity-depth recorders were

175 deployed on seven gannets that completed 16 foraging trips in 2001, DA compass loggers were

176 attached to seven gannets that completed 14 foraging trips in 2002, and Earth & Oceans compass

177 Tlog devices (length = 65 mm, diameter = 16 mm, 14.5 g, 2 MB memory) with horizontal direction

178 recorders were also used to track 10 successive foraging flight paths of three gannets in 2003 (2)

179 and 2004(1). The data recording intervals set on each bird-borne device (below) allowed continuous

180 recording for up to 3 - 4 days, and the weight of each device weighed $\leq$ ~1% of a gannet's body

181 mass. With the exception of the Lotek LTDs (see below), all loggers were attached with Tesa® tape

182 to feathers on the lower back about 5 cm above the uropygeal gland or atop four central tail

183 feathers. When an equipped gannet was recaptured, devices were removed quickly, and data were

184 downloaded onto a laptop computer.

185   *LTD loggers*: LTD_100 tags (Lotek Marine Technologies, St. John's, Newfoundland, Canada;

186 57 mm length, 18 mm diameter, 16 g, 1 MB memory) were attached with Tesa ® tape to two plastic

187 bands on one leg. Activity was inferred from records every 30 s of thermal fluctuations (following

188 Wilson et al. 1995, Garthe et al. 1999); dive depth data are reported elsewhere (Garthe et al. 2000,

189 2003).When temperature indicated sea surface temperature (SST) and remained constant, the bird

190 was considered to be swimming or resting on the water with the logger submerged. When tempera-

191 ture varied slightly within the range of recorded air temperature (some degrees higher than SST),

192 the bird was considered to be flying. When the temperature varied in higher ranges (as the logger

193 was warmed by the bird's and chick's body heat and often solar and terrestrial radiation) and with

194 other diurnal thermal rhythms, the bird was considered to be in the colony (i.e. at the nest most of

195   the time). These occurrences were validated by observations using a spotting scope from outside the

196   colony to check when marked birds carrying loggers were present at nest-sites (Garthe et al. 2003).

197   *DA activity-depth loggers*: Dall'Antonia devices (80 mm length, 22 - 31 mm width, 13 - 18.5

198   mm height, 28 g, 128 kB memory) recorded activity (from a motion sensor) every 6 s and depth

199   (from a pressure sensor) every 4 s (Dall'Antonia et al. 1993, Benvenuti et al. 1998). In previous

200   research (e.g. Garthe et al. 2000, 2007), we have demonstrated that U-shaped dives for capelin and

201   V-shaped dives for large pelagic fishes like post-smolt Atlantic salmon are typically in excess of 4

202   s, and we are confident that we recorded the foraging dives by the gannets in our study. The activity

203   sensor (a 5 mm diameter modified microphone membrane) was activated by flight signals produced

204   by accelerations and/or body vibrations, caused by wing beats. During diving, signals are produced

205   by wing and/or foot propulsions. Flight activity was identified on graphs as regular high-level

206   deflections, easily distinguishable from the low-frequency signals produced when the bird is on the

207   sea surface and from weak irregular or absent signals when the bird is at the nest. Devices were

208   attached either to feathers on the lower back about 5 cm above the uropygial gland or the four

209   central tail feathers with Tesa ® tape.

210   *Compass loggers*: DA compass loggers (length = 93 mm, width = 22 - 33 mm, height = 15 - 20

211   mm, 33 g, 128 kB memory) with direction recorders, flight and pressure sensors and one with a

212   flight recorder but no pressure sensor were used to track flight directions and activities (Benvenuti

213   et al. 1998, 2001). Intervals between successive recordings were 6 – 8 s for both the compass and

214   flight sensor and 4 s for the pressure sensor. Used in conjunction with satellite tags, these loggers

215   indicated similar general foraging areas (Falk et al. 2001). Earth & Oceans compass Tlog devices

216   (length = 65 mm, diameter = 16 mm, 14.5 g, 2 MB memory) with horizontal direction recorders

217   were also used to track foraging routes. Intervals between successive directional records were 6 s.

218   **Foraging routes, ranges and diving activity.** Twenty-four compass routes from 10 parental

219   gannets were plotted; one of these birds had four consecutive foraging routes recorded, three had

220   three, five had two, and one had one route recorded. Foraging routes and ranges were reconstructed

221 by multiplying an estimated average flight speed of 14.9 m s^{-1} (54 km h^{-1}; Pennycuick 1997) by the

222 summed flight time along outbound and inbound foraging routes, time on water, a corrected

223 magnetic declination (-28°) and wind influences (wind speeds and directions were recorded at the

224 colony (above) and also obtained from the Environment Canada weather station at Pool's Island

225 near the mouth of Bonavista Bay and within the gannets' foraging range). Potential sources of error

226 include imperfect alignment of a device with a gannet's body axis, drift when birds are on water and

227 variable flight speeds in different wind conditions (Grémillet et al. 2004; Fifield & Montevecchi

228 unpubl data). For the seven gannets equipped in 2002, we estimated distances to all diving bouts

229 (groups of dives, excluding those shallower than 1 m, separated by long intervals of flying or

230 swimming) and from the last dives of a foraging trip to the colony. Points of maximum trip distance

231 were mapped for all 10 compass-equipped birds by extrapolating distances and directions from

232 Funk Island on a 1:250,000 map of the northeast Newfoundland coast.

233   Scanned images of foraging trip routes during 2002 printed on 27.9 x 43.2 cm paper were

234 subjected to box-counting fractal analysis using the HarFa Harmonic and Fractal Image Analyzer

235 (www.fch.vutbr.cz/lectures/imagessci/download/harfasp.html). Fractal dimensions of the a) entire

236 route, b) outbound route to the most distant point and c) to the last or terminal dive, d) inbound

237 route from the most distant point and e) from the last or terminal dive. Fractal dimensions of b

238 versus d and of c versus e were compared with t-tests for related samples and with binomial tests of

239 differences (Siegel 1957). We describe the number and temporal and spatial patterning of diving

240 bouts performed throughout trips; depth profiles of different diving patterns are reported by Garthe

241 et al. (2000). We also assessed the consistency of foraging route directions on successive trips by 10

242 individual gannets.

243

244   RESULTS

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246   **Prey landings**. Capelin comprised 77 % of the prey loads returned to the colony, ranging from

247   51 to 100 % on per annum bases from 1998 – 2002 (Table 1). Atlantic salmon was the next most

248   common prey with high annual variation ranging from 0 to 34 % of landings. Atlantic saury, herring

249   and mackerel made up relatively minor dietary components. During 1998 – 2000, capelin

250   comprised more than 80 % of prey landings, though the situation was somewhat different in 2001

251   and very different in 2002, when Atlantic salmon made up significant dietary components and when

252   dietary diversity was greatest (Table 1). Gannet landings of capelin contained six to 20 fish

253   compared to landings of salmon that contained one to three much larger fishes.

254   **Directions and sizes of returning flocks and prey landings at colony.** The flight directions

255   of incoming gannets are shown in Fig. 2. In all years, most birds returned to the colony from

256   inshore foraging sites southwest of the island, except during 2002 when most returned from

257   offshore sites north of the colony (χ^2 = 902.7, df = 12, p < 0.001).

258   Comparisons of the directions of returning birds and proportions of prey species landed at the

259   colony revealed significant relationships between inshore returns and landings of capelin (Y =

260   0.49X + 38.5, n = 12, R^2 = 0.33, p = 0.049) and between offshore foraging and landings of Atlantic

261   salmon (Y = 1.15X+ 19.1, n = 12, R^2 = 0.60, p = 0.003; Fig. 3). No relationships for other common

262   prey (herring, Atlantic saury) were detected (p > 0.05). The sizes of flocks returning from inshore

263   were significantly larger than those returning from offshore in each year and in all years combined

264   (Fig. 4). Flock sizes were lowest in the year (2002) when capelin was least abundant.

265   **Distributions of gannets along vessel transects.** Observers on research vessels noted consistent

266   general travel routes of gannets to and from Funk Island from areas southwest of the colony.

267   Capelin abundance was substantially lower in 2002, showing a 7-fold decrease from 2001 (Fig. 5;

268   Table 2). The number of gannets per km along the survey route was also significantly lower during

269   2002, being less than a third of those recorded in 2000 and 2001 (Table 2). Interestingly, 2002 was

270   the only year when more foragers returned from offshore areas north of the island (Fig. 2) and the

271   year when most Atlantic salmon were landed at the colony (Table 1).

272   **Foraging trips, range and area.** Foraging trips consisted of alternated series of flights and stops

273   of variable durations that include dives and sitting on the water, with one or two longer flights

274   performed most often at the beginning and end of the trips. Most diving activity occurred during the

275   middle segments of foraging flights (χ^2 = 48.26, df = 4, p < 0.001; Fig. 6), indicating that there was

276   little foraging activity in close proximity to the colony. Colony departures occurred between sunrise

277   and sunset with no apparent diurnal concentration (see also Garthe et al. 2003). Foraging trip

278   durations of birds with compass loggers were variable, ranging from 3.3 to 26.2 hr, with mean and

279   median durations of 9.5 ± 5.8 (± SD) and 8 hr (Table 3). Birds that departed in the morning usually

280   returned before sunset, whereas those that left in the afternoon usually remained at sea overnight

281   and returned the next morning.

282   On foraging trips, gannets with compass loggers spent about half (49 %) of the daylight time

283   away flying, with a range from 31 to 71 %. Birds remained on the water and did not fly after dark.

284   Total flight durations ranged between 1.9 and 13.7 hr, with mean (± SD) and median durations of

285   3.8 ± 3.0 and 2.9 hr. Time spent flying increased with trip duration (r = 0.90, n = 14, p < 0.001),

286   indicating more travelling and potentially more searching on longer foraging trips. The more birds

287   dived the longer they rested on water after diving (r = 0.82, n = 18, p < 0.001 for first dive bouts,

288   and for all dive bouts r = 0.53, n = 75, p < 0.001).

289   Based on a flying speed of 54 km h^{-1} (Pennycuick 1997), values for maximum outbound

290   distances from the colony (foraging range) on individual trips during 2002 averaged (± SD) 61 ± 44

291   km (n = 14 trips; median and mode = 50 km and ranged from 30 - 200 km (Table 4, Fig. 7).

292   Estimated flight distances between the colony and the first feeding site ranged from 10 - 193 km.

293   Foraging ranges were shorter in 2003 and 2004, when capelin again predominated gannet landings

294   (Montevecchi 2007), and averaged 41± 21 km (n = 10 trips; Table 4).

295   The mean number of activity changes from swimming to flying and vice versa was significantly

296   greater on outbound (5.3) than on inbound flights (2.8; t = 2.986, n = 24, p = 0.007). The mean (±

297   SD) fractal dimensions of outbound flights (1.29 ± 0.12) were not significantly different from those

298   of inbound ones (1.24 $\pm$ 0.13; t = 0.12, n = 14, p > 0.05) nor were the mean ($\pm$ SD) fractal

299   dimensions foraging routes out to (1.26 $\pm$ 0.14) and back from terminal dive bouts (1.18 $\pm$ 0.15; t =

300   0.12, n = 14, p > 0.05). Yet, 11 of 14 outbound routes had higher fractal dimensions than

301   corresponding inbound routes on the same trips by the same individuals (binomial test, p = 0.029),

302   and 10 of 12 routes to the terminal dive bout had higher fractal dimensions than their corresponding

303   inbound routes (binomial test, p = 0.019).

304   There was no significant difference in the average ($\pm$ SD) number of dives during the last or

305   terminal diving bouts of a trip (5.1 $\pm$ 4.1, range = 1 – 16) compared to previous diving bouts on the

306   same trip (4.7 $\pm$ 7.2, range = 1 – 30; F = 0.61; df = 1,31, p > 0.05). Eleven of 12 terminal diving

307   bouts involved multiple dives compared to 10 of 19 previous diving bouts on the same trip (χ^2 =

308   5.13, df = 1, p = 0.024). On a foraging trip, the time spent resting on the water after terminal diving

309   bouts (20.8 $\pm$ 23.0 min) was about half that than after previous diving bouts (36.8 $\pm$ 31.5 min)

310   though owing to variability this tendency was not statistically significant (t = 0.157, df = 1,12, p >

311   0.05).

312   Individual gannets returned to the colony from all directions, ranging from 30° t 355° (Table 4).

313   Consistent with the scan data in 2002, mean ($\pm$ SD) and median return directions of foraging flocks

314   were 187° $\pm$ 100° and 200°. Six of seven successive trips were within 90° of one another, and the

315   average difference in flight direction between successive foraging trips by the same individual was

316   45° $\pm$ 17° (Table 4). Again in 2003 and 2004, mean and median return directions of foraging trips

317   were from the south at 181° $\pm$ 78° and 192°. As well, six of seven of foraging trips by three

318   individuals tracked during 10 foraging trips a were also within 90° of one another, averaging 46° $\pm$

319   35° directional differences between successive foraging trip (Table 4). Combing data for the 10

320   compass-equipped gannets, the average and median directions of returning foraging flocks were

321   191° $\pm$ 92° and 200°, and the overall mean angular deviation between 14 successive foraging trips

322   by these individuals was 43° $\pm$ 40°, with a median angular difference between successive trips of

323   34°.

324

325   DISCUSSION

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327   **Responses of gannets to device attachments**

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329   Birds were likely influenced by device attachments. Yet as in our other studies that have

330   employed some of the same attachments on gannets in this same colony, there was little evidence to

331   indicate deleterious effects (Garthe et al. 2000, 2003, 2007a). Following attachments, birds returned

332   quickly to nest-sites, and parental behaviour, feeding and chick care and condition appeared normal.

333   The foraging trip durations of equipped birds were not significantly different from those of their

334   unequipped mates (Garthe et al. unpubl.). Of 24 birds equipped with loggers, only three were not

335   recaptured (two of these were at sea when we had to depart the island due to weather), indicating

336   that the stress related to capture, handling and attachments was surmountable. The other bird that

337   we did not recapture had an approximately 8-day old chick that was knocked from the nest and

338   died. This was the only chick mortality observed during the study, and the only time we equipped a

339   bird with a chick this young.

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341   **Prey exploitation**

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343   Following a centennially-significant cold water perturbation in1991 (Drinkwater 1996), large

344   warm-water pelagic fishes and squid did not migrate into the region and the dietary diversity of

345   gannets decreased markedly (Montevecchi & Myers 1995). During 1998-2002, the gannets preyed

346   mostly on capelin, which are among the smallest prey that they exploit, often carrying 20 or more in

347   a single load. Most capelin were spent females and males, with very few gravid females. Male

348   capelin are larger than females, but gravid females have the highest energy density (Montevecchi &

349   Piatt 1984) and are the preferred prey of common murres (*Uria aalge*; Davoren & Montevecchi

350 2003). The large multi-prey loading gannets do not discriminate among these small forage fish.

351 Rather, the gannets' landings likely reflect capelin availability (determined by temperature-

352 dependent spawning times) within the constraints of their maximum 20 m dive depths and 200 km

353 foraging ranges.

354   When capelin stocks decreased, gannets landed substantial numbers of Atlantic salmon and

355 other large pelagic fishes. Salmon were a minor prey the gannets' diets during the 1980s and 1970s

356 but increased significantly after an anomalous cold-water perturbation in 1991 (Montevecchi et al.

357 2002, Montevecchi & Cairns 2003, Montevecchi 2007). Due to shifting pelagic food webs during

358 the 1990s, the gannets' prey options were fewer and their diet breadth narrowed.

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360   **Foraging tactics and foraging sites**

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362   Large seabird colonies occur in proximity to robust predictable prey fields, giving individuals

363 opportunities to learn about productive foraging sites and to use memory-based foraging strategies

364 (Hamer et al. 2001, Davoren et al. 2003b). Gannets from the large offshore Funk Island colony

365 foraged consistently inshore when persistent shoals of capelin provided the bulk of their prey.

366 Common murres from Funk Island and other large predators also forage consistently on these

367 persistent inshore shoals of capelin, i.e. hotspots (Davoren et al. 2003a). During 2002, when these

368 shoals were reduced in abundance and dispersed, more gannets foraged opportunistically offshore

369 from the colony and exploited post-smolt Atlantic salmon.

370   Individual gannets showed consistency in successive foraging trips, returning to areas where they

371 were recently successful (Benvenuti et al. 1998, Irons 1998, Hamer et al. 2001, Watanuki et al.

372 2003). Fidelity to feeding areas on successive foraging trips is indicative of memory-based foraging

373 tactics. In the long-term such tactics could facilitate the development of behavioural "traditions" or

374 hinterlands as has been demonstrated in other studies of seabird foraging ecology (Furness &

375 Birkhead 1984, Cairns 1989, Grémillet et al. 2004; Garthe et al. 2007a).

376   Generally, the gannets used a mixed foraging strategy that involved a general fidelity to inshore

377   areas and some wider offshore foraging when capelin were less available and when post-smolt

378   Atlantic salmon moved through the area. Flocks returning from inshore sites were significantly

379   larger than those from offshore, suggesting that it might also have been easier for gannets to exploit

380   information (local enhancement) from conspecifics foraging inshore on concentrated shoals of

381   capelin (Wittenberger & Hunt 1985, Fleming & Greene 1990). Larger inshore flocks are likely

382   related to the high numbers of gannets foraging there, giving greater opportunity to return to the

383   colony in linear aggregations thereby gaining aerodynamic and energetic benefits. Like other

384   opportunistic generalists (Watanuki et al. 2004), the gannets integrated a mixed array of flexible and

385   repetitive tactics to engage changes in prey availability driven by dynamic oceanographic

386   conditions.

387

388   **Foraging trip patterning**

389

390   Gannets flew for about half of their daylight time at sea and stayed on the water at night (see also

391   Hamer et al. 2001, Garthe et al. 2003). The longer birds were at sea, the more they flew and the

392   farther they traveled. Gannets tended to make relatively long initial and final flights from and to the

393   colony in the order of 50 to 60 km. Outbound flights were interrupted more by time on the water

394   than were return flights. Following more intense diving bouts, gannets spent more time on the

395   water, likely for digestion, resting and self-maintenance (Diamond et al. 1986); very long pauses

396   likely follow self-feeding bouts and shorter ones followed by direct returns to the colony are

397   indicative of chick-provisioning activity (see also Ropert-Coudert et al. 2004).

398   Prey depletion (Birt et al. 1987) and conspecific interference hypotheses (Hunt et al. 1986,

399   Lewis et al. 2001) predict longer foraging ranges at large colonies. Maximum foraging distances of

400   birds carrying compass loggers ranged between 10s and 100s of km with ranges that extended up to

401   262 km (Garthe et al. 2007a.). These ranges are similar to those of gannets nesting in Shetland

402 (Garthe et al. 1999) but shorter than those at larger colonies in the North Sea (Hamer et al. 2000,

403 Lewis et al. 2001) and Gulf of St. Lawrence (Garthe et al. 2007a). Substantial inter-annual changes

404 in foraging ranges from a single colony are also associated with major shifts in prey bases (Garthe

405 & Montevecchi 2007).

406

407   **Coping with changing prey conditions**

408

409   Gannets use flexible tactics to cope effectively with changes in prey availability and diversity

410 over seasonal, annual and decadal scales. In the northwest Atlantic, the prey landings of gannets

411 shifted from a predominance of large migratory warm-water pelagic fishes and squid during the

412 1970s and 1980s, to what appears to be a "default" diet of primarily small forage fish (capelin)

413 through to 2004 (Montevecchi 2007). Yet this major alteration in feeding ecology and diet has had

414 no negative influence on the gannets' breeding populations that have grown considerably during

415 these decades (Chardine 2000, pers. comm.).

416   Under lower availability of capelin (biomass, number of shoals) in 2002, gannets responded

417 by foraging farther offshore. This is evidenced by foraging locations and lower densities and total

418 numbers of gannets observed during the inshore vessel survey. Gannets caught more large pelagic

419 fishes, increasing dietary diversity during 2002. The single gannet equipped with a compass logger

420 that foraged offshore in 2002 exhibited the greatest effort of any bird in our study, i.e. highest

421 percentage of time flying (63 %) and most dives during a foraging trip (66 % higher than the next

422 highest effort). The gannets' ability to alter their foraging strategies (e.g. foraging location, prey-

423 type) under varying conditions (see also Watanuki et al. 2004) is essential for their success in a

424 dynamic pelagic environment.

425

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588 Table 1. *Sula bassana.* Percentages of regurgitations of each prey species in regurgitations
589 (numbers in parentheses) by gannets on Funk Island, 1998 - 2002
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591 _____
592 Prey/Year   1998   1999   2000   2001   2002   1998-02
593 _____
594
595 Capelin   84 (384)   87 (86)   100 (183)   72 (153)   51 (145)   77 (951)
596
597 Atl Salmon 1 (5)   0   0   25 (54)   34 (95)   12 (154)
598
599 Atl Saury   12 (56)   10 (10)   0   1 (3)   3 (9)   6 (78)
600
601 Herring   3 (15)   3 (3)   0   2 (4)   3 (8)   2 (30)
602
603 Mackerel   0   0   0   0   9 (25)   2 (25)
604
605 Totals   100 (460)   100 (99)   100 (183)   100 (214)   100 (282)   99 (1,238)
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620   Table 2. *Sula bassana* and *Mallotus villosus.* Number, aggregation scales and tracking scales of
621   northern gannets to capelin and the number, density, biomass estimates, and aggregation scales of
622   capelin within the survey area in 2000, 2001, 2002. A different hydroacoustic technique was used in
623   2000 (see Methods), so capelin biomass could not be quantified and compared with 2001 and 2002.
624   * = significant difference
625

	2000	2001	2002
No. gannets *1	685	962	220
% Flying	65	70	94
% Plunge diving	1	1	0
% Sitting on the water	34	29	6
Mean ± SE number of gannets per km *2	0.13 ± 0.03	0.10 ± 0.01	0.03 ± 0.01
No. capelin shoals	204	358	79
Mean capelin length (mm)	159.5	151.2	151.4
Mean capelin mass (g)	18.7	17.7	19.7
Mean capelin density (fish/m^2)	-	53.2	7.3
Total areas of the survey (x 10^6 m^2)	5,487	5,487	5,487
Estimated number of capelin (x 10^6)	-	291,942	39,821
Estimated biomass of capelin (t)	-	5,171	785
Survey Length (km)	610	431	373

626
627   *1 (χ^2 test: df = 4, χ^2 = 68.74, p < 0.0001); *2 (F = 5.963, df = 1020, p = 0.003)
628

Table 3. *Sula bassana.* Durations (hr) of compass logger attachments, foraging trips (and numbers of trips), and flight activity during each trip of 7 northern gannets rearing 4 to 6 week old nestlings on Funk Island during 2001.

Gannet	1	2	3	4	5	6	7
No. trips	2	3	2	2	2	2	1
Duration							
Equipment attachment	29.3	51.1	44.0	44.0	49.9	40.2	51.5
Trip 1	5.8	14.4	9.1	3.3	12.1	5.4	5.7
Trip 2	6.7	4.7	4.9	14.5	26.2	11.9	
Trip 3		8.0					
Flight Trip 1	2.7	4.6	2.9	1.8	2.7	2.8	3.6
Trip 2	2.7	2.9	1.9	5.1	13.7	3.2	
Trip 3		2.5					

Table 4. *Sula bassana.* Foraging trip directions and maximum distances (ranges) during first, second, third and fourth foraging trips by gannets equipped with compass loggers.

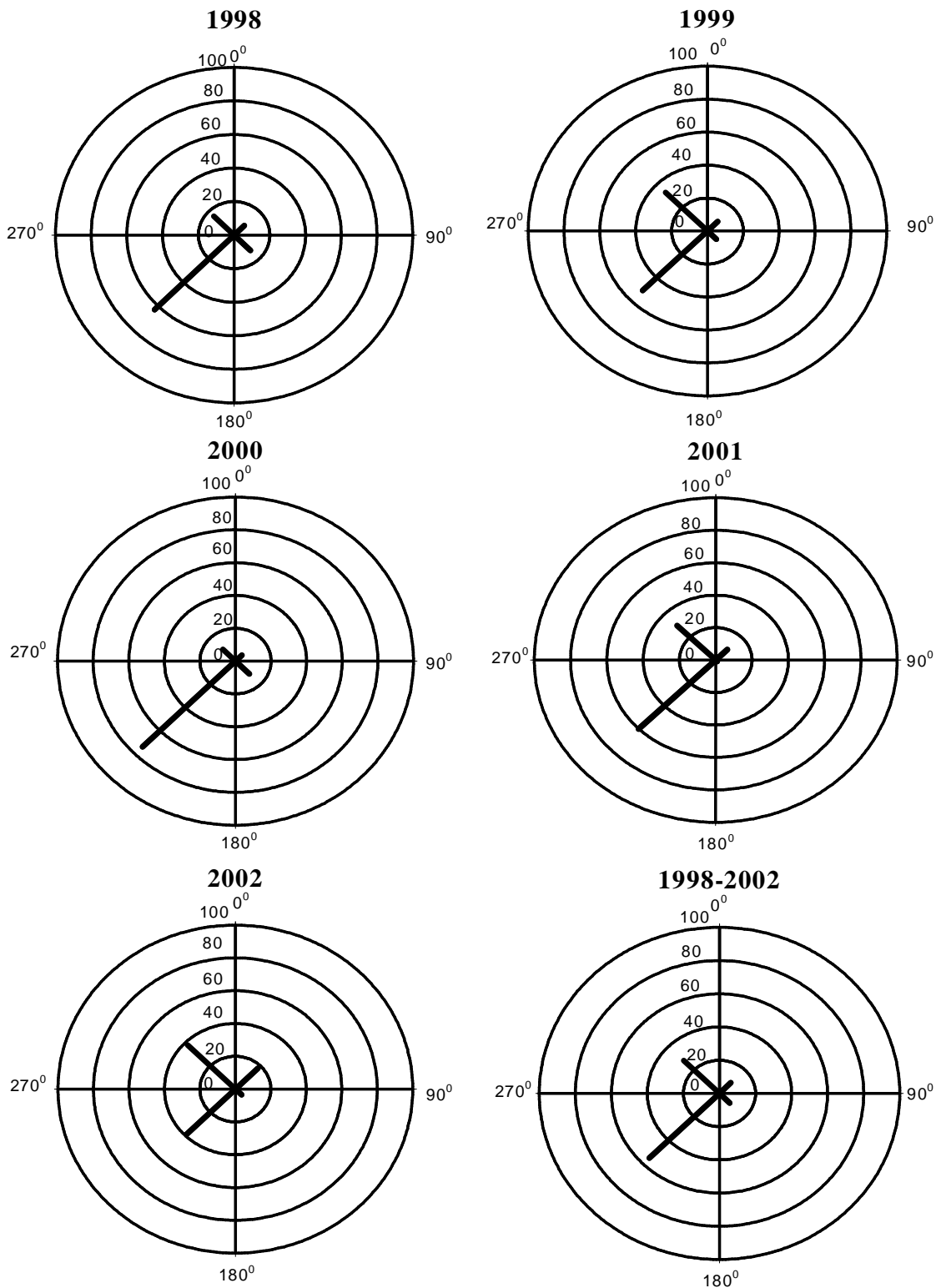| Gannet	Direction (^{o})				Maximum Distance (km)			
	1st	2nd	3rd	4th	1st	2nd	3rd	4th
2001								
1	200	190			50	50		
2	355	345	30		70	60	60	
3	205	190			40	30		
4	130	80			40	90		
5	205	340			30	200		
6	200	250			50	50		
7	40				40			
2003								
8	278	278	228		63	47	25	
9	173	222	199	185	67	12	46	53
2004								
10	51	152	65		62	16	19	

689 **FIGURE CAPTIONS**

690

691

692 Fig. 1. Chart of study area showing Funk Island and vessel survey routes off the northeast coast of
693 Newfoundland

694

695 Fig. 2. *Sula bassana*. Polar plots of directions (in 90° sectors) of flocks of foraging gannets
696 returning to the colony on Funk Island, 1998 – 2002 and all years combined

697

698 Fig. 3. *Sula bassana* Percentages of flocks A) returning from inshore and associations with the
699 percentages of capelin loads landed at the colony ($Y = 0.49X + 38.5$, $R^2 = 0.33$)and B) returning
700 from offshore foraging sites and associations with salmon loads landed at colony on Funk Island (Y
**701** $= 1.15 + 19.1$, , $R^2 = 0.60$)

702

703 Fig. 4. *Sula bassana.* Average sizes of flocks returning from inshore (white bars) and offshore
704 (black bars) foraging areas, 1998 -2002

705

706 Fig. 5. *Sula bassana* and *Mallotus villosus.* Abundances of gannets and capelin on vessel transects
707 within the gannets' foraging range from Funk Island, 2000-2002. Dashed lines represent the survey
708 track in each year

709

710 Fig. 6. *Sula bassana.* Percentages of dives during each 20 % flight segment of foraging trips

711

712 Fig. 7. *Sula bassana.* Maximum distances from the colony during foraging trips by parental
713 gannets (dots) and first dives, median and maximum foraging range estimates (circles) for northern
714 gannets nesting on Funk Island off the northeast Newfoundland coast

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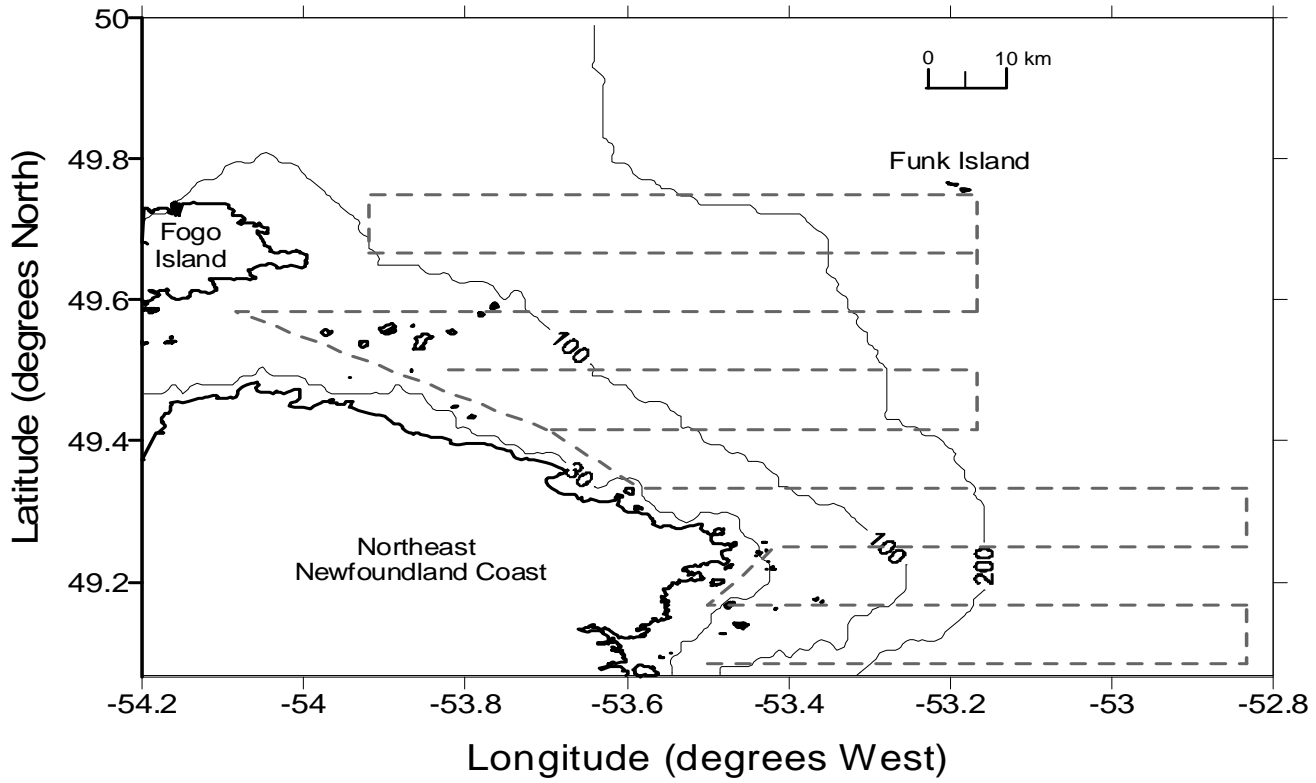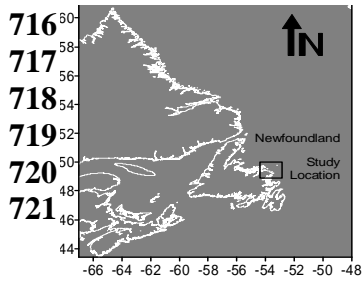
Fig. 1. Chart of study area showing Funk Island and the vessel survey route
(dashed line) off the northeastern coast of Newfoundland

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Fig. 2. *Sula bassana.* Polar plots of directions (in 90° sectors) of gannets returning to the colony on
Funk Island from foraging areas, 1998 – 2002 and all years combined
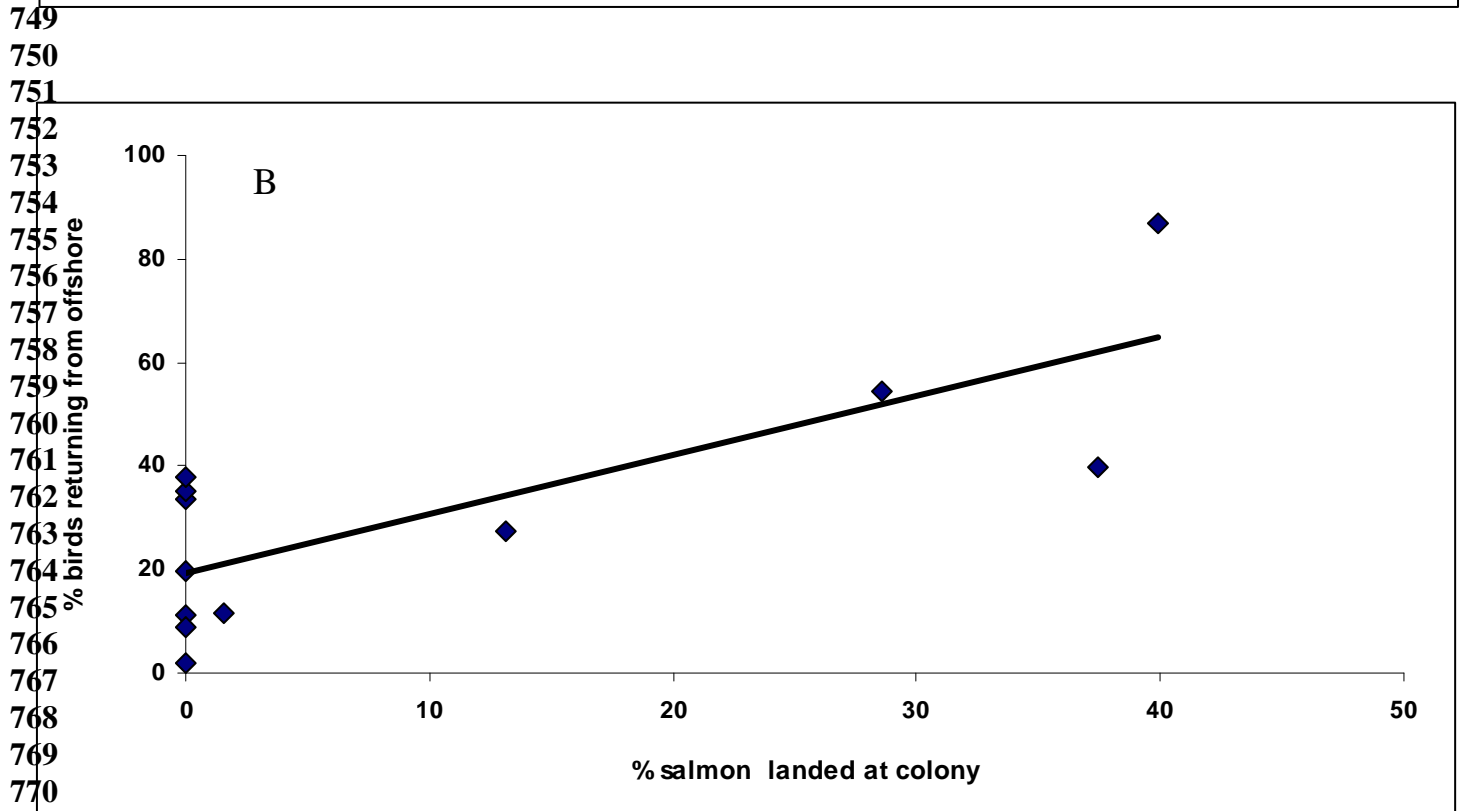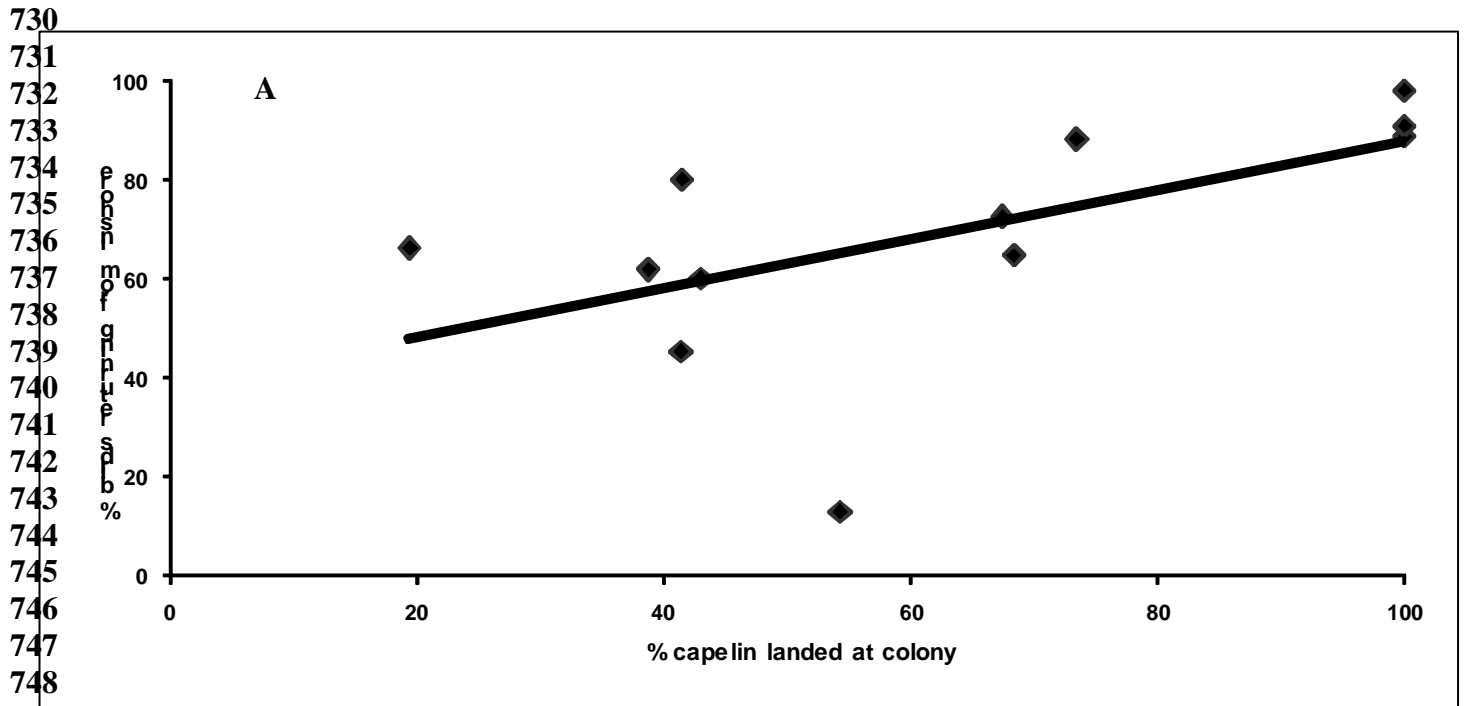
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Fig. 3. *Sula bassana* Percentages of flocks A) returning from inshore and associations with the percentages of capelin loads landed at the colony (Y = 0.49X + 38.5, R^2 = 0.33)and B) returning from offshore foraging sites and associations with salmon loads landed at colony on Funk Island (Y = 1.15X+ 19.1, , R^2 = 0.60)

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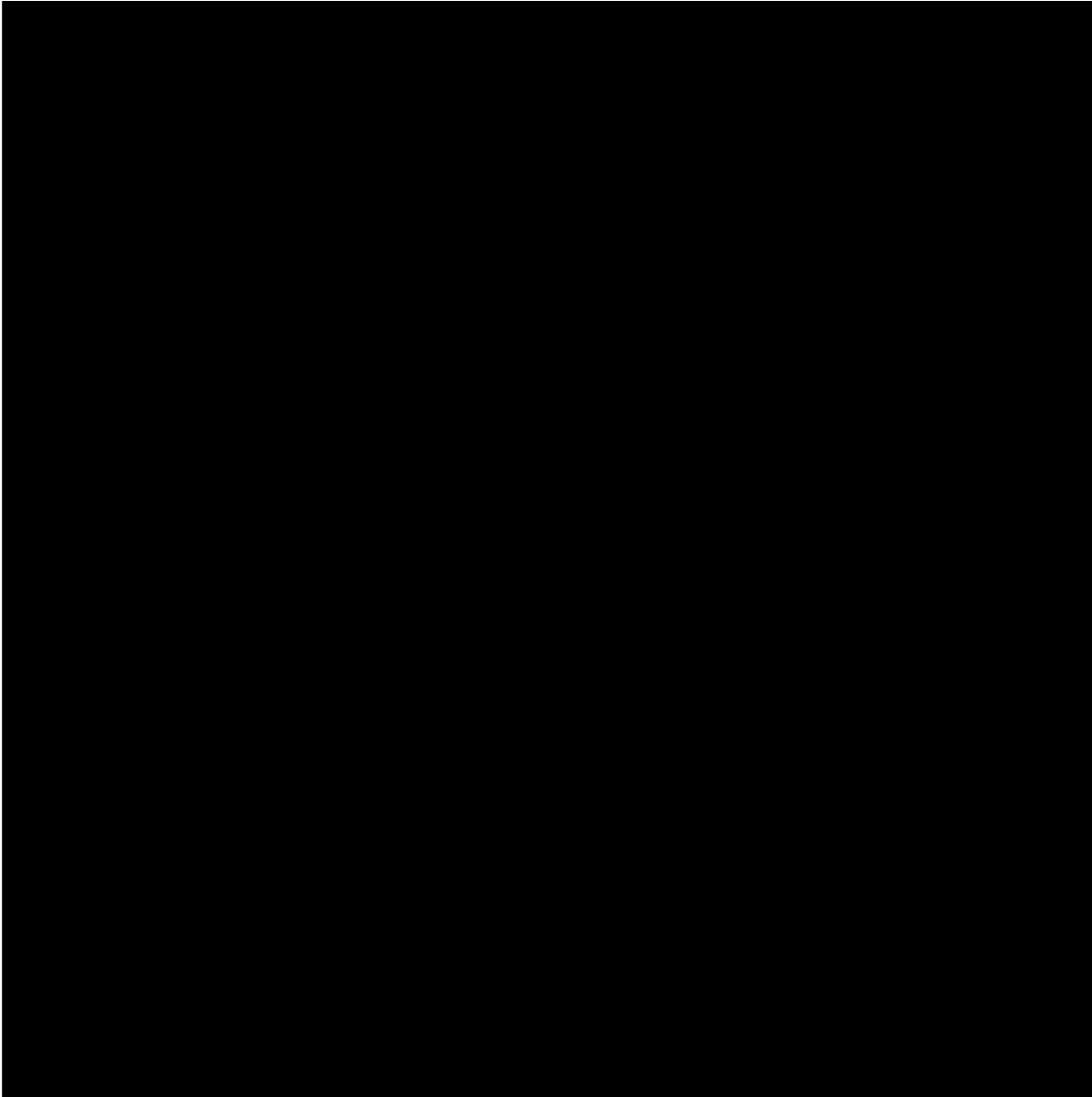
813 Fig. 4. *Sula bassana.* Mean sizes of flocks of gannets returning from inshore (white bars) and
814 offshore (black bars) foraging sites, 1998-2002; comparisons during each year and for all years
815 combined are statistically significant (all Ps < 0.001)
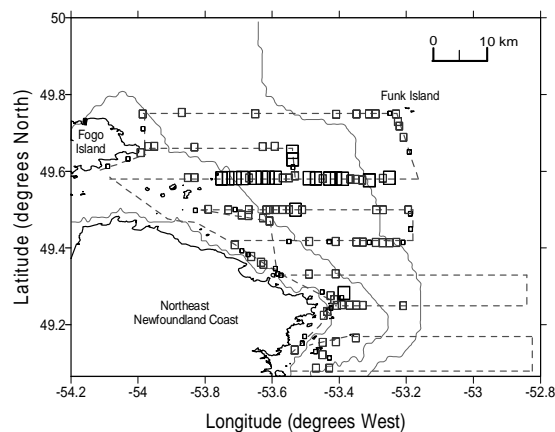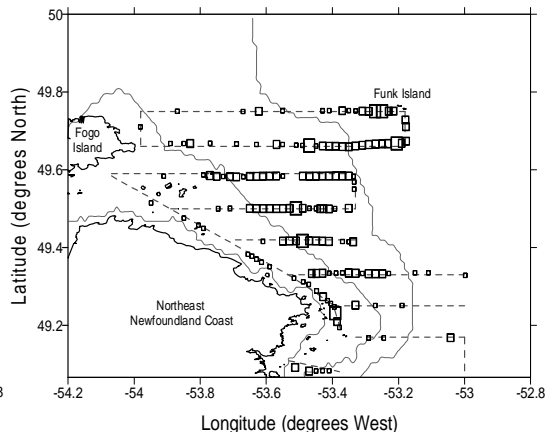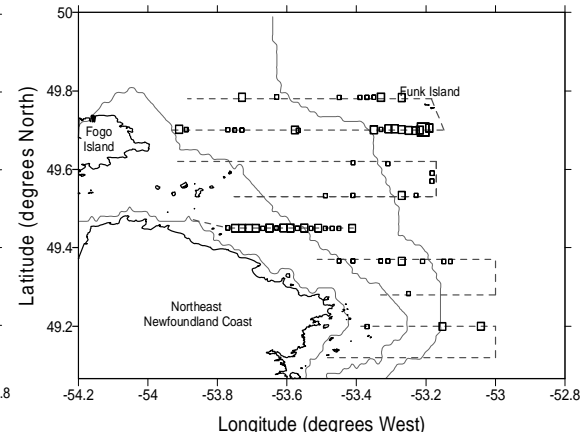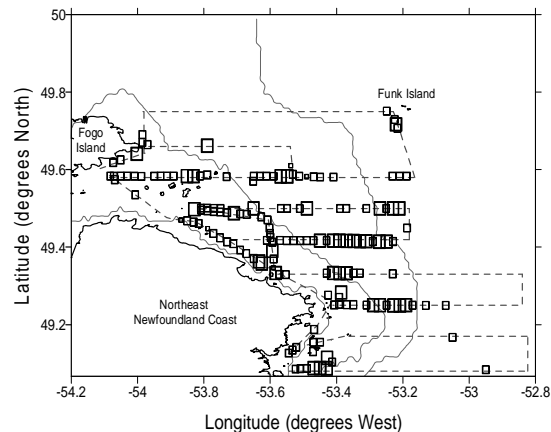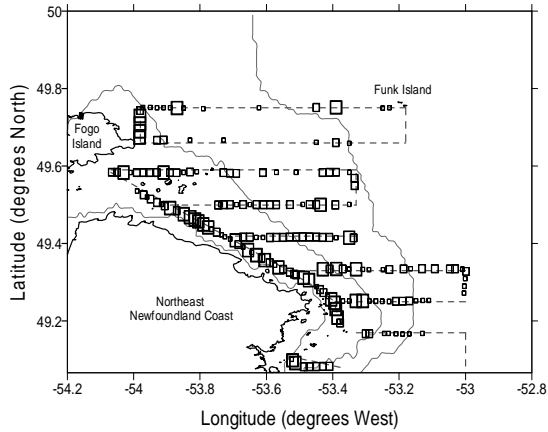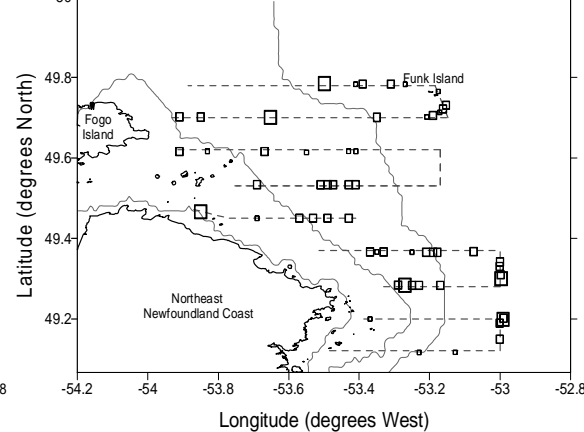
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817 Fig. 5. *Sula bassana* and *Mallotus villosus.* Abundances of gannets and capelin on vessel transects within the gannets foraging range from Funk
818 Island, 2000-2002. Dashed lines represent the survey track in each year

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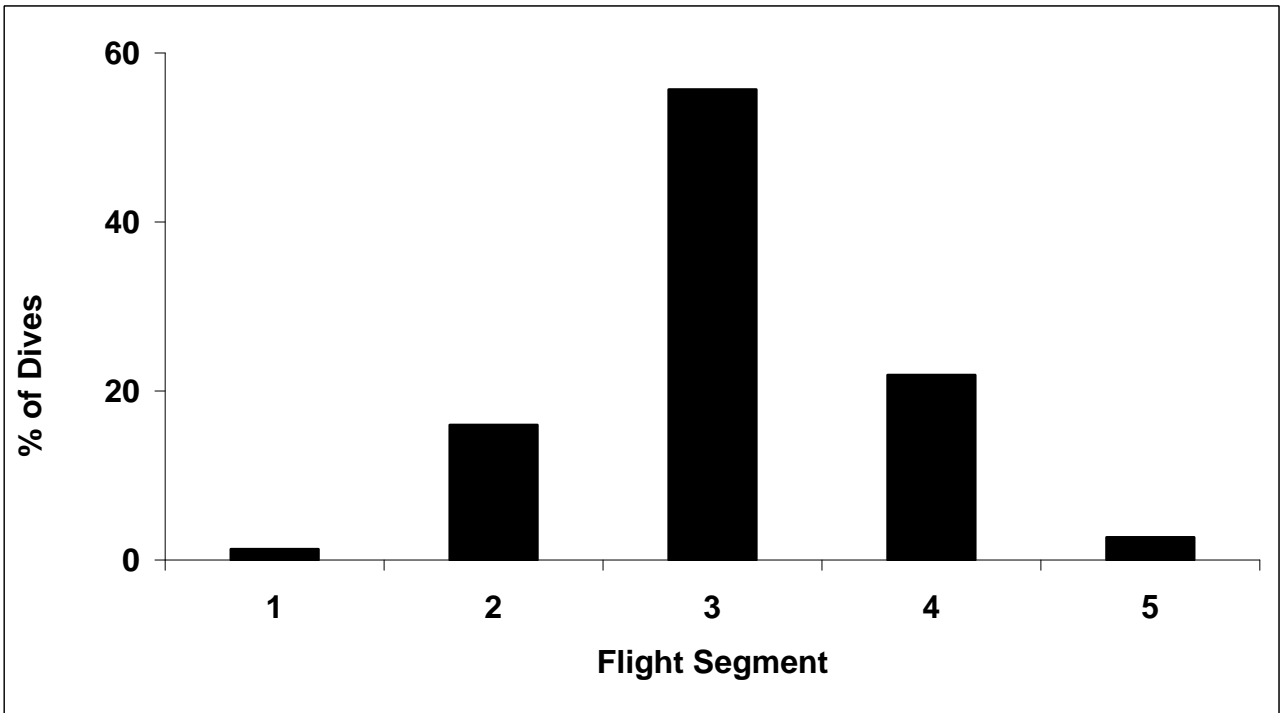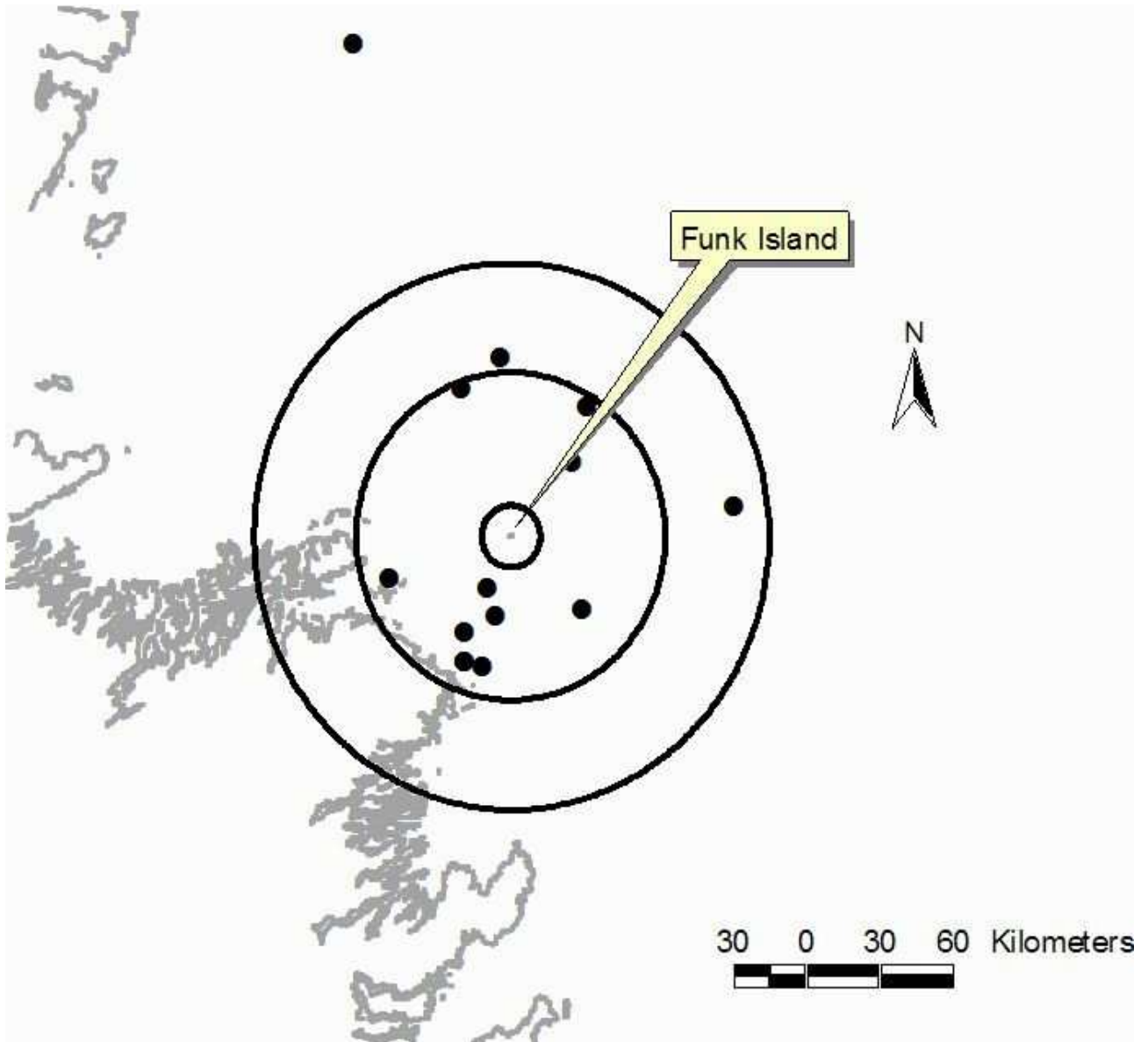839
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Fig. 6. *Sula bassana*. Percentages of dives during each 20 % flight segments of foraging trips

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853 Fig. 7. *Sula bassana.* First dives, median (inner circle) and mean maximum (outer circle) 2002
854 foraging range estimates for seven northern gannets nesting on Funk Island off the northeast
855 Newfoundland coast
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