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MIGRATORY TACTICS AND WINTERING AREAS OF NORTHERN GANNETS (*MORUS BASSANUS*) BREEDING IN NORTH AMERICA

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ABSTRACT.—Migration has evolved to allow organisms to undertake life-history functions in the most appropriate place at the most appropriate time. Migration creates seasonal ecological linkages that have important implications for survival, population dynamics, response to climate change, and conservation. Although advances in bird-borne tracking technology have promoted knowledge of avian migratory ecology, major information gaps remain for most avian species, including seabirds. Ours is the first study to electronically track the migration and wintering of Northern Gannets (*Morus bassanus*; hereafter “gannets”) from almost all of their North American breeding range, in multiple years and with multiple tracks from individual birds.

Gannets used distinct wintering areas and aggregated in several major hotspots. Most adults remained along the northeast North American coast, and breeding populations displayed only weak migratory connectivity. Unexpectedly, the Gulf of Mexico was revealed to be an important wintering area for adults. Individual gannets displayed remarkable winter-site fidelity with extensive range overlap across years. Timing, rates of movement, and use of stopovers during migration depended strongly on winter destination and also on sex, colony, and year. Females left the colony prior to males in fall, but, contrary to expectation, earlier spring arrival of males was not detected. Variation in seasonal constraints was emphasized by faster and shorter spring migrations compared with fall. Migratory duration, distance, and timing of arrival and departure from the winter grounds were all repeatable, suggesting strong individual conservation in these traits, while variability in the timing of colony departure and arrival, migratory speed, and the extent of stopovers en route imply greater environmental influences on these behaviors.

Three of 46 gannets displayed a radically different round-trip migration and overwinter strategy by undertaking the first recorded (and repeated), round-trip trans-Atlantic migrations to the coast of Africa, where gannets breeding in Europe overwinter. Trans-Atlantic crossings were as rapid as 5 days. Gannets breeding at all of the North American colonies located in easternmost Canada in Newfoundland made trans-Atlantic migrations. This contrasts with no such crossings by a much larger sample of gannets breeding in the species' largest North American colony (Bonaventure Island) in the Gulf of St. Lawrence. Similar trans-Atlantic migrations have not been recorded in the well-studied European colonies. The discovery of this trans-Atlantic connection has implications for interaction, connectivity, and phylogeographic radiation between the eastern and western Atlantic populations and suggests that migratory animals have a surprising capacity for successful movement beyond their known migrations.

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We discuss our results in the broader context of seabird migration. The observed patterns of migratory timing and scale-dependent connectivity present a novel opportunity to assess the ecological and conservation implications during migration and on the wintering grounds. The overall weak connectivity suggests that gannets, as a population, may have the capacity to respond to modest environmental change. However, the repeatability of some characters implies that any response may be slow because the population will respond, but not necessarily the individuals. The lability of migratory tactics in the population as a whole combined with remarkable individual consistency in some, but not all, migration parameters offers rare insight into the relative contributions of genetic and environmental factors controlling migration. *Received 31 January 2013, accepted 25 April 2013.*

Key words: geolocators, migration tactics, migratory connectivity, Northern Gannet, site fidelity, winter areas.

Stratégies migratoires et aires d'hivernage des Fous de Bassan (*Morus bassanus*) nichant en Amérique du Nord

RÉSUMÉ.—La migration a évolué pour permettre aux organismes d'accomplir les fonctions de leur cycle biologique à l'endroit et au moment les plus appropriés. La migration crée des liens écologiques saisonniers ayant des répercussions importantes sur la survie, la dynamique, l'adaptation aux changements climatiques et la conservation des populations. Bien que les avancées technologiques relatives aux dispositifs fixés sur les oiseaux pour les suivre aient permis d'améliorer nos connaissances de l'écologie des migrations aviaires, il subsiste d'importantes lacunes à ce sujet pour la plupart des espèces d'oiseaux, y compris les oiseaux marins. Notre étude est la première qui permette de suivre électroniquement la migration et l'hivernage de Fous de Bassan (*Morus bassanus*; ci-après « fous ») répartis dans presque toute leur aire de nidification nord-américaine, sur plusieurs années et avec des tracés multiples pour les mêmes individus.

Les fous ont utilisé des aires d'hivernage distinctes et se sont rassemblés dans quelques zones de concentration majeure. La plupart des adultes sont demeurés le long de la côte nord-est de l'Amérique du Nord, et les populations nicheuses n'ont présenté qu'une connectivité migratoire faible. Fait inconnu jusque-là, le golfe du Mexique s'est avéré être une aire d'hivernage importante pour les adultes. Individuellement, les fous ont été remarquablement fidèles à leur site d'hivernage, l'aire utilisée se chevauchant de façon importante d'une année à l'autre. La chronologie de migration, le taux de déplacement et l'utilisation des haltes migratoires étaient fortement liés à la destination d'hivernage de même qu'au sexe, à la colonie et à l'année. Les femelles ont quitté la colonie avant les mâles à l'automne, mais contrairement aux attentes, l'arrivée plus hâtive des mâles au printemps n'a pas été détectée. Les migrations printanières étaient plus rapides et plus courtes que celles à l'automne, faisant ressortir la variation des contraintes saisonnières. La grande reproductibilité de la durée et de la distance de la migration, de même que de la chronologie d'arrivée et de départ de l'aire d'hivernage donne à penser qu'il existe une forte rétention individuelle de ces caractéristiques, tandis que la variabilité de la chronologie de départ et d'arrivée à la colonie, de la vitesse de migration et de l'importance des haltes migratoires implique l'existence d'une influence environnementale plus grande sur ces comportements.

Trois des 46 fous ont accompli un cycle migratoire et adopté une stratégie d'hivernage radicalement différents des autres, en effectuant (et de façon répétée) les premiers allers-retours migratoires transatlantiques jusqu'aux côtes de l'Afrique jamais enregistrés, rejoignant sur leur aire d'hivernage les fous nichant en Europe. Les traversées de l'Atlantique prenaient aussi peu que 5 jours. Les fous provenant des colonies nord-américaines les plus à l'est au Canada, soit à Terre-Neuve, ont fait ces migrations transatlantiques. Ce résultat contraste avec le fait qu'aucun fou provenant de la plus grande colonie d'Amérique du Nord (l'île Bonaventure, dans le golfe du Saint-Laurent) n'a effectué une traversée de cet ordre, même avec un échantillon beaucoup plus grand d'oiseaux. Des migrations transatlantiques de ce genre n'ont jamais été rapportées chez les colonies d'Europe, pourtant bien étudiées. La découverte de cette connexion transatlantique a des incidences quant à l'interaction, la connectivité et la radiation phylogéographique entre les populations des deux côtés de l'Atlantique, et laisse croire que les animaux migrants ont la capacité surprenante d'effectuer des déplacements profitables au-delà des migrations connues.

Nous mettons en perspective nos résultats dans le contexte plus large de la migration chez les oiseaux marins. Les tendances observées pour la chronologie de migration et la connectivité selon l'échelle considérée présentent une nouvelle possibilité d'évaluer les effets sur le plan de l'écologie et de la conservation au moment de la migration et de l'hivernage. La connectivité relativement faible dans l'ensemble indique que les fous, considérés en tant que population, pourraient avoir la capacité de répondre à des changements environnementaux modestes. Cependant, le caractère reproductible de certains attributs implique que toute réaction pourrait être lente puisque la population réagira, mais pas nécessairement les individus. L'adaptabilité des stratégies migratoires dans l'ensemble de la population, combinée avec la remarquable constance individuelle pour certains des paramètres de migration (mais pas tous), offre un rare aperçu de la contribution relative des facteurs génétiques et environnementaux qui contrôlent la migration.

INTRODUCTION

ORGANISMS UNDERTAKE DIFFERENT life history functions in the most appropriate place at the most appropriate time in order to maximize fitness (Gauthreaux 1982, Stearns 1992). To get to these places, migration—defined here as the “seasonal return movement between breeding and wintering grounds” (Newton 2008)—has proved to be a remarkably labile trait. It has evolved across a broad range of taxa many times as an adaptive response to temporal and spatial variation in resource availability (Piersma et al. 2005, Dingle and Drake 2007, Griswald et al. 2010). It is likely to evolve whenever winter-season survival is enhanced away from the breeding grounds and reproduction is more successful outside the winter area (Lack 1954).

Populations may be limited by both biotic and abiotic factors, including a suitable climate, habitat, food, predators, anthropogenic influence, parasites, and disease (Lack 1968, Croxall and Rothery 1991, Cairns 1992, Both et al. 2006, Schwemmer et al. 2011). Food, both for provisioning young during breeding and for winter survival, is likely the most important ultimate factor limiting migrant bird populations (Lack 1968). The relative importance of population-limiting factors that operate in the breeding versus winter seasons has been widely debated (reviewed in Gauthreaux 1982). But it is becoming clear that a more holistic viewpoint is required, because effects in one season carry over into subsequent ones (Marra et al. 1998, Norris and Marra 2007, Inger et al. 2010, Bogdanova et al. 2011, Catry et al. 2013).

Seasonal ecological linkages (Fretwell 1972) in migratory organisms affect individual survival and population dynamics (Harris et al. 2005, Pütz et al. 2006, Norris and Marra 2007, Sorensen et al. 2009, Altizer et al. 2011), local

adaptation and evolutionary response to climate change (Both et al. 2006, Wilcove and Wikelski 2008, Carey 2009), disease epidemiology (Olsen et al. 1995, Rappole et al. 2000), and species conservation (Haney et al. 1998, Webster et al. 2002, Martin et al. 2007). To understand how these linkages affect a species' ecology, evolution, and conservation (Webster et al. 2002, Boulet and Norris 2006), it is essential to assess animals' spatial distribution and movement throughout the annual cycle.

Migratory connectivity.—The concept of migratory connectivity characterizes the degree to which breeding populations overlap in space and time during the winter (Webster et al. 2002). Weak (or diffuse) migratory connectivity occurs when separate breeding populations mix freely on the wintering grounds (or vice versa; e.g., Mallory et al. 2008), whereas with strong connectivity a wintering area is spatially partitioned among breeding populations (Webster et al. 2002). These are two extreme ends of a continuous spectrum, and most species likely fall somewhere in between. Variable winter conditions can reduce survival in some populations, but subsequent effects on population dynamics depend on the degree of migratory connectivity between breeding and wintering populations.

Migratory connectivity may play a role in local adaptation to wintering grounds. Under strong migratory connectivity, breeding populations generally migrate to the same wintering area and therefore experience similar selective pressures during both breeding and winter seasons. This may lead to strong local adaptation if birds consistently use the same wintering areas in subsequent years (Webster et al. 2002). Under weak migratory connectivity, birds from a single breeding population migrate to a variety of winter locations and, thus, gene flow between these winter populations limits local adaptation

(Webster et al. 2002). This, of course, assumes a strong genetic component to migratory behavior and random mating of birds from different winter populations on the breeding grounds (Berthold 1996, Gillis et al. 2008). On the other hand, weak migratory connectivity will likely permit a more rapid and favorable evolutionary response to shifting selective pressure from climate change and habitat loss or modification, due to genetic variation or plasticity in migratory behavior (Dolman and Sutherland 1994, Webster and Marra 2005, Norris et al. 2006, Dias et al. 2010). The spread of parasites and diseases (e.g., Lyme disease, West Nile virus, and avian influenza virus) among avian populations and, subsequently, to humans can also be affected by the extent to which breeding and wintering populations overlap (Webster et al. 2002, Ricklefs et al. 2005, Lebarbenchon et al. 2009). For example, the transhemispheric spread of Lyme disease was likely due, at least in part, to seabirds that migrate between high-latitude breeding and wintering areas in different hemispheres (Olsen et al. 1995, McCoy et al. 2003).

Effective avian conservation planning in marine environments depends on knowledge of biogeographic linkages between breeding and wintering populations (Lopes et al. 2006, Norris et al. 2006, González-Solís et al. 2007, Harris et al. 2010, Bogdanova et al. 2011, Fort et al. 2013a) and their relative threats from sources including wind farms (Garthe and Hüppop 2004, Fox et al. 2006, Masden et al. 2009), oil spills and other contaminants (Wiese et al. 2001, Álvarez and Pajuelo 2004, Wiese and Robertson 2004), fishery interactions (Weimerskirch et al. 1997, Suryan et al. 2007, Benjamins et al. 2008, Delord et al. 2008, Grémillet et al. 2008), artificial nocturnal lighting (Montevicchi 2006), changing environmental conditions (Sandvik et al. 2005, 2012; Grémillet and Boulinier 2009; Harris et al. 2010), and their interactions (Hebert 1998, Rolland et al. 2008). The implications of migratory connectivity can be understood only with knowledge of the migratory routes and wintering areas of individual animals and, by extension, populations (Webster et al. 2002). This knowledge is missing for most bird species.

Migration and timing.—Migration has been characterized in many ways, and much of the literature has focused on birds to provide the most cogent examples. Migration can be considered facultative where the breeding grounds are

survivable in winter or obligate where they are not (Dingle and Drake 2007). Migration is considered partial if only some individuals leave the breeding or wintering grounds (Dingle and Drake 2007, Sekercioglu 2010), thereby trading off the risk of remaining in a suboptimal landscape against the cost of migrating to a better one. Different migration strategies may be undertaken by different (sub-)populations (Kren and Zoerb 1997, González-Solís et al. 2007, Lopes et al. 2008), by failed and successful breeders (Bogdanova et al. 2011, Catry et al. 2013), or by different ages or sexes (Gauthreaux 1982, González-Solís et al. 2008). The latter is referred to as “differential migration” (Catry et al. 2005, Dingle and Drake 2007), where the sexes or age classes undertake migration to different locations or at different times in order to gain some advantage (e.g., earlier return to breeding grounds) or avoid competition (Ketterson and Nolan 1983, Cristol et al. 1999).

Different selective forces shape the spring and fall migrations. In most bird groups, there is a decrease in reproductive success as the breeding season advances, producing selective pressure for early spring arrival and laying (Weber et al. 1998, 1999; Drent et al. 2003; Gaston et al. 2009). Yet arriving too early can impose survival risks due to harsh environmental conditions and/or limited food supply (Møller 1994, Drent et al. 2003). Birds must therefore time their departure from winter grounds in order to reach the breeding area at the most appropriate time. This is accomplished by an endogenous rhythm that is further fine tuned by local and global environmental cues including weather and photoperiod (Gwinner 1986, Forchhammer et al. 2002, Newton 2008). Arrival (and breeding) synchrony may play a more important role than absolute arrival date in colonially breeding seabirds (Hatchwell 1991, Reed et al. 2009).

Birds may not be under the same pressure to reach the wintering grounds, and thus migrate more slowly during fall (Stutchbury et al. 2009). The date of fall departure from the breeding site is fairly consistent between years for many species (Newton 2008). But spring arrival timing may carry over into fall departure time, given that birds arriving late in the spring will generally require the same amount of time to breed as their early-arriving conspecifics and, thus, their fall departure will be delayed (Daunt et al. 2006, Gunnarsson et al. 2006).

The location of the wintering area can affect the timing of migration and subsequent arrival for breeding. In general, spring migration starts earlier in the more distant portions of the winter range, allowing more distant birds to catch up (Bregnballe et al. 2006, Newton 2008). Although birds wintering closer may arrive earlier and enjoy greater success (Hötker 2002, Mehl et al. 2004), this is not universal (Bregnballe et al. 2006). Timing of arrival on the breeding grounds may also be affected by conditions at stopover sites (Weber et al. 1998, Drent et al. 2003) and by breeding success or failure in the previous season (Catry et al. 2013). Individuals may need to reach a specific nutrient threshold for egg production (Perrins 1996), and the extent to which species are income versus capital breeders (Drent and Daan 1980, Bond and Diamond 2010) may dictate resource accumulation needs at stopover sites (Drent et al. 2006). Thus, breeding date may be determined by conditions en route or in previous breeding seasons, including weather and interspecific or intraspecific competition for food, which carry over to the breeding grounds (Drent et al. 2003, 2006; Catry et al. 2013).

Large-scale climate affects the timing of migration (Forchhammer et al. 2002, Hüppop and Hüppop 2003, Vähätalo et al. 2004, Bauer et al. 2008) and timing of breeding (Both and Visser 2001, Crick 2004, Frederiksen et al. 2004, Durant et al. 2007, Gaston et al. 2009). Birds are constrained in how much they can advance their breeding timing by the timing of migration (Senner 2012). Because timing of migration is likely genetically controlled by endogenous rhythms (Gwinner 1986, Van Buskirk et al. 2012), there is a limit to how much birds can adjust their breeding timing to match prey availability (Both and Visser 2001, Geinapp et al. 2008).

Sex differences in migration.—Differential migration is common in many avian species, and this pattern is likely the rule rather than the exception, particularly among temperate and polar birds (Cristol et al. 1999, Catry et al. 2005, Bogdanova et al. 2011, Catry et al. 2013). Males often arrive before females in the spring and/or depart after females in the fall (Morbey and Ydenberg 2001, Mills 2005). The difference in relative timing of migration is greatest in species with different parental roles. For example, male ducks do not provide parental care, and they leave the breeding grounds well before

the females (Newton 2008). Avian differential migration research has tended to focus on waterfowl, raptors, shorebirds, and passerines (e.g., Arnold 1991, Carbone and Owen 1995, Komar et al. 2005, Mathot et al. 2007). A comprehensive review by Cristol et al. (1999) included only a single seabird species that displayed differential migration by the sexes, the Great Cormorant (*Phalacrocorax carbo*). More recently, sex-based differences in migration timing, routes, and/or destination have been found in several, but mostly procellariiform, seabirds (Weimerskirch and Wilson 2000; Álvarez and Pajuelo 2004; Phillips et al. 2004b, 2005, 2009; González-Solís et al. 2008; Bogdanova et al. 2011).

Site fidelity.—Fidelity to breeding and winter sites occurs to a variable extent across avian species, with some displaying fidelity in both seasons, greater fidelity in one season than in the other, or no fidelity at all (Newton 2008). Generally, far more is known about breeding-site fidelity than about winter-site fidelity, although the extent of even breeding-site fidelity is unknown for most species. Individuals displaying winter-site fidelity may have an advantage over dispersers due to both local knowledge of resources and genetic local adaptation, but dispersing to novel sites may allow individuals to find better habitat (Newton 2008, Dias et al. 2010). The extent of winter-site fidelity may depend on age, sex, and variability in winter habitat and food supply (Newton 2008) and may be influenced by mating systems (Robertson et al. 2000). Winter-site fidelity has been shown in waterfowl (Robertson and Cooke 1999), shorebirds (Burton 2000, Johnson et al. 2001), and passerines (Holmes and Sherry 1992, Staicer 1992), but in few seabird species because of the difficulty of observing birds away from the breeding colony. The availability of tracking devices suitable for seabirds is changing this (Wilson et al. 2002), and recent studies in a few (mostly procellariid) seabirds have found mixing among (González-Solís et al. 2007) as well as fidelity to (Frederiksen et al. 2002; Croxall et al. 2005; Phillips et al. 2006, 2008; Dias et al. 2010; Quillfeldt et al. 2010; Kopp et al. 2011) nonbreeding sites or routes (Guilford et al. 2011). Fidelity to stopover sites, like breeding and wintering sites, varies by taxonomic group (Newton 2008). Theoretical and empirical evidence suggests that the stopover-site fidelity of passerines decreases with increasing distance

from migratory end points (Merom et al. 2000, Catry et al. 2004, Yohannes et al. 2007, Vogt et al. 2012). Higher fidelity is expected with species that follow specific migratory pathways, such as raptors (Shiu et al. 2006), or that have few suitable refueling sites, such as waterfowl (Fox et al. 2002) and shorebirds (Harrington et al. 1988, Minias et al. 2010).

Seabird migration and overwintering.—Assessing migratory connectivity in seabirds has been challenging because tracking them through the annual cycle is difficult (Webster and Marra 2005). After breeding, many seabird species cross vast oceanic and hemispheric expanses to reach distant shelf-edge, coastal, and pelagic wintering areas (Harrison 1983, Nelson 2002). Traditional assessments of migration routes and wintering areas and their associated connectivity have relied on at-sea surveys, band recoveries, or even variation in plumage and morphology (Boulet and Norris 2006). Analyses of these data provided an important broad-scale picture of occurrence and movements for some species (Bairlein 2003), but limited plumage and morphological differentiation and low band-encounter rates have hampered progress (Boulet and Norris 2006). Band recoveries are essentially one-off records that do not yield information about the destinations, timing, or travel routes of individual migrations and are often more associated with the distribution of human populations on the coasts (Gaston et al. 2008). Major insights into seabird migrations and their spatial and temporal movement tactics over the world's oceans have recently been forthcoming from miniaturized bird-borne tracking and data-logging devices (Weimerskirch and Wilson 2000; Phillips et al. 2004a; Croxall et al. 2005; Shaffer et al. 2006; Kubetzki et al. 2009; Dias et al. 2010; Ismar et al. 2010a, 2011; Yamamoto et al. 2010; Bogdanova et al. 2011; Frederiksen et al. 2012; Fort et al. 2012, 2013a; Hedd et al. 2012; Catry et al. 2013), from intrinsic biological markers (Lopes et al. 2008; Phillips et al. 2009; Ramos et al. 2009a, b), and from both techniques used in combination (Phillips et al. 2007). These techniques, especially when integrated with banding data, can generate a comprehensive understanding of the movement ecology of marine birds over a range of spatial and temporal scales and provide insights into the implications of population connections (González-Solís et al. 2007, Navarro et

al. 2009, Strandberg et al. 2009). Each of these techniques carries with it attendant biases, cost-benefit tradeoffs, and constraints on the spatiotemporal scales and types of inferences that can be drawn. The most successful studies are likely to be those that combine two or more of these approaches (Furness et al. 2006, Phillips et al. 2007, Strandberg et al. 2009). Yet few authors have explicitly compared inferences drawn from multiple methods for a given species (but see Anker-Nilssen and Aarvak 2009, Strandberg et al. 2009, Harris et al. 2010).

Patterns of seabird migration and wintering sites are highly variable across species, but there are some general trends within and across taxa. Movement between breeding and wintering areas does not occur on a broad front but instead follows recognizable routes defined by oceanographic processes that concentrate prey (Yoder et al. 1994, Elphick 2007, Fort et al. 2012). Adult round-trip migration typically occurs over smaller spatial and temporal scales than that of juveniles (Nelson 2002, Newton 2008). Migratory movements vary from short (or not at all in some partial or nonmigrants) to long-distance, whole-ocean movements (Fort et al. 2013b). For example, North American cormorants undertake a partial migration that is largely restricted to coastlines (Nelson 2006). At the other end of the spectrum, many procellariiforms migrate across open ocean in association with oceanic fronts and stable wind patterns (Weimerskirch and Wilson 2000, Shaffer et al. 2006), and Arctic Terns (*Sterna paradisaea*) complete annual trips of >70,000 km by migrating along coastal shelves and across open ocean (Egevang et al. 2010).

Spring arrival at the breeding colony (and subsequent laying) is highly synchronized in many seabird species (e.g., Hatchwell 1991, Reed et al. 2009), which may require birds wintering at more distant locations to initiate migration earlier in order to arrive on time (Bregnballe et al. 2006). The consistency of migration timing across years has received little attention in seabirds, although consistent timing has been found in Barau's Petrel (*Pterodroma barau*; Pinet et al. 2011), Black-browed Albatross (*Thalassarche melanophrys*; Phillips et al. 2005), and Cory's Shearwater (*Calonectris diomedea*; Dias et al. 2010).

Use of stopover areas, or "hotspots," a common feature of migration in other orders (Beauchamp 2009, Stutchbury et al. 2009),

has recently been observed in some seabirds (Phillips et al. 2005, Guilford et al. 2009, Dias et al. 2010, Egevang et al. 2010) but is not universal (Shaffer et al. 2006, Yamamoto et al. 2010). Finally, individual animals may display markedly different migratory patterns (Kubetzki et al. 2009, Dias et al. 2010) that aggregate into population-level migratory strategies.

Study species.—The Northern Gannet (*Morus bassanus*), the largest breeding seabird in the North Atlantic (Nelson 2002), is the focus of this monograph. It and its two Southern Hemisphere congeners, the Cape Gannet (*M. capensis*) and the Australasian Gannet (*M. serrator*), are the only migratory high-latitude sulids, relying on cool, productive waters for breeding. The rest of the sulids (the boobies) are essentially nonmigratory tropical residents (Nelson 2006).

The Northern Gannet (hereafter “gannet”) breeds at 45 colonies in the North Atlantic: 31 in Europe (from France to northern Norway), 8 in Iceland, and 6 in North America (Nelson 2006). The world population (measured in apparently occupied sites [AOS] at colonies) totals ~432,000 AOS (315,000 in the eastern Atlantic and 117,000 in the northwest Atlantic; Wanless and Harris 2004, Wanless et al. 2005, Murray 2011, Chardine et al. 2013). From banding studies and observations of birds at sea, Nelson (2002) ascertained that juvenile gannets that fledge in the United Kingdom migrate down the west coast of Europe, into the Mediterranean, as far south as the highly productive waters off Senegal and Mauritania in the Canary Current, where extensive fisheries produce large amounts of discards (Camphuysen and van der Meer 2005). However, Nelson (2002) deduced that most adults remain closer to the breeding colony in the North Sea, in the Bay of Biscay and along the Iberian coast.

Kubetzki et al. (2009) used geolocator tracking to reveal that adult gannets breeding at Bass Rock, Scotland, occupied relatively small home ranges within one of four distinct geographic zones in proportions that differed from expectation. Surprisingly, almost half wintered off western Africa, indicating the existence of weak to moderate connectivity in this population (Kubetzki et al. 2009). This represents a likely change in migratory strategy or, alternatively, the effect of bias in previous banding studies. Prior to geolocator-based studies, there was no evidence of colony-based differences in winter

destination for European gannets, although most studies focused on the Bass Rock colony (Nelson 2002). Repeated tracking of individuals was recommended to interrogate the extent of consistency within individual schedules across years (Kubetzki et al. 2009). More recently, evidence from five European colonies suggested that gannet migrations are oriented toward particular wintering hotspots, have similar maximum distances (~4,000 km, resulting in chain migration), but are bimodal (distance-wise) at some colonies (Fort et al. 2012). Large-scale differences in winter locations have not been found between the sexes, but there was a tendency for Bass Rock females to winter farther from the colony than males (Kubetzki et al. 2009).

Far less is known about the migration and wintering of gannets in North America. Current knowledge of their migration is due to at-sea surveys and long-term banding studies, conducted mainly at two of the gannets’ six North American colonies (Bonaventure Island and Funk Island; Gaston et al. 2008). They migrate from eastern Canadian breeding colonies along the continental margin to wintering areas along the U.S. east coast and Gulf of Mexico, covering up to ~5,000 km one way at speeds of 24–32 km day⁻¹ (Nelson 2006, Gaston et al. 2008). The main target locations for wintering were considered to be off the east coast of Florida and in the Gulf of Mexico, based on the large number of (mostly immature) band recoveries in these areas (Nelson 2002, Gaston et al. 2008). At-sea surveys in Canadian waters indicate that gannets were observed south and east of Newfoundland and on the Scotian Shelf during November–December (Brown 1986, Fifield et al. 2009). Gannets were present over the continental shelf from the Gulf of Maine to Chesapeake Bay during December–February, with the highest densities (and survey effort) occurring between New Jersey and Cape Cod (Powers 1983). Juveniles and immatures reportedly migrate farther than adults; this is supported by the fact that only 8% of adult band recoveries were in the Gulf of Mexico (Nelson 2002). Spring migration begins as early as February, and birds arrive at the breeding area in mid-April having covered the return distance more quickly than in fall, at a speed of 56–112 km day⁻¹ (Nelson 2006, Gaston et al. 2008), via a route that may be farther offshore than in fall (Perkins 1979). Many of these band recoveries are decades old, and



FIG. 1. Study area, showing colony locations and places mentioned in the text.

the extent to which inferred winter areas have remained constant over time is unknown, as is their reliance on band-recovery biases. Indeed, geolocators have indicated different wintering areas for gannets than those shown by banding data (Montevecchi et al. 2011).

Gannets are birds of continental shelf waters (Nelson 2002), and the Atlantic Ocean likely acts as a rarely crossed barrier to restrict interactions between Nearctic and Palearctic populations. Only nine gannets banded in North America have been reported in the eastern Atlantic (Gaston et al. 2008). Most of these were immature birds in their first year of life, so it is not clear whether they purposefully or accidentally crossed the Atlantic. The risk and energy demand associated with trans-Atlantic movements underscore the evolutionary forces that shape migratory behavior, with important ramifications for population interactions and species range radiations (Alerstam 1981,

Able 1999, Berthold 2001). To date, questions of trans-Atlantic population interactions, historical range expansions, and ancestral source population remain unresolved for gannets.

Our goal in this monograph is to examine the migratory movements and winter areas of adult Northern Gannets breeding in North America. This research addresses three important questions: (1) What degree of migratory connectivity and overlap in winter area exists in the population as a whole, among colonies, and between sexes (i.e., where do they go)? (2) How and when is the migration accomplished, with respect to timing of movements and stopovers by different populations and sexes (i.e., how and when do they get there)? And (3) how consistent are these patterns for individuals across years? We address these questions in the context of comparison and integration of signals derived from band recoveries and electronic tracking of individual birds. We compare different levels of

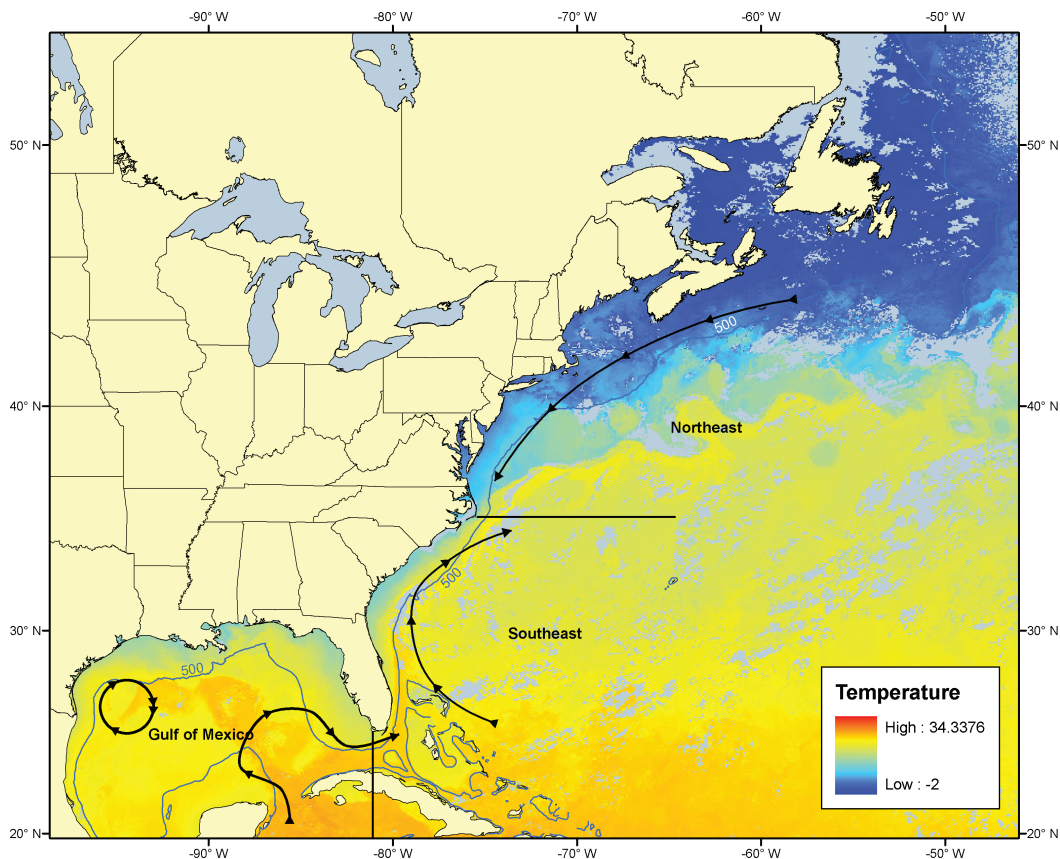


FIG. 2. Locations of North American overwinter zones, predominant currents, and typical mid-February sea surface temperatures that characterize continental shelf waters.

ecological organization (population, colonies, sexes, and individuals) and discuss the evolutionary, ecological, and conservation implications of the observed patterns.

METHODS

Study sites.—Research was conducted at four of the six Northern Gannet colonies in the northwest Atlantic (Fig. 1): (1) the species' largest colony (~59,600 pairs), at Bonaventure Island (48°29'N, 64°09'W) in the Gulf of St. Lawrence, Quebec; (2) the third-largest North American colony (~14,800 pairs) and the species' southernmost colony at Cape St. Mary's, Newfoundland (46°49'N, 54°49'W); (3) the fourth-largest (~10,000 pairs) and most oceanic North American colony, on Funk Island (49°45'N, 53°11'W) off the northeast Newfoundland coast; and (4) the fifth-

largest (~2,300 pairs) colony at Baccalieu Island (48°07'N, 52°47'W) on the eastern Newfoundland coast (Chardine 2000, Chardine et al. 2013). Only the inaccessible colony at Bird Rocks and the smallest colony at Anticosti Island (both in the Gulf of St. Lawrence) were not included.

Winter zones.—We partitioned the gannet's North American winter range (Nelson 2002) into three oceanographic zones for analysis (Montevecchi et al. 2011): (1) the northeast (NE) zone, including all the east coast of North America north of Cape Hatteras; (2) the southeast (SE) zone, from Cape Hatteras to the tip of Florida (east of 81°W); and (3) the Gulf of Mexico (GoMex) zone (west of 81°W). The boundaries of these zones (Fig. 2) were selected on the basis of characteristic thermal regimes and current systems that typify each region and influence prey species assemblages (Rabalais

and Boesch 1987). Additionally, each zone has its own unique set of industrial activity levels (e.g., fishing and petroleum extraction) that could affect wintering gannet populations (Rattner and McGowan 2007). In the NE zone, the continental shelf is strongly influenced by the cold Labrador Current that flows south along the Labrador and Newfoundland coasts (Rabalais and Boesch 1987). In the SE zone, the warm northward-flowing Gulf Stream dominates the continental shelf until Cape Cod, where it deflects sharply to the northeast. The clockwise-circulating Loop Current, along with the eddies it generates, and outflow from the Mississippi River delta typify the warm Gulf of Mexico (Rabalais and Boesch 1987).

Banding data.—The North American bird-banding database provided records of all gannet banding and recovery records as of 30 April 2010, including 13,946 deployments and 832 known-location recoveries (also see Montevecchi et al. 2011). Birds were characterized as “adult” ($n = 315$) if they were in at least their fifth year of life when encountered, “immature” ($n = 469$) if they were younger, or “unknown” ($n = 48$). Recoveries were filtered to extract only those found during the nonbreeding season (15 October–15 April; $n = 288$) or the winter season (January–February; $n = 62$). The nonbreeding season was defined to coincide with typical gannet colony departure and arrival dates (Nelson 2002). Winter was restricted to January–February to allow for comparison with geolocator-tracked birds that had ceased large-scale migratory movements by then (see below).

Geolocators.—Three models of light-sensing geolocators were used. (1) Fifty Geo-LT (cylindrical, 14 × 45 mm; weight: 8.5 g in air, 16.2 g including attachment; static accuracy: 30–180 km [product literature]; Earth and Ocean Technologies, Kiel, Germany) were deployed at all colonies. (2) Ten LTD 2400 (cylindrical, 11 × 32 mm; weight: 8 g in air, 8.8 g including attachment; static accuracy: 109 ± 58 km, deployed accuracy: 400 ± 298 km [Shaffer et al. 2005]; Lotek Wireless, St. John’s, Newfoundland) were deployed at Bonaventure Island and Cape St. Mary’s. (3) Six BAS MK5 (square, 18 × 18 × 5 mm; weight: 3.6 g total; static accuracy: 85 ± 47 km, deployed accuracy: 186 ± 114 km [Phillips et al. 2004a]; British Antarctic Survey, Cambridge, United Kingdom) were deployed at Baccalieu Island. The Geo-LT geolocators recorded light level every 30 s and

temperature every 120 s. The LTD 2400 geolocators sampled light every 60 s and temperature and pressure every 32 s. The BAS loggers sampled light every 30 s and recorded the maximum level every 10 min.

Between 2004 and 2009, these 66 devices were deployed once or twice (in successive years) on 76 gannets (31 at Bonaventure Island, 15 at Funk Island, 14 at Cape St. Mary’s, and 16 at Baccalieu Island), for a total of 105 deployments (Table 1). Breeding adults with large chicks were captured late in the breeding season from nest sites with a 5-m telescoping noose pole. Birds were held for ~5 min while devices and identification bands were attached; geolocators were retrieved during subsequent breeding seasons. Gannets were captured from colony peripheries to reduce disturbance, but individuals from the third or fourth row from the edge were selected, to avoid young or inexperienced breeders that may nest at the colony edge (Nelson 2002), although even peripheral breeders may be experienced in some colonies (Pettex et al. 2012). All animals were cared for in accordance with guidelines of the Canadian Council on Animal Care.

On Bonaventure Island, 25 birds were fitted with devices on 11 September 2004, and all were recaptured between 24 May and 14 July 2005 (except one recaptured on 3 July 2007; Table 1). One bird lost its device and 4 devices failed, yielding 20 datasets. During 4–8 September 2005, 23 birds (17 of the same birds from the previous year and 6 others) were equipped, and all were recaptured between 12 June and 13 July 2006. Three birds lost devices, yielding 20 datasets.

On Funk Island, 14 birds were fitted with geolocators during 5–10 August 2005, and 10 were recaptured during 8–14 August 2006, 9 of which yielded datasets (Table 1). Eleven gannets (10 of the same birds from the previous year) were equipped during 8–15 August 2006, and 8 were recaptured during 24–25 July 2007 or 26–29 July 2008, yielding 7 datasets.

At Cape St. Mary’s, on 3 September 2005, a single geolocator was deployed, and it was retrieved on 15 September 2006 (Table 1). Five gannets were equipped on 15 September 2006, and 1 was retrieved on 4 September 2007. Seven gannets were equipped on 16 September 2007, and 4 were retrieved between 10 August and 22 September 2008. On 31 August 2008, 2 gannets were equipped (one same bird from previous year) and one was recaptured on 4 July 2009.

TABLE 1. Overall and annual numbers of Northern Gannets equipped and recaptured, and datasets recovered at each study colony.

Colony	Overall						Annual details			
	Unique birds equipped	Unique birds recaptured	Unique birds providing data ^a	Birds tracked twice ^b	Datasets recovered		Year	Deployments	Recaptures	Datasets recovered
					All	Full ^c				
Bonaventure Island	31	31	28	11	40	34	2004–2005	25	25	20
							2005–2006	23	23	20
Funk Island	15	10	9	6	16	14	2005–2006	14	10	9
							2006–2007	11	8	7
Cape St. Mary's	14	7	4	0	4	3	2005–2006	1	1	1
							2006–2007	5	1	1
							2007–2008	7	4	2
							2008–2009	2	1	0
							2009–2010	1	0	0
Baccalieu Island	16	6	5	0	5	5	2009–2010	16	6	5
Total	76	54	46	17	65	56		105	79	65

^aIncludes birds that provided partial datasets.

^bIncludes only birds with two complete round-trip tracks.

^cDatasets containing complete round-trip tracks.

This bird was re-equipped and not recaptured in 2010. From the 7 devices retrieved at this site, 4 datasets were recovered.

On Baccalieu Island, between 15 and 20 August 2009, 16 birds were equipped, 1 was retrieved on 14 April 2010 from a fishing net in eastern Newfoundland, and 5 were retrieved during 17–25 August 2010, yielding 5 datasets (Table 1).

Thus, 65 datasets (63 Geo-LT, 2 LTD 2400, and 0 BAS MK5) were collected from 46 separate individuals, each tracked in 1 or 2 years. Seventeen birds were tracked (with complete round-trip datasets) in 2 consecutive years. All 65 datasets included positions up to the end of December, and 95%, 92%, and 89% ($n = 62, 60,$ and 58) till the end of January, February, and March, respectively; 86% ($n = 56$) yielded complete round-trips. Different numbers of devices or birds are included in each analysis, depending on device failure date; sample sizes are given with the description of each analysis.

Geolocator position estimation.—Raw light data from Geo-LT geolocators were analyzed using MULTITRACE for Windows (Jensen Software Systems, Laboe, Germany), which produced two

daily position estimates. Longitude was estimated by comparing the time of local noon (or midnight) to Greenwich Mean Time (GMT), and latitude was estimated from day length (Wilson et al. 1992, Hill 1994). For LTD 2400s, internal tag software computed a single daily position based on measured light parameters. The error in the light-based latitude can be more than twice the corresponding longitude error estimated by geolocators (Phillips et al. 2004a, Teo et al. 2004, Shaffer et al. 2005). Light-based latitude cannot be estimated during the solar equinoxes, when day length is the same at all latitudes (Hill 1994). However, light-based latitude estimates can be improved (or recovered during equinoxes) by reconciling geolocator-measured sea surface temperatures (SSTs) with remotely sensed satellite SSTs. Teo et al. (2004) described an algorithm that uses the geolocator longitude estimates and finds the most plausible latitude for each day based on three indices of match between geolocator and remotely sensed SSTs near that longitude. This method was originally developed for bluefin tuna (*Thunnus thynnus*) and was subsequently validated for use in seabirds, reducing overall mean great-circle error from 400 km to

202 km (Shaffer et al. 2005). The software developed by Teo et al. (2004) was not available for use in the present study, so the algorithm was implemented in Matlab (Mathworks, Natick, Massachusetts) according to their published description and was used to adjust gannet daily latitude estimates accordingly. The SST-corrected positions were filtered to remove positions requiring unreasonable speeds ($n = 31$), using a forward-backward averaging filter (McConnell et al. 1992) with a maximum speed of 84 km h^{-1} (Garthe et al. 2007b). Missing positions (e.g., due to failure of light-based geolocation during equinoxes and/or failure of the SST correction algorithm; $n = 1,714$, or 7.5%), were linearly interpolated between surrounding positions (Guilford et al. 2009). Tracks of individual birds were smoothed using a sliding window boxcar smoother (with a window size of 5) whereby the coordinates of each smoothed position were the weighted mean (in a 1:2:3:2:1 ratio) of the second previous, previous, current, subsequent, and second subsequent position's coordinates. This resulted in a total of 22,871 filtered and smoothed positions. Smoothed positions were characterized as either "travel" or "stopover," based on an examination of interposition displacements and turning angles. Travel is characterized by relatively small turning angles and displacements exceeding a minimum threshold, whereas stopovers are characterized by relatively large turning angles or small displacements (Turchin 1988). Travel and stopovers were assessed using a sliding window of five consecutive positions, with each bird initially defined to be in the stopover state (i.e., starting at the colony). Transition to the travel state was defined when any three or more positions (within a block of five) had turning angles $\leq 35^\circ$ and interposition distances $\geq 40 \text{ km}$. Likewise, transition from travel to stopover was defined when three or more positions failed to meet the turning angle or displacement criteria.

Data analysis.—The geolocator data were notably unbalanced across colonies and years, complicating statistical analysis. The bulk of the data came from Bonaventure Island and Funk Island from 2004–2006, but Bonaventure Island was the only colony sampled in 2004–2005, Cape St. Mary's and Baccalieu Island had small sample sizes, and Baccalieu Island was the only colony sampled in 2009–2010. Including all data across all years in statistical models made it

impossible to distinguish year effects from colony effects, because these two were completely confounded. Furthermore, estimates of variance components in linear mixed-effects models (LMMs; Pinheiro and Bates 2000) are unstable in the presence of such highly unbalanced data (Raudenbush and Bryk 2002). Therefore, for colony effects, comparisons were made between Bonaventure and Funk islands in 2005–2006 only, because this was the only year with a sufficient sample at more than one colony. Year comparisons were made between Bonaventure Island in 2004–2005 and 2005–2006, and between Funk Island in 2005–2006 and 2006–2007. The data for sexes and winter destination were better balanced, with a good spread across colonies and years, and models investigating the effect of these parameters used all available data. For all analyses, except those involving LMMs, statistical significance was set at a critical $\alpha = 0.05$. P values from LMMs are known to be approximate (Zuur et al. 2009), so for these models $P \leq 0.01$ was considered significant, $0.01 < P \leq 0.05$ was considered "weak" evidence, and $0.05 < P \leq 0.1$ was considered "marginal" evidence. For all boxplots, the thick horizontal line shows the median, the box edges depict the first and third quartiles, the dashed lines extend to $1.5\times$ the interquartile range, and outliers are plotted as individual open circles. All statistical analysis was performed using R, version 2.11.0 (R Development Core Team 2010).

Gannet wintering areas were assessed using both bands and geolocators. The numbers of bands recovered in each oceanographic zone during nonbreeding and winter seasons were examined, and the hypothesis of equal zonal use across colonies of origin was tested. For geolocators, the winter centroid was determined for each gannet whose device functioned until at least the end of February ($n = 56$ datasets from 40 birds) by calculating the mean latitude and longitude of all positions between the end of fall migration and the start of spring migration. Proportions of birds with centroids in each oceanographic zone were compared among years and colonies. Because all birds tracked more than once had centroids in the same winter zone across years (except one), data were combined across years (excluding the one bird) to test the effect of sex on the proportion wintering in each zone. Likewise, the proportion of birds wintering in each North American oceanographic zone was

compared between bands and geolocators. All comparisons described in this section were conducted with Fisher exact tests.

To investigate areas of high use during the entire nonbreeding season (including both migration and overwintering), the Spatial Analyst Density tool in ARCGIS, version 9.3 (ESRI, Redlands, California), was used to create a map showing the pattern and locations of hotspots (areas of intense use) for all birds combined. More in-depth analysis employed volume-contoured kernel utilization distributions (UDs; van Winkle 1975, Silverman 1986, Worton 1989) for two purposes: (1) to set the boundary of the wintering area in order to define the end of fall migration and the start of spring migration, and (2) to give estimates of space use in the wintering area. These were constructed from fixed bivariate normal kernels with a grid size of 10 km using the 'adehabitat' package (Calenge 2006) in R. The 50% volume contour defined the winter "core range," and the 95% contour defined the "home range." These values are commonly used in other seabird studies and in ecology in general (Wood et al. 2000, Laver and Kelly 2008, Dias et al. 2010). Examination of bird positions revealed that most birds had stopped large-scale movements and reached the farthest extent of their migrations by January, after which they remained in relatively restricted areas, with mostly stopover days until at least the end of February. Thus, January–February stopovers were used to compute the winter core and home-range kernels. Non-stopover positions were excluded because an examination of migration tracks indicated that some birds had obviously not reached their winter destination by 1 January or had started their spring migration before the end of February. Use of these positions would have included (in some cases large) areas that were used for migration and not for overwintering.

The choice of the kernel smoothing bandwidth, h , has the greatest influence on resulting UD (Silverman 1986). This parameter affects the relative contribution of surrounding points at a given distance to the kernel density estimate at any given point (Gitzen et al. 2006). Choice of h by least-squares cross validation (LSCV) has been suggested to produce the most accurate results (Worton 1995, Seaman et al. 1999), but the LSCV algorithm may fail to converge for datasets in which

many positions are tightly clumped or coincident (Hemson et al. 2005, Gitzen et al. 2006); indeed, the algorithm failed to converge for many gannet datasets ($n = 12$). Additionally, LSCV can potentially produce a different smoothing bandwidth (and, thus, level of detail) for each individual, making it difficult to differentiate variation in behavior from that due to choice of smoothing parameter (Pellerin et al. 2008). Other authors have used an ad hoc value, h_{ref} , which is based on the latitudinal and longitudinal variances of the positions (Worton 1989). This approach can also produce a different smoothing parameter for each bird and may overestimate area use (by oversmoothing) for animals with multimodal distributions (Seaman et al. 1999, Gitzen and Millspaugh 2003). A constant value of h is thus preferred to clarify comparisons between individuals, colonies, and sexes (Pellerin et al. 2008, Sternalski et al. 2008, Tolon et al. 2009), and a value of 75 km was chosen for all analyses, based on the mean h_{ref} (73.5 km, $n = 56$) for all winter datasets.

The sizes of North American core and home ranges were tested for differences between colonies, years, destination zones, and sexes. LMMs with bird identity as a random effect were used to account for multiple tracking of some birds. The likelihood of concurrent shared space use for a mated pair from Bonaventure Island tracked during 2005–2006 was assessed using the utilization distribution overlap index (UDOI; Fieberg and Kochanny 2005), which measures the amount of overlap between UD, compared with two individuals using the same space in a uniform manner. A UDOI value of 1 indicates 100% overlap between two individuals using space uniformly; values <1 indicate less overlap in relation to uniform space use; and values >1 indicate greater overlap (Fieberg and Kochanny 2005).

Winter-site fidelity was assessed in three ways for birds tracked in 2 consecutive years. First, regional-scale fidelity was assessed by comparing the zonal location (NE, SE, or GoMex) of centroids in successive years. Second, the distribution of distances between successive winter centroids was compared with the distribution of distances between centroids of datasets paired at random ($n = 10,000$ randomizations; Dias et al. 2010) with a Kolmogorov-Smirnov (K-S) test; the medians were also compared for both

distributions. This approach can detect a shift in the location of the winter centroid but is insensitive to changes in range size. To address this, a third analysis compared the percentage overlap between consecutive core and home ranges. For each individual, two indices were computed for each of the core or home ranges: $CR_{t,t+1}$ or $HR_{t,t+1}$, the percentage of the core range or home range in year t overlapped by the core or home range in year $t + 1$; and the converse, $CR_{t+1,t}$ or $HR_{t+1,t}$ (Kernohan et al. 2001, Fieberg and Kochanny 2005). The observed distribution of indices was compared to randomized distributions of overlap indices ($n = 10,000$ core or home ranges paired at random; Dias et al. 2010) with a K-S test, and the medians were compared for both distributions.

Fall migration duration was defined as the period from colony departure until first entry into the 95% winter home range, and spring duration as the period from final exit of the 95% winter home range until colony return (Ramírez et al. 2013). Geolocator temperature data indicated dates of colony departure and return. High and variable nighttime temperatures indicated colony attendance, and constant low nighttime temperatures were characteristic of time at sea (Shaffer et al. 2005). Migration speed (km day^{-1}) was defined as the total distance covered along the migration track divided by the migration duration. LMMs were used to test the effects of colony, year, winter destination, and sex on migration start–end date, distance, duration, speed, and number of stopover days, and to compare the same parameters during fall versus spring migrations. Means \pm SD and ranges for migration timing parameters are presented in tabular form throughout the results, in order to provide a clear summary of these data. Estimated effect sizes from LMMs, which may differ slightly from raw means, are presented in the text. One individual, gannet 14932 breeding at Cape St. Mary's, had no chick, departed prematurely, and was thus removed from the departure-date analysis.

Consistency of migration parameters through time for birds tracked twice was tested using repeatability (Lessells and Boag 1987). Repeatability is the portion of variation attributable to differences between individuals (as opposed to within individuals) in the population

as a whole and may (Falconer 1981) set an upper limit on heritability (but see Dohm 2002). Repeatability, also known as the intraclass correlation coefficient (Sokal and Rohlf 1981), is calculated as $r = s^2_A / (s^2 + s^2_A)$, where s^2_A is the among-individual variance and s^2 is the within-individual variance (Lessells and Boag 1987). A large value of r indicates consistent behavior, because most of the variation is between individuals and not within individuals.

The masses of eight geolocator-equipped adults taken before deployment and after retrieval in 2005–2006 served as an indicator of potential gross device effects. Additionally, survival and fecundity rates were compared with published accounts (Mowbray 2002).

RESULTS

Forty-three of 46 tracked gannets migrated to winter destinations in North America; the other 3 individuals migrated to the west coast of Africa. Results for North American migrants are presented first, followed by trans-Atlantic migrants.

Device effects.—All (31) equipped birds were recaptured at Bonaventure Island (in both years), as were 10 of 15 birds at Funk Island (the two colonies where most resighting and recapture effort was concentrated). Birds carrying 46 of 48 (95.8%) deployments at Bonaventure Island and Funk Island were seen in the colony the following year, as were 10 of 14 at Cape St. Mary's, and all but one recaptured gannet had an egg or chick. Two equipped gannets seen in the colony, but not recaptured, had lost an egg or chick. The mass of the devices used ranged from only 0.1% to 0.5% of the typical mass (3,000 g; Nelson 2002) of a gannet. Mean body masses were not detectably different before and after carrying loggers overwinter (paired t -test, $t = -0.24$, $df = 7$, $P = 0.82$).

North American wintering areas from banding data.—In North America, 13,946 gannets have been banded. Of these, up to 2010, only 85 non-breeding-season and 20 winter adult recoveries have occurred in North America (Table 2). The mostly coastal recoveries occurred over a large geographic range from the breeding grounds to the southern tip of Florida and into the Gulf of Mexico as far west as Texas (Table 2 and Fig. 3). Recoveries did not occur in equal proportions among the oceanographic zones during the

TABLE 2. Numbers (proportion) of adult Northern Gannets recovered in North America during nonbreeding (15 October–15 April) and winter (January–February) in three winter zones: northeast (NE), southeast (SE), and Gulf of Mexico (GoMex).

Banding location	Recoveries							
	Nonbreeding				Winter			
	NE	SE	GoMex	Total	NE	SE	GoMex	Total
Bonaventure Island	43 (0.60)	24 (0.34)	4 (0.06)	71	8 (0.50)	7 (0.44)	1 (0.06)	16
Funk Island	6 (0.46)	6 (0.46)	1 (0.08)	13	1 (0.33)	2 (0.67)	–	3
Baccalieu Island	1 (1.0)	–	–	1	1 (1.0)	–	–	1
Total	50 (0.59)	30 (0.35)	5 (0.06)	85	10 (0.50)	9 (0.45)	1 (0.05)	20

nonbreeding season: 59% occurred in the NE zone, 35% in the SE zone, and only 6% in the GoMex zone. No difference was detected when data were restricted to the winter period (Fisher exact test, $P = 0.77$; Table 2).

Only Bonaventure Island and Funk Island had enough recoveries for colony comparison. More than 3× as many birds were banded at Bonaventure Island compared with Funk Island, and there were more recoveries at the former. There was little temporal overlap in recoveries of adults outside the breeding season between the two colonies (Bonaventure Island recoveries: 1939–1989; Funk Island recoveries: 1982–1998). Recoveries of Bonaventure Island adults during the nonbreeding season produced 60% in the NE zone, 34% in the SE zone, and only 6% in the GoMex zone (Table 2). A similar pattern emerged for Funk Island, where 46% of recoveries occurred in each of the NE and SE zones, compared with only 8% in the GoMex zone, and no detectable difference in zonal proportions of recoveries was found for either the nonbreeding (Fisher exact test, $P = 0.68$) or winter (Fisher exact test, $P = 1.0$) periods. Only a single known-sex recovery occurred: a female from Funk Island in the SE zone.

North American wintering areas from geolocators.—Geolocators yielded the first round-trip migration records for North American gannets (Fig. 4). Gannets mainly occupied continental shelf and slope waters during the nonbreeding season but were not randomly distributed throughout their winter range (Fig. 5). They aggregated at several primary hotspots: off the coast of New Jersey and around Chesapeake Bay in the NE zone, and along the Louisiana coast in the GoMex zone. Secondary areas of aggregation occurred in the Gulf of Maine and in the South Atlantic Bight.

Of the 40 birds that provided 56 North American datasets complete to the end of February, the location of the winter centroids varied among individuals (Fig. 6). Many birds wintered in the NE zone, occupying shelf waters from the Gulf of Maine to Cape Hatteras. Others had centroids in the SE zone, along the coasts of North Carolina, South Carolina, Georgia, and northern Florida. Still others occupied the shelf waters of the Gulf of Mexico from Florida to Texas. Gannets did not use each of the three zones in equal proportions. The percentages of wintering gannets using each zone were 62% in the NE zone, only 10% in the SE zone, and 28% in the GoMex zone (Table 3).

There was variation in the wintering area within each zone. For example, within the NE zone, some birds remained in the northern portion of the zone, almost entirely within the Gulf of Maine (Figs. 4 and 6). Others congregated in the southern part of the zone around Delaware and Chesapeake Bays. Birds in the SE zone tended to frequent the coasts of North Carolina, South Carolina, Georgia, and northern Florida, avoiding the rest of Florida's Atlantic coast. Most birds in the Gulf of Mexico inhabited coastal Louisiana waters, but three gannets restricted themselves to either the extreme east or west of the Gulf. The longest and shortest (great-circle route) distances between the breeding colony and winter centroids were 3,947 km and 1,041 km, respectively.

Bonaventure Island and Funk Island were the only colonies with enough data to compare across years (Table 3). The proportion in each zone did not show a detectable difference at Bonaventure Island between 2004–2005 and 2005–2006 (Fisher exact test, $P = 0.66$) or at Funk Island between 2005–2006 and 2006–2007 (Fisher exact test, $P = 0.56$).

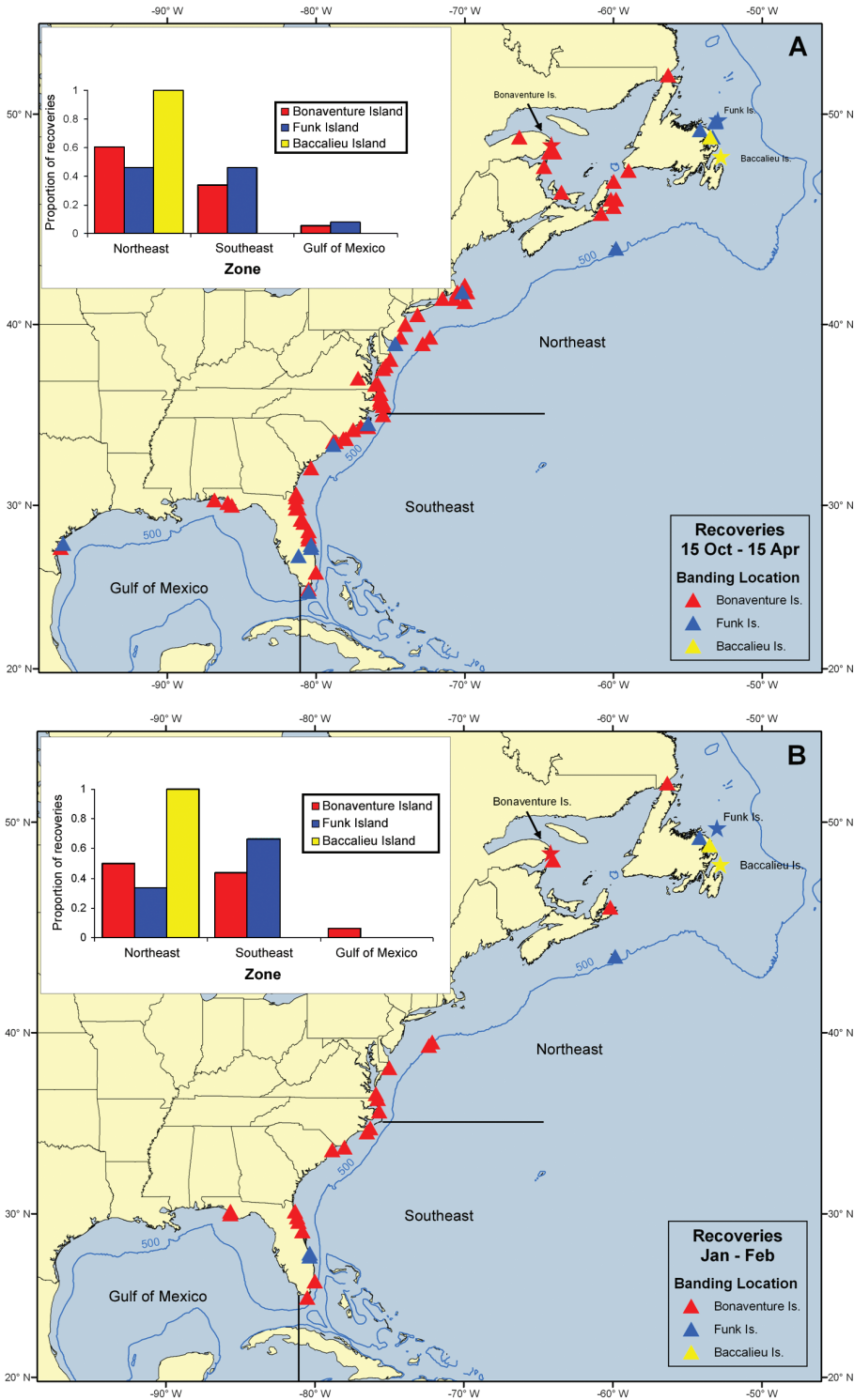


FIG. 3. Colony proportion of (A) nonbreeding season (15 October–15 April) and (B) winter (January–February), and frequency distribution (inset) of band recoveries of adult Northern Gannets in each oceanographic zone.

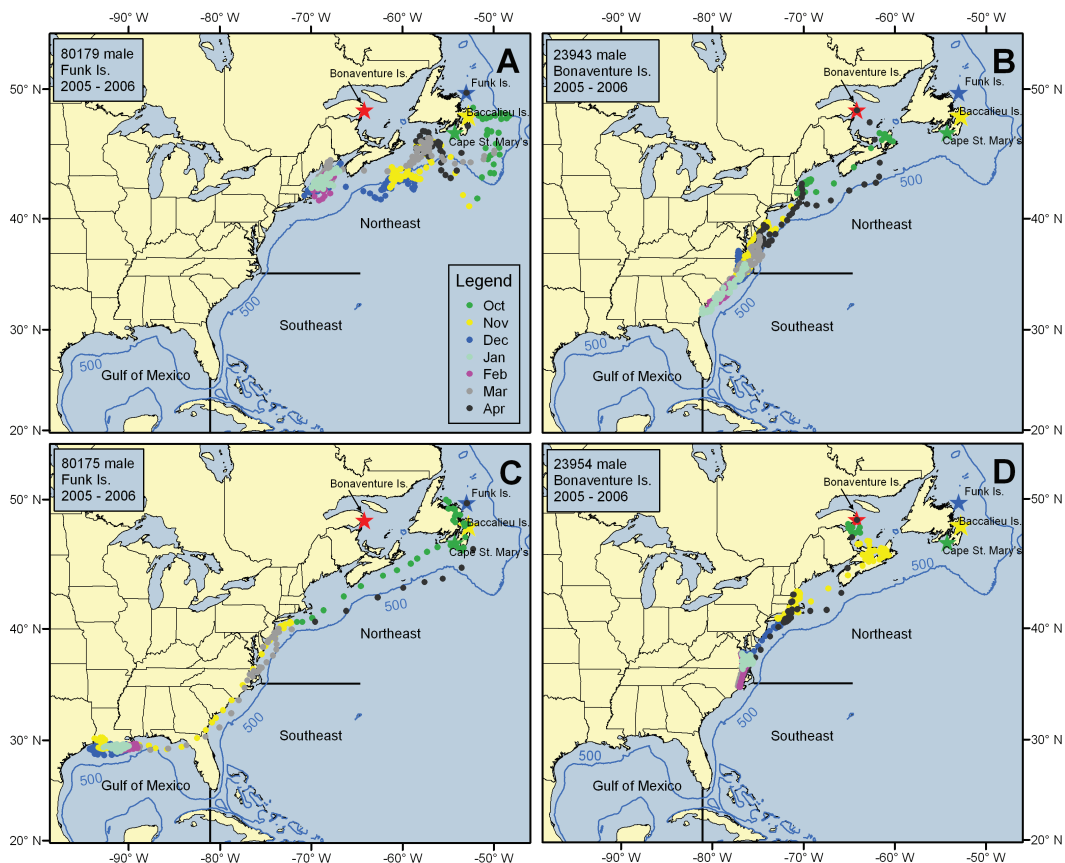


FIG. 4. At-sea positions of four individual geolocator-equipped Northern Gannets, showing typical patterns of wintering (January–February) in the three North American oceanographic zones: (A) northeast (NE zone), (B) southeast (SE zone), (C) Gulf of Mexico (GoMex zone), and (D) NE zone. January–February positions were restricted to the Gulf of Maine, Carolinas, Gulf of Mexico, and Chesapeake Bay areas, respectively. Dots represent bird positions (2 day^{-1}).

More birds from Bonaventure Island had winter centroids in the NE zone than in either of the other two zones in both 2004–2005 and 2005–2006 (Fig. 6 and Table 3). Over both years combined, 60% of Bonaventure Island birds had winter centroids in the NE zone and were the only ones with centroids in the SE zone. Birds from Funk Island had centroids in only the NE zone (62%) and GoMex zone (38%). Three of the four Baccalieu Island birds wintered in the NE zone, and the fourth was in the GoMex zone. Of the two Cape St. Mary's gannets, one was in the NE zone and the other was in the GoMex zone. When colonies were compared (Bonaventure Island vs. Funk Island in 2005–2006), there was no detectable difference in proportional use of each zone (Fisher exact test, $P = 0.34$).

There was a difference in the pattern of how winter centroids of birds from different colonies were distributed within the NE zone (Figs. 4 and 6). Birds from Funk Island tended to have a more northerly distribution, with two birds hardly venturing farther south than the Gulf of Maine during the entire winter (e.g., Fig. 4A). Centroids of birds from Bonaventure Island were concentrated in the southern half of the zone, particularly around Delaware and Chesapeake Bays, as were those from Baccalieu Island (although Baccalieu Island birds were tracked in a different year than all others). Further, no Newfoundland-breeding gannet had any positions south of Cape Hatteras, unless it was in transit to or from the Gulf of Mexico.

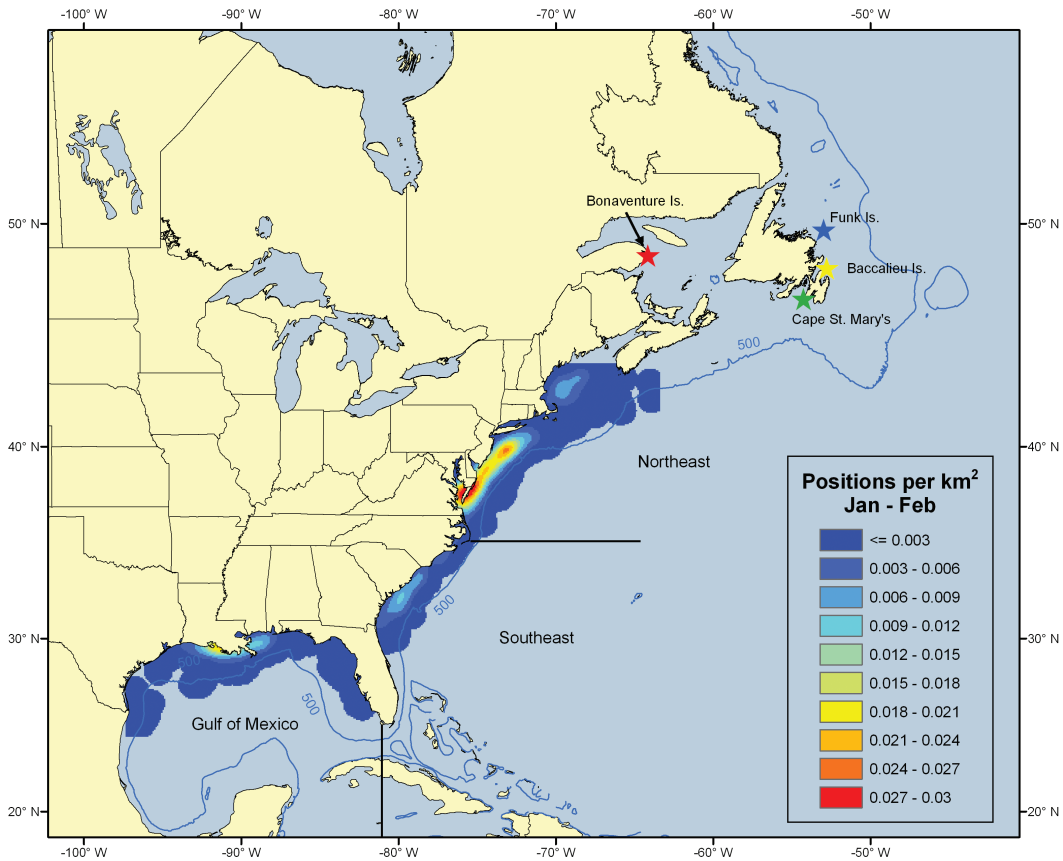


FIG. 5. Density of twice-daily positions from geolocator-equipped Northern Gannets during January–February (all birds combined), showing location of primary hotspots in the northeast (NE) and Gulf of Mexico (GoMex) zones and the secondary hotspots in the Gulf of Maine and South Atlantic Bight.

Across all years, 31 known-sex gannets (21 males and 10 females) were tracked to winter areas within North America. Contrary to expectation, both sexes were found throughout the species' winter range (Fig. 7 and Table 3), with no evidence that males wintered closer to the breeding colony than females. The proportion with centroids in each oceanographic zone did not detectably differ between the sexes (excluding gannet 23943, which switched from the GoMex zone to the SE zone between years; Fisher exact test, $P = 0.85$). This result did not differ if 23943 was included in the GoMex or SE sample (Fisher exact test, both $P \geq 0.73$). One mated pair (male 23951 and female 23952) was tracked from Bonaventure Island in 2005–2006, during which the male's winter centroid was in Chesapeake Bay in the NE zone and the female's was ~630 km away, off the coast of South Carolina in the SE zone.

Examination of home and core ranges provided more insight into individual variation than winter centroids. Most birds spent the winter period in relatively small areas and did not range widely (Figs. 8 and 9), although there was significant individual variation. Home and core range sizes ranged from 153,600 to 606,300 km² and 34,600 to 137,100 km², respectively. The mean (\pm SD) home range size was 273,605 \pm 87,211 km², which is equal to the area of a circle with a radius of only 292 \pm 45 km (range: 221–439 km); whereas mean core range size, 58,877 \pm 19,246 km², was equal to that of a circle with a radius of only 135 \pm 21 km (range: 105–209 km). Some birds ($n = 8$) with centroids in the NE and SE zones had a small portion of their home range that crossed the NE–SE dividing line in 1 or more years. Three other birds with centroids in the NE zone made considerable excursions

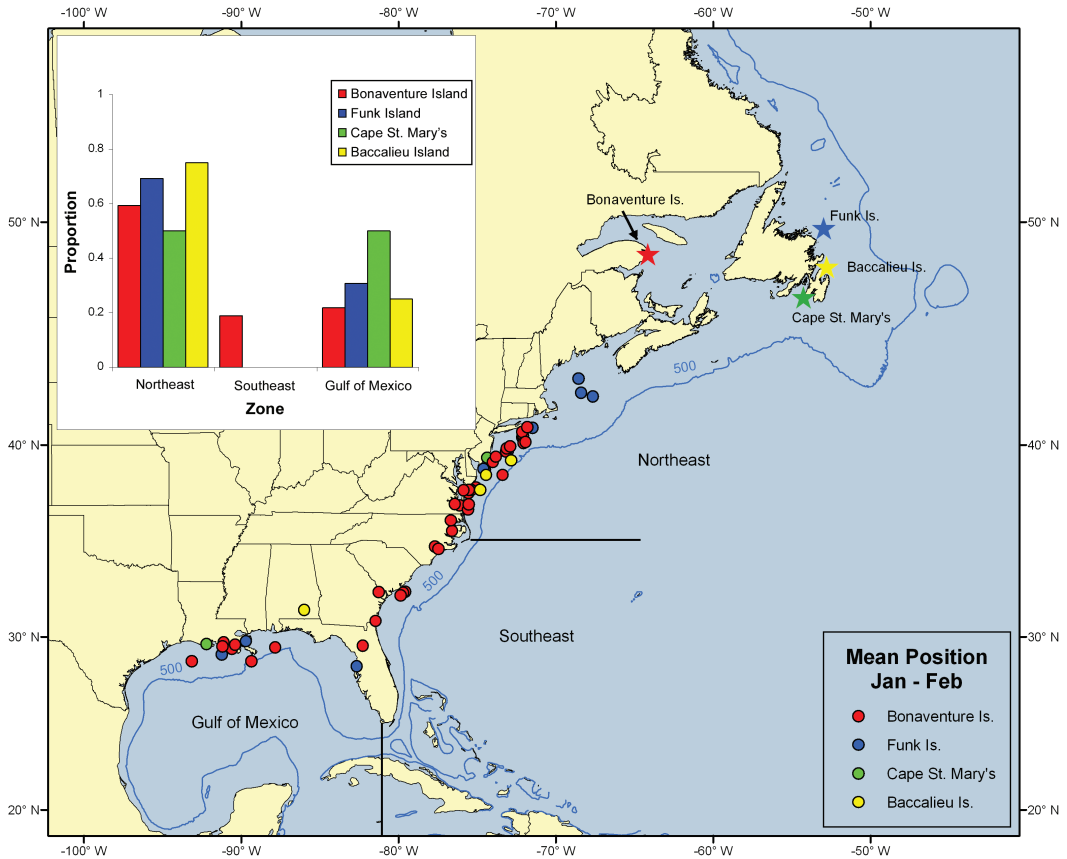


FIG. 6. Location of winter (January–February) centroids from 56 datasets of 40 adult geolocator-equipped Northern Gannets tracked in 1 or 2 years between 2004 and 2010, and frequency distribution (inset) according to oceanographic zone and colony. One Baccalieu Island centroid is on land in Alabama because of an early January stopover in the southeast (SE) zone, followed by wintering along the Louisiana coast.

into the SE zone (e.g., Fig. 9D). The most extensive of these, gannet 23954, remained entirely in the NE zone in 2004–2005, with core and home ranges centered in Chesapeake Bay and the Gulf of Maine. But in 2005–2006, its home range covered most of the area from the northern Gulf of Maine to the coast of Georgia. In this year, its core range consisted of three similarly sized disjoint areas, one in the Gulf of Maine, one in Chesapeake Bay, and one in the South Atlantic Bight. Another gannet (gannet 16207) stopped in the SE zone for the first 2 weeks of January and then moved to the GoMex zone for the rest of the winter. Its home range was partially in the SE zone and partially in the GoMex zone, but its core range was entirely in the Gulf of Mexico.

Neither home-range nor core-range size differences were detected among winter destinations, sexes, or year (at Bonaventure Island; all $P > 0.05$). There was weak support for Funk Island birds' home ranges being larger ($76,698 \pm 19,398 \text{ km}^2$ larger) in 2006–2007 than in 2005–2006 (LMM, $F = 15.63$, $df = 1$ and 4 , $P = 0.017$). Home range sizes for the only other gannets tracked in 2006–2007 (two from Cape St. Mary's) were similar to those for Funk Island ($310,200$ and $266,400 \text{ km}^2$). There was also weak support for a difference between colonies in 2005–2006 (LMM, $F = 5.11$, $df = 1$ and 25 , $P = 0.03$). In that year, Bonaventure Island home ranges were larger ($61,514 \pm 27,203 \text{ km}^2$) than those for Funk Island birds, although this difference was not detected when birds with the two largest home

TABLE 3. Numbers (proportion) of geolocator-equipped Northern Gannets with complete winter (January–February) dataset centroids in each of the North American oceanographic zones, northeast (NE), southeast (SE), and Gulf of Mexico (GoMex), by year, colony, and sex. Birds tracked across multiple years are included only once in combined and total rows.

		NE	SE	GoMex	Total	
Year	2004–2005	11 (0.65)	2 (0.12)	4 (0.23)	17	
	2005–2006	15 (0.56)	5 (0.18)	7 (0.26)	27	
	2006–2007	5 (0.83)	0	1 (0.17)	6	
	2007–2008	1 (0.50)	0	1 (0.50)	2	
	2009–2010	3 (0.75)	0	1 (0.25)	4	
Colony	Bonaventure Island	2004–2005	11 (0.65)	2 (0.12)	4 (0.23)	17
		2005–2006	11 (0.55)	5 (0.25)	4 (0.20)	20
		Combined ^a	15 (0.60)	4 (0.16)	6 (0.24)	25
	Funk Island	2005–2006	4 (0.57)	0	3 (0.43)	7
		2006–2007	5 (0.83)	0	1 (0.17)	6
		Combined	5 (0.62)	0	3 (0.38)	8
	Cape St. Mary's	2007–2008	1 (0.50)	0	1 (0.50)	2
	Baccalieu Island	2009–2010	3 (0.75)	0	1 (0.25)	4
	Sex	Male ^a	14 (0.70)	2 (0.10)	4 (0.20)	20
		Female	6 (0.60)	2 (0.20)	2 (0.20)	10
Grand totals^a		24 (0.62)	4 (0.10)	11 (0.28)	39	

^a Excludes one male bird that was in the GoMex zone in 2004–2005 and the SE zone in 2005–2006.

ranges at Bonaventure Island (gannets 23954 and 23959) were excluded (LMM, $F = 3.03$, $df = 1$ and 23 , $P = 0.1$). The most extreme bird, 23954, ranged widely (described above), while gannet 23959 had a winter home range from the central Gulf of Maine to Cape Hatteras. Although the centroids for the mated pair were separated by ~630 km in 2005–2006, a portion of their home ranges overlapped during January–February, but their overlap index (UDOI = 0.031) was extremely low, indicating little likelihood of shared space use.

The wintering areas of most birds tracked to North American regions in 2 consecutive years ($n = 16$) were remarkably consistent. All birds except one exhibited winter centroids in the same zone in consecutive years (Fig. 10). The median distance observed between consecutive winter centroids was only 87 km (range: 5–746 km). By contrast, the median distance between random pairings of centroids was 763 km. The observed distribution of interannual centroid distances was significantly different than the randomized distribution (K-S test, $D = 0.61$, $P < 0.0001$). There was no detectable difference in the

size of home (paired t -test, $t = -0.08$, $df = 15$, $P = 0.94$) or core (paired t -test, $t = 0.49$, $df = 15$, $P = 0.63$) ranges of individuals in consecutive years.

All home ranges and all but two core ranges overlapped for birds tracked in 2 years (Fig. 11). The median observed overlap of core ranges for year t on year $t + 1$ (39%, range: 0–78%) and for year $t + 1$ on year t (33%, range: 0–87%) were both significantly different than expected by chance (0% for both, K-S tests, both $D = 0.62$, $P < 0.0001$). Likewise, for home ranges, the median observed overlap for year t on year $t + 1$ was 70% (range: 0–96%) (K-S test, $D = 0.62$, $P < 0.0001$), and that for year $t + 1$ on year t was 60% (range: 0–97%), both greater than expected by chance (K-S test, $D = 0.66$, $P < 0.0001$).

North American timing and movement.—Fifty-six complete fall ($n = 40$ individuals) and 51 complete spring ($n = 37$ individuals) migration tracks were recorded. Birds generally migrated over continental shelf waters, but some birds made occasional excursions into much deeper water (Fig. 12). Gannets departed breeding colonies in October and moved southwestward along the eastern coast of North America and, for some,

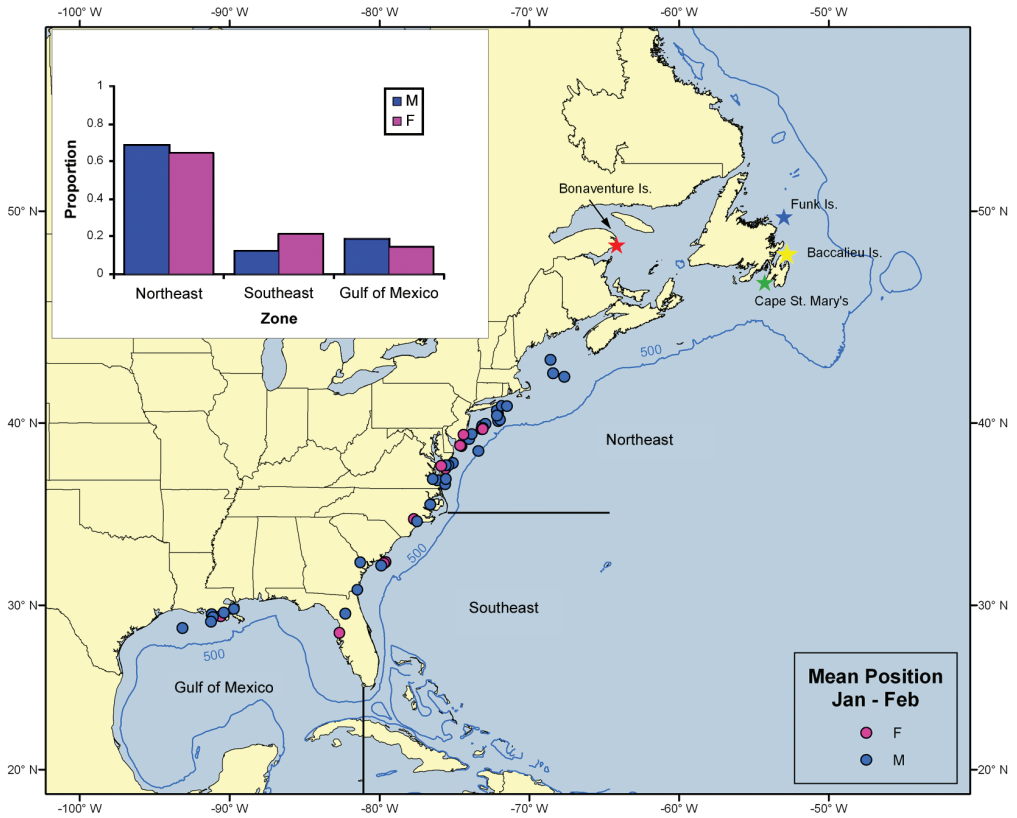


FIG. 7. Location of winter (January–February) centroids, and frequency distribution (inset) of 47 datasets from 31 adult known-sex geolocator-equipped Northern Gannets tracked in 1 or 2 years, according to sex and oceanographic zone.

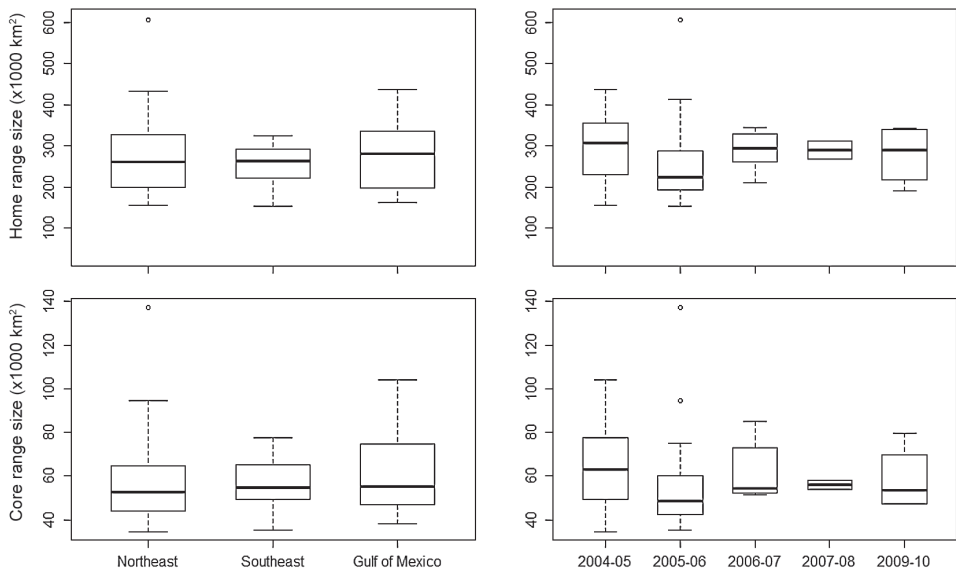


FIG. 8. Home (95%, top) and core (50%, bottom) range sizes by winter destination (left) and year (right) of Northern Gannets. Note the differing scales for home-range versus core-range plots.

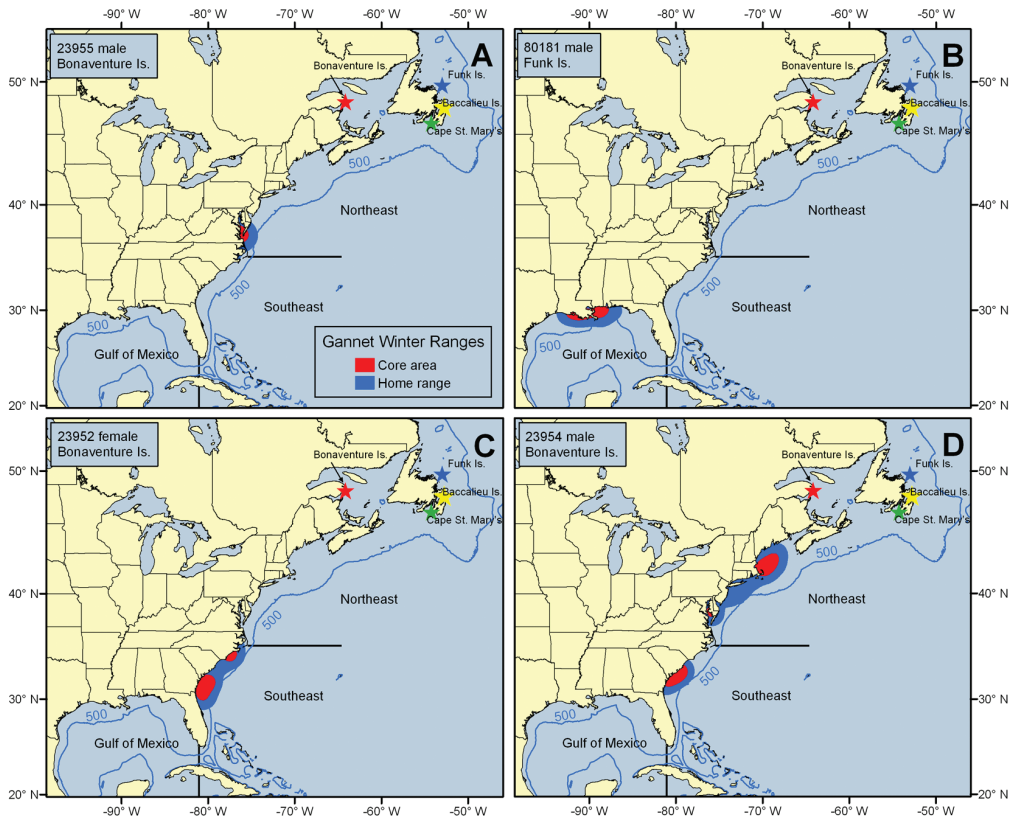


FIG. 9. Typical (A–C) North American winter (January–February) home and core ranges of Northern Gannets, showing restriction to a relatively small core area. (D) Atypical pattern of one bird that ranged widely during January–February.

into the Gulf of Mexico. There was great individual variability in the progress of movement toward wintering areas. Most October positions were north of Cape Cod, but by the last week of the month some birds had reached Cape Hatteras (~35°N). During November, birds were distributed widely, with some remaining near the breeding area while many occurred along the eastern North American coast. The earliest bird arrived at its (NE zone) winter area on 8 November (Table 4). Incredibly, one bird reached its winter area along the coast of Louisiana by 12 November. Gannets vacated the Gulf of St. Lawrence and the continental shelf waters of Newfoundland by mid-December, whereas in the Gulf of Mexico birds reached eastern Texas by early December. All birds (except 8) had finished their migration by 1 January, and by the end of January the most distant had reached the Texas–Mexico border. By then, the limit of

their northern range had retracted to the Gulf of Maine and southern Scotian Shelf. Mean arrival date on the wintering grounds (4 December \pm 21 days) was much more variable than colony departure date. The latest arrival on the wintering grounds occurred in the Gulf of Mexico on 4 February. The duration of the migratory period was also highly variable, ranging from 12 to 110 days (mean: 46 \pm 23 days). Birds had 23 \pm 14 stopover days (range: 1.5–59.5 days) during fall migration, with high stopover concentrations on the Scotian Shelf (especially near Sable Island and The Gully), the mouth of the Bay of Fundy, the western Gulf of Maine, and the Delaware Bay–Chesapeake Bay region, and lesser concentrations on the Grand Bank and along the coast in the SE zone (Fig. 13). The distance traveled between colony departure and arrival on the winter grounds (including distance covered on stopover days) varied from 1,304 to 13,584 km

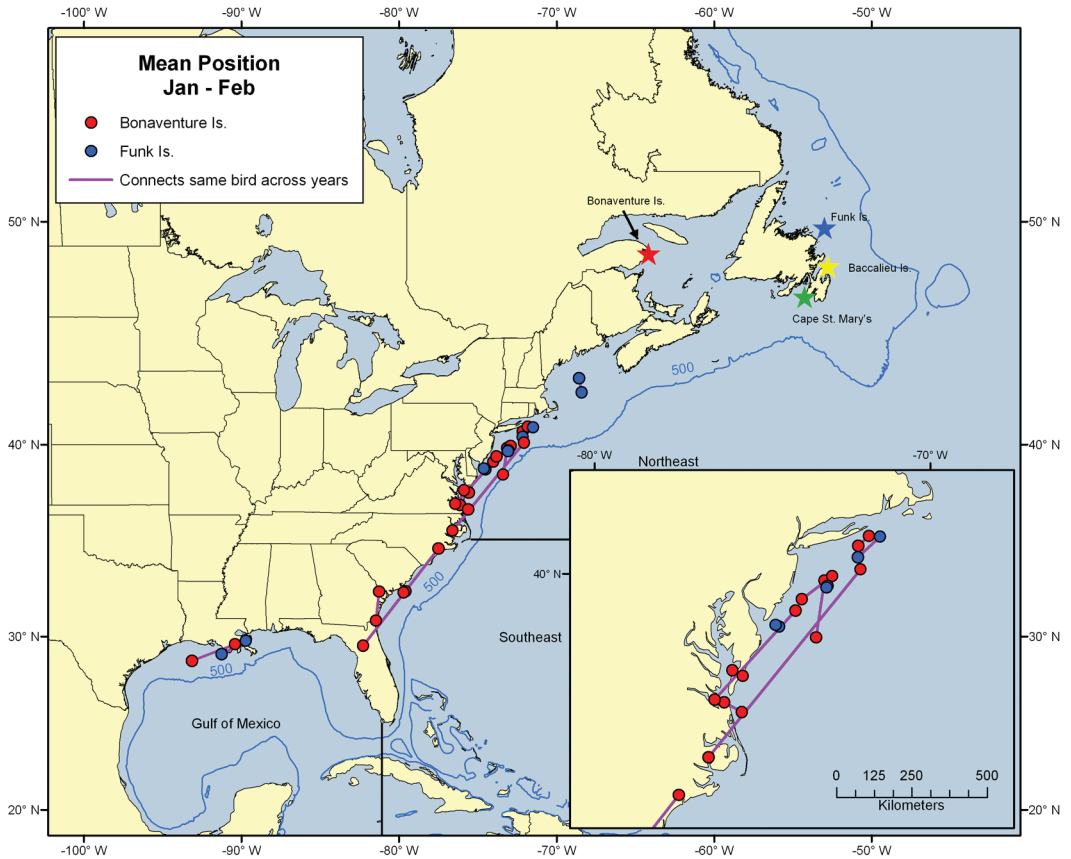


FIG. 10. Interannual consistency of winter (January–February) centroids of Northern Gannets tracked in 2 consecutive years ($n = 16$). Purple lines connect the centroid locations of each bird between years. Inset presents close-up view of the region from Cape Cod to Cape Hatteras for clarity.

(mean: $4,947 \pm 2,500$). There was a strong correlation between migration duration, distance, number of stopover days, and migration end date (all Pearson $r > 0.7$). But there was also considerable individual variation. For example, gannets wintering in the Gulf of Mexico had both the highest and lowest number of stopover days. The mean number of stopover days per day of migration was 0.48 ± 0.15 but ranged from 0.05 to 0.81. The smallest of these, a bird from Funk Island, migrated to the Gulf of Mexico in 28 days at a speed of 184 km day^{-1} with only 2 stopover days. Mean speed of migration was $110 \pm 20 \text{ km day}^{-1}$ (range: $71\text{--}184 \text{ km day}^{-1}$) and did not detectably differ by date of departure (LMM, $F = 0.15$, $df = 13$, $P = 0.70$). Time spent in the winter area varied from 48 to 152 days (mean: 118 ± 26 days, median: 125 days).

Initiation of spring migration ranged from 22 February to 25 April (mean: 29 March ± 14 days; Table 4). Only one departure from the winter grounds occurred in February, the rest occurring in March ($n = 25$) and April ($n = 25$). By the last 2 weeks of March, the earliest birds had reached the Scotian Shelf and Grand Bank ($n = 8$ trips). By 2 April, all birds had vacated the Gulf of Mexico; and by the third week of April, all positions were north of Cape Hatteras. Colony arrival date was less variable than departure from the winter area. Arrival for six trips occurred during the first 2 weeks of April, for 41 trips during the last 2 weeks of April, and 4 occurred during the first week of May, producing a mean colony arrival date of 22 April. The duration of spring migration varied from 2 to 64 days, with a mean of 24 ± 14 days, and

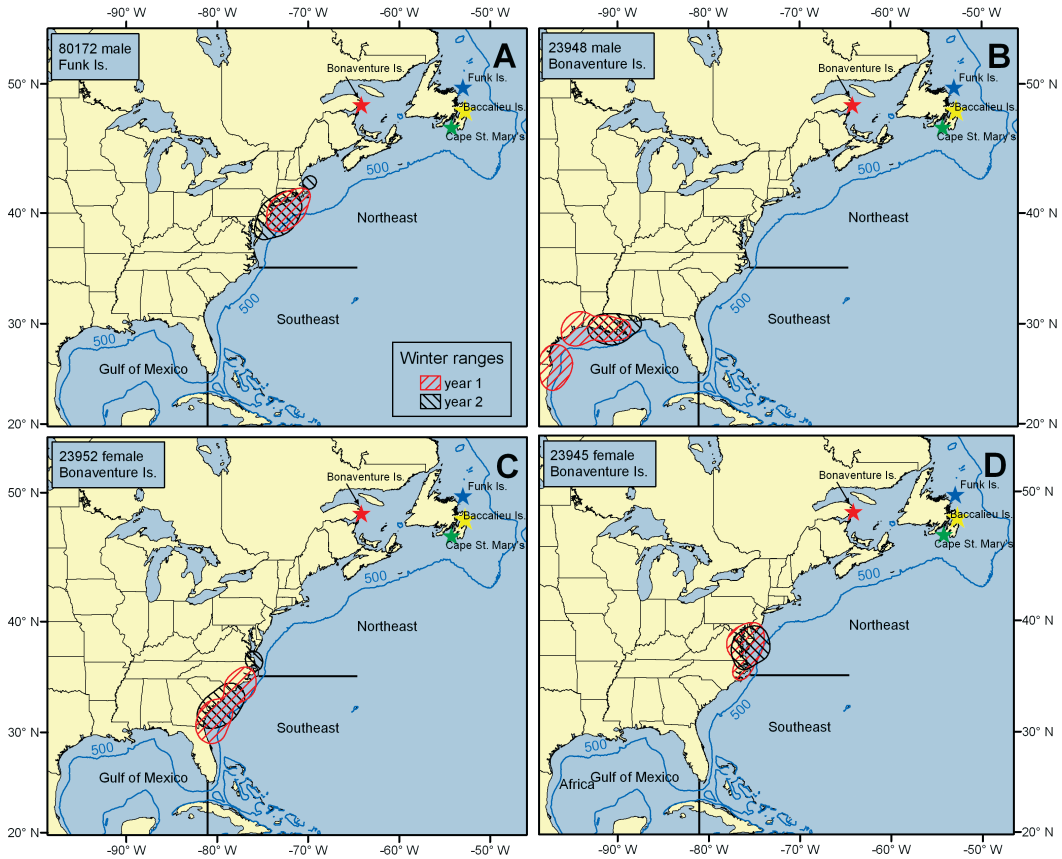


FIG. 11. Typical home-range overlap for Northern Gannets tracked in two consecutive winters. For Bonaventure Island, “year 1” is 2004–2005 and “year 2” is 2005–2006; for Funk Island, “year 1” is 2005–2006 and “year 2” is 2006–2007.

involved 11 ± 8 stopover days (range: 0.5–32.5) en route. Seven birds had no stopover days during spring migration. Important stopover areas during spring migration included the Delaware Bay–Chesapeake Bay region, the area south-east of Long Island, and, to a lesser extent, the western Gulf of Maine and Scotian Shelf (Fig. 13). Surprisingly, geolocator temperature data revealed that two birds spent one or more nights on land (one gannet on 9 and 16 April 2005, and one during most nights 19–28 March 2005) in the vicinity of Sable Island, which suggests that they roosted on this offshore island. The mean number of stopover days per day of migration was similar to that in fall, at 0.42 ± 0.18 (range: 0.02–0.80). The distance covered during spring migration (including distances moved on stopover days) was $3,408 \pm 1,840$ km

(range: 619–9,641 km) at an overall speed of 164 ± 72 km day⁻¹ (range: 84–486 km day⁻¹). Migrations initiated later in spring were 1.9 ± 0.8 days shorter per day of delayed departure than those initiated earlier (LMM, $F = 5.43$, $df = 1$ and 11 , $P = 0.04$).

There was little detectable evidence of colony-specific differences in migration parameters between Bonaventure Island and Funk Island in 2005–2006 (Table 4). One exception, contrary to expectation, was that birds returned to the more northerly colony at Funk Island 11 ± 2 days earlier (LMM, $t = -5.06$, $df = 23$, $P < 0.0001$) in spring than at Bonaventure Island in 2005–2006 (all other $P > 0.01$). Colony arrival at Funk Island in this year was also earlier than in the subsequent year.

Winter destination had a significant effect on most timing and movement parameters for

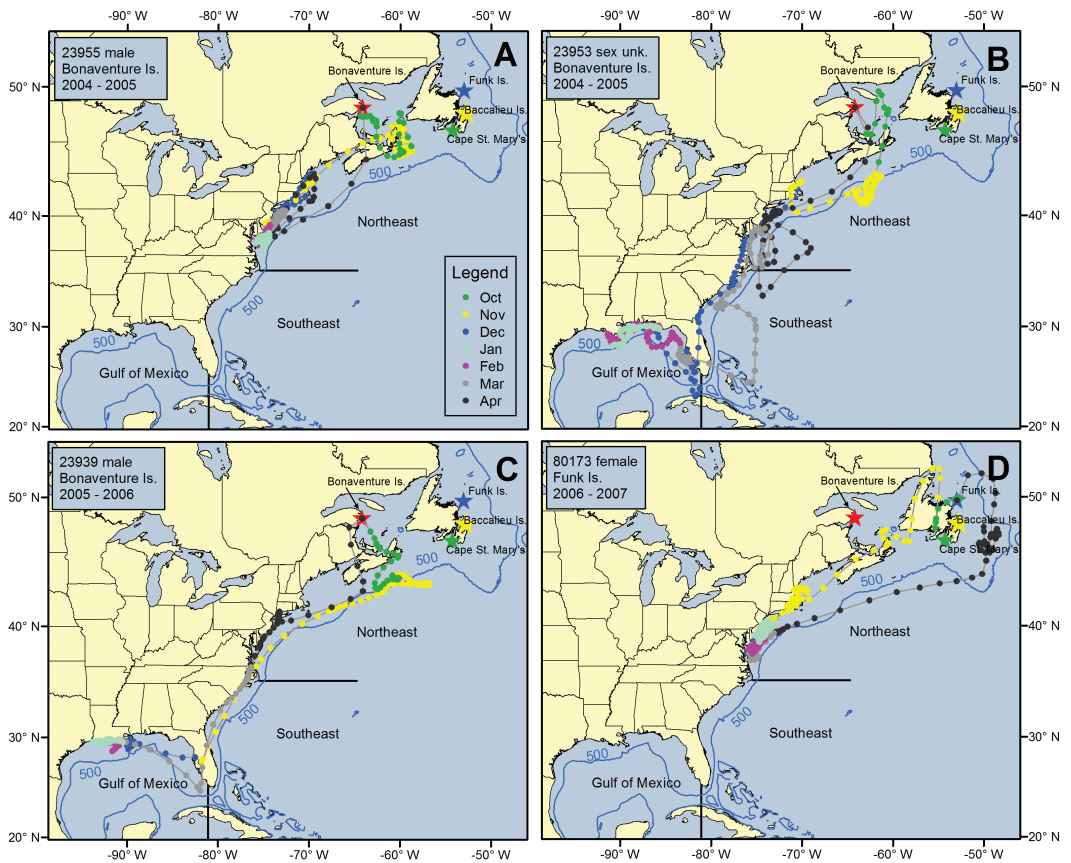


FIG. 12. Migration routes of four individual geolocator-equipped Northern Gannets, showing (A) much shorter spring versus fall migration, (B) unusual extensive offshore excursions during spring migration, (C) direct migration punctuated by significant fall stopover on the Scotian Shelf and a brief stop at Long Island in spring, and (D) fall migration through the Strait of Belle Isle and along the west coast of Newfoundland with faster and more offshore spring migration. Dots represent bird positions (2 day^{-1}), and stars indicate colony locations.

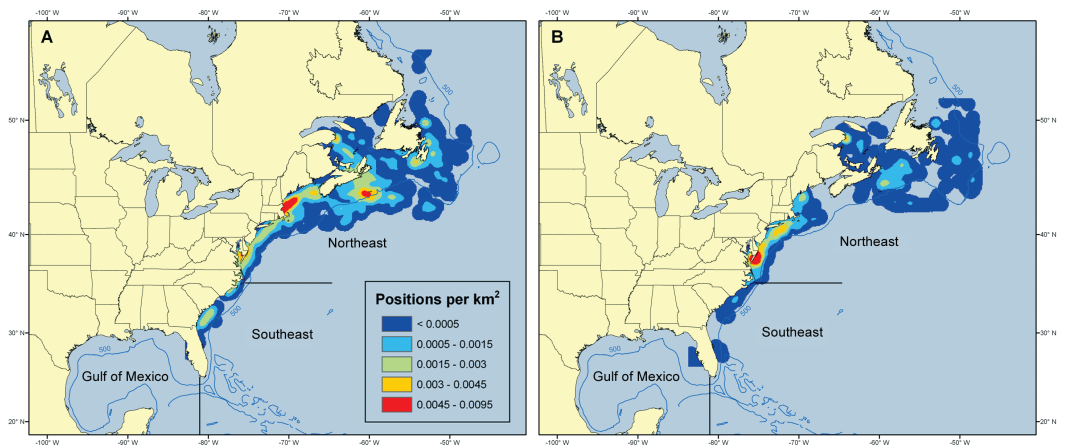


FIG. 13. Maps of (A) fall and (B) spring density of stopover days for Northern Gannet migrations in North America.

TABLE 4. Migration parameters (means \pm SD; range in parentheses) of Northern Gannets in North America.

		Start date	End date	Duration (days)	Stopovers (days)	Distance (km)	Speed (km days ⁻¹)
Fall							
All birds	<i>n</i> = 56	20 Oct \pm 6 (3–28 Oct) ^a	4 Dec \pm 21 (8 Nov–4 Feb)	46 \pm 23 (12–110)	23 \pm 14 (1.5–59.5)	4,947 \pm 2,500 (1,304–13,584)	110 \pm 20 (71–184)
Females	<i>n</i> = 14	17 Oct \pm 7	27 Nov \pm 19	42 \pm 19	19.5 \pm 12.5	4,601 \pm 1,983	114 \pm 17
Males	<i>n</i> = 33	(3–26 Oct) 22 Oct \pm 5 (10–28 Oct)	(7 Nov–12 Jan) 3 Dec \pm 17 (8 Nov–12 Jan)	(22–86) 43 \pm 19 (12–82)	(4.5–51) 22 \pm 13 (1.5–48)	(2,580–8,655) 4,390 \pm 1,760 (1,304–9,328)	(77–132) 107 \pm 23 (71–184)
Bonaventure Island	2004–2005 <i>n</i> = 17	23 Oct \pm 5 (9–28 Oct)	4 Dec \pm 20 (8 Nov–18 Jan)	43 \pm 23 (22–102)	22 \pm 13.5 (4.5–45)	4,540 \pm 2,834 (2,518–13,584)	107 \pm 23 (71–143)
	2005–2006 <i>n</i> = 20	19 Oct \pm 7 (3–27 Oct)	28 Nov \pm 17 (8 Nov–3 Jan)	40 \pm 17 (12–82)	21 \pm 12.5 (3–48)	4,320 \pm 1,667 (1,304–7,224)	110 \pm 17 (81–135)
Funk Island	2005–2006 <i>n</i> = 7	16 Oct \pm 5 (10–22 Oct)	3 Dec \pm 17 (9 Nov–21 Dec)	47 \pm 18 (28–72)	20.5 \pm 11 (1.5–31.5)	5,524 \pm 1,900 (3,408–8,655)	121 \pm 31 (84–184)
	2006–2007 <i>n</i> = 6	22 Oct \pm 3 (18 Oct–26 Oct)	8 Dec \pm 23 (15 Nov–1 Dec)	46 \pm 23 (22–80)	21 \pm 15.5 (7.5–48)	4,912 \pm 2,368 (2,740–9,328)	108 \pm 16 (84–122)
Spring							
All birds	<i>n</i> = 51	29 Mar \pm 14 (22 Feb–25 Apr)	22 Apr \pm 6 (5 Apr–4 May)	24 \pm 14 (2–64)	11 \pm 8 (0.5–32.5)	3,408 \pm 1,840 (619–9,461)	164 \pm 72 (84–486)
Females	<i>n</i> = 13	31 Mar \pm 10 (15 Mar–17 Apr)	22 Apr \pm 7 (8 Apr–4 May)	22 \pm 15 (4–49)	10.5 \pm 10.5 (0.5–32.5)	3,119 \pm 1,362 (1,257–5,702)	188 \pm 85 (84–385)
Males	<i>n</i> = 31	30 Mar \pm 14 (2 Mar–25 Apr)	22 Apr \pm 6 (5 Apr–4 May)	23 \pm 13 (2–64)	10.5 \pm 6 (0.5–23)	3,283 \pm 1,850 (619–9,461)	159 \pm 72 (103–486)
Bonaventure Island	2004–2005 <i>n</i> = 15	3 Apr \pm 15 (1 Mar–25 Apr)	23 Apr \pm 5 (16 Apr–4 May)	21 \pm 15 (2–55)	11 \pm 9 (0.5–32.5)	3,014 \pm 2,114 (619–9,205)	182 \pm 103 (84–486)
	2005–2006 <i>n</i> = 19	30 Mar \pm 11 (13 Mar–19 Apr)	24 Apr \pm 4 (17 Apr–3 May)	25 \pm 13 (7–49)	11 \pm 7 (0.5–24.5)	3,223 \pm 1,426 (1,365–5,702)	137 \pm 29 (102–218)
Funk Island	2005–2006 <i>n</i> = 6	21 Mar \pm 13 (3 Mar–2 Apr)	13 Apr \pm 6 (5–20 Apr)	23 \pm 13 (6–40)	10 \pm 9.5 (0.5–23)	3,823 \pm 1,338 (1,867–5,133)	189 \pm 62 (119–287)
	2006–2007 <i>n</i> = 6	25 Mar \pm 16 (2 Mar–14 Apr)	26 Apr \pm 4 (21 Apr–4 May)	32 \pm 18 (12–64)	12.5 \pm 5.5 (4–19)	4,886 \pm 2,607 (2,040–9,461)	156 \pm 23 (133–195)

^aNumber of trips for fall start date is 53 because one bird lost its chick and departed early.

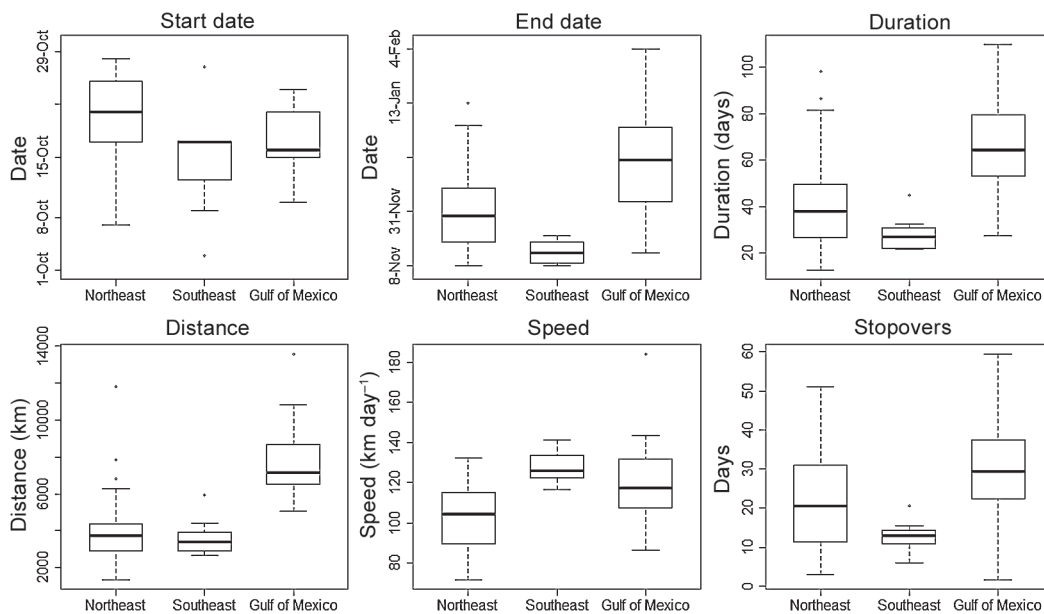


FIG. 14. Boxplots of fall migration parameters by winter destination for Northern Gannets: northeast (NE) zone, $n = 35$; southeast (SE) zone, $n = 7$; and Gulf of Mexico (GoMex) zone, $n = 14$ (except for start date, where GoMex = 13).

both the fall and spring migrations. In comparison to the NE zone, trips to the GoMex zone departed on similar dates but took 27 ± 7 more days (LMM, $t = 3.77$, $df = 14$, $P = 0.002$), covered greater distance ($3,686 \pm 765$ km; LMM, $t = 4.81$, $df = 14$, $P = 0.0003$) at a faster speed (18 ± 7 km day⁻¹; LMM, $t = 2.67$, $df = 14$, $P = 0.018$), and, contrary to expectation, used a similar number of stopover days to reach the more distant wintering area (Fig. 14). Expectedly, the gannet with the shortest distance (1,304 km) wintered in the NE zone and the one with the longest distance (13,584 km) in the GoMex zone, but the gannet with the second-longest distance (11,778 km) wintered in the NE zone. It made a trip to the central Labrador shelf immediately after colony departure, vastly increasing its migration distance.

Surprisingly, migration parameters for trips to the SE zone were not intermediate between those for the NE zone and the GoMex zone (Fig. 14). Instead, in comparison to the NE zone, they had earlier fall departure dates (5.5 ± 2.5 days; LMM, $t = -2.24$, $df = 14$, $P = 0.042$) and covered similar distances during similar migration durations (LMM, both $P > 0.1$) by taking less circuitous routes at a faster speed (25 ± 4 km day⁻¹;

LMM, $t = 5.59$, $df = 14$, $P = 0.0001$), using 9.5 ± 3 fewer stopover days (LMM, $t = -3.20$, $df = 14$, $P = 0.006$; Fig. 14). In comparison to the GoMex zone, trips to the SE zone departed on similar dates (LMM, $P > 0.1$), took 41 ± 8 fewer days (LMM, $t = -4.89$, $df = 15$, $P = 0.0002$), covered $4,173 \pm 1,060$ fewer kilometers (LMM, $t = -3.95$, $df = 15$, $P = 0.0013$) at a similar speed (LMM, $P > 0.1$), and used 17 ± 4.5 fewer stopover days (LMM, $t = -3.97$, $df = 15$, $P = 0.0012$; Fig. 14).

In contrast to fall, spring migration conformed better to expectations. In most cases, parameters for gannets wintering in the SE zone were intermediate between those in the NE zone and those in the GoMex zone and were more similar to the latter. There were significant differences detected between one or more winter zones in all measured parameters, except date of arrival on the wintering grounds, and the greatest differences were between the most widely separated areas (i.e., NE vs. GoMex; Fig. 15). Comparison of spring migrations between nearer (to the colony) and more distant zones included earlier departure from the wintering area (GoMex vs. NE: 24 ± 4 days; LMM, $t = -6.20$, $df = 12$, $P < 0.0001$; SE vs. NE: 16 ± 4 days; LMM, $t = -3.22$, $df = 12$, $P = 0.0074$), longer

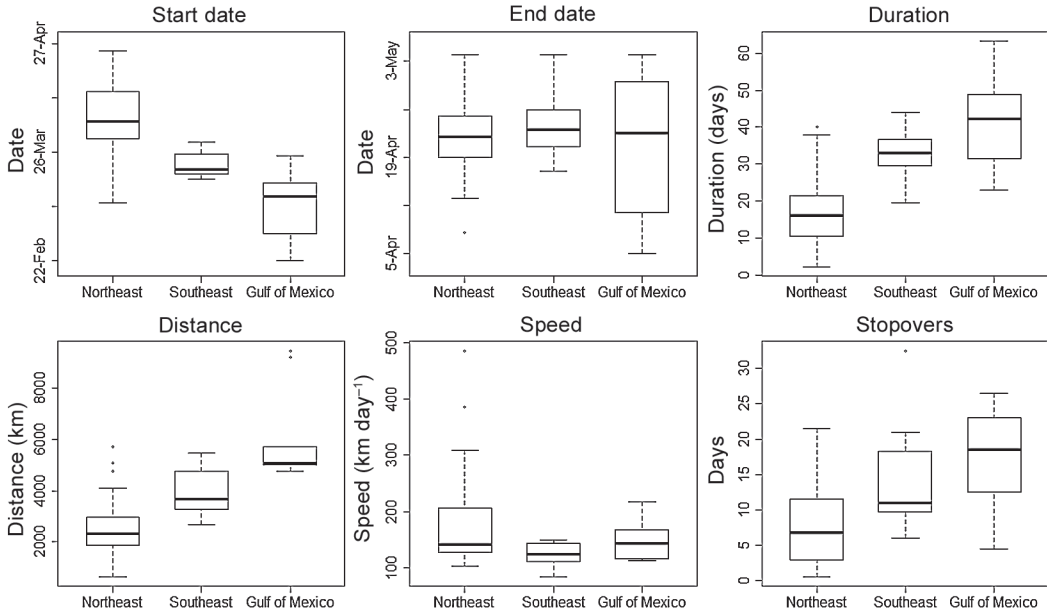


FIG. 15. Boxplots of spring migration parameters by winter destination for Northern Gannets: northeast (NE) zone, $n = 34$; southeast (SE) zone, $n = 7$; and Gulf of Mexico (GoMex) zone = 10.

migration duration (GoMex vs. NE: 24 ± 4 days; LMM, $t = 5.91$, $df = 12$, $P < 0.0001$; SE vs. NE: 16 ± 5 days; LMM, $t = 3.32$, $df = 12$, $P = 0.006$), greater travel distances (GoMex vs. NE: $3,373 \pm 653$ km; LMM, $t = 5.17$, $df = 12$, $P = 0.0002$; SE vs. NE: $1,415 \pm 621$ km; LMM, $t = 2.29$, $df = 12$, $P = 0.0412$), using more stopover days (GoMex vs. NE: 10 ± 2.5 days; LMM, $t = 3.79$, $df = 12$, $P = 0.003$; SE vs. NE: 7.5 ± 3 days; LMM, $t = 2.30$, $df = 12$, $P = 0.041$) but with a lack of detectable difference in speeds (except SE vs. NE: 53 ± 17 km day⁻¹ slower; LMM, $t = 12$, $df = -3.03$, $P = 0.01$). In contrast to fall migration, the top 10 fastest (speed-wise) spring migrations were all by birds from the NE zone, except one migrating from the GoMex zone (the same bird that had the fastest migration in fall).

Only colony departure date provided a detectable difference between the sexes: males departed the colony 5 ± 2 days later than females (LMM, $t = 2.97$, $df = 29$, $P = 0.006$; Table 4). In the only mated pair tracked, the male departed 6 and 11 days later than the female in 2004 and 2005, respectively. Contrary to expectation, we failed to detect a difference in colony return date between males and females in spring (LMM, $P > 0.1$; Table 4). This result did not change when each colony was examined separately in each

year (all $P > 0.1$). The male of the mated pair returned 3 days before the female in 2006.

There was weak evidence that departures from Bonaventure Island were 4 ± 2 days later (LMM, $t = -2.24$, $df = 10$, $P = 0.049$) in 2004–2005 than in 2005–2006, with marginal evidence for earlier departure (6 ± 2 days; LMM, $t = 2.68$, $df = 4$, $P = 0.056$) at Funk Island in 2005–2006 than in 2006–2007. Birds also returned to Funk Island 13 ± 3 days earlier (LMM, $t = 4.18$, $df = 4$, $P = 0.014$) in 2005–2006 than in 2006–2007 (Table 4). There was no evidence for a detectable difference between years for any other migration parameters (LMM, all $P > 0.1$).

Spring migration routes generally retraced those of fall, and, contrary to the suggestion by Perkins (1979), only 16 of 51 migrations had significant portions of the spring migration more offshore than during fall. Overall, spring migrations were faster and shorter than fall migrations. Spring migrations were 21 ± 3 days shorter (LMM, $t = -6.98$, $df = 66$, $P < 0.0001$), covered $1,277 \pm 269$ fewer kilometers (LMM, $t = -4.71$, $df = 66$, $P < 0.0001$) at 54 ± 10 km day⁻¹ faster speed (LMM, $t = -5.03$, $df = 66$, $P < 0.0001$), and used 12 ± 2 fewer stopover days (LMM, $t = -5.72$, $df = 66$, $P < 0.0001$; Fig. 16). However, the number of stopover days per day of migration was

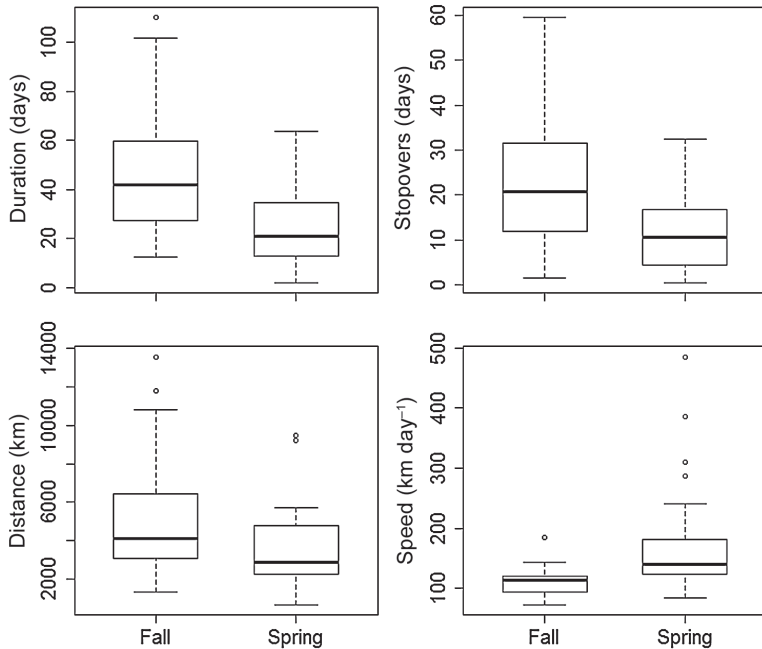


FIG. 16. Comparison of fall and spring migration parameters in Northern Gannets.

quite similar (0.48 ± 0.15 vs. 0.42 ± 0.15). This overall pattern did not show a detectable difference between males and females (all $P > 0.1$), but it differed depending on winter destination for all parameters (all interactions of season and destination; $P < 0.01$). Inspection of interaction plots (Fig. 17) showed that the difference between fall and spring migrations to or from the NE zone and the GoMex zone were consistent for all parameters, whereas the difference between fall and spring migrations to or from the SE zone did not follow the same pattern. In all cases (except speed), spring migration parameters for the SE zone were intermediate between those for trips migrating from the NE zone and the GoMex zone, as expected (Fig. 17). The lack of consistency with the other two zones was due to the uncharacteristically fast and short migrations to the SE zone in fall.

In the population as a whole, there was no indication that individuals shifted the timing of their migratory movements in successive years (paired t -tests, all $P > 0.05$). However, repeatability scores were significant only for certain timing parameters (Table 5). All migration parameters showing significant repeatability had r scores ≥ 0.42 . Fall migration end date,

duration, and distance, all of which were highly correlated (Pearson $r \geq 0.8$), exhibited significant repeatability. Similarly, spring departure date, duration, and distance showed significant repeatability within individuals; again these three parameters are highly correlated (Pearson $r \geq 0.9$). These results did not change when colonies were considered separately, except that spring colony arrival date was significantly

TABLE 5. Repeatability (r) of migration behaviors between years for Northern Gannets.

	r	F	P
Fall ($n = 16$)			
Start date	<0.01	0.94	0.55
End date	0.42	2.47	0.04
Duration (days)	0.42	2.47	0.04
Stopovers (days)	0.30	1.78	0.13
Distance (km)	0.61	4.08	0.004
Speed (km day ⁻¹)	0.32	1.92	0.1
Spring ($n = 14$)			
Start date	0.90	17.41	<0.0001
End date	<0.01	0.84	0.62
Duration (days)	0.75	6.87	0.0005
Stopovers (days)	0.37	2.20	0.08
Distance (km)	0.64	4.59	0.004
Speed (km day ⁻¹)	<0.01	0.93	0.55

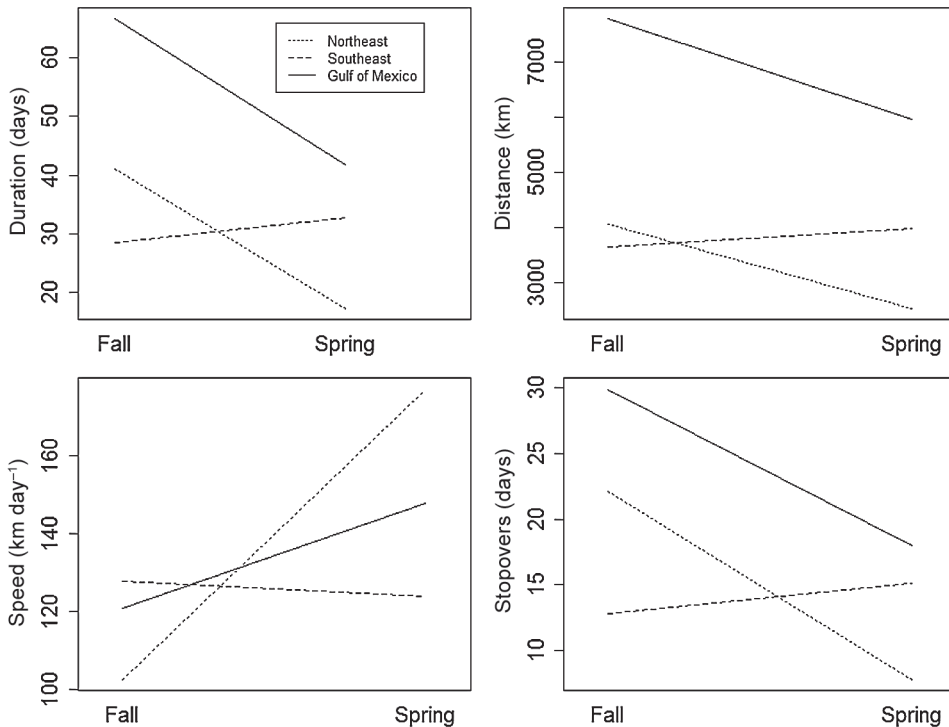


FIG. 17. Interaction plots of spring and fall migration parameters versus winter destination in Northern Gannets. Dotted lines = northeast (NE) zone, dashed lines = southeast (SE) zone, and solid lines = Gulf of Mexico (GoMex) zone.

repeatable for Bonaventure Island birds ($r = 0.59$, $F = 3.97$, $df = 8$ and 9 , $P = 0.03$) but did not show a detectable difference for Funk Island birds ($r < 0.01$, $F = 0.099$, $df = 4$ and 5 , $P = 0.98$).

Trans-Atlantic migration and wintering areas from banding data.—Nine recoveries of gannets banded in North America (Table 6) occurred in the eastern Atlantic (also see Gaston et al. 2008). Most ($n = 6$) were recovered as immature birds, though three were adults when recovered. Gannets from Funk Island were recovered in Iceland, Ireland, Portugal, Morocco, and Madeira; the single (immature) gannet from Bonaventure Island was recovered in northern Spain (Fig. 18). Birds banded as chicks comprised the most Atlantic-crossing gannets (6 of 8 at Funk Island, 1 at Bonaventure Island), and four recoveries occurred in the first year of life (all from Funk Island; Table 6). Most recoveries occurred during the nonbreeding season, except for two fledglings banded at Funk Island: one banded in August 1986 and recovered in Morocco one month later, and one banded in

August 1984 and recovered as an adult in Iceland in May 1991. About 5 \times more gannets have been banded in eastern Atlantic colonies ($n = 62,328$ banded, 3,218 recoveries; Wanless 2002) than in North America ($n = 13,946$ banded, 832 recoveries; Table 7). Yet not a single gannet banded in the eastern Atlantic Ocean has been recovered in the western Atlantic. The difference in the frequency of Atlantic crossings by North American (9 of 832) versus European (0 of 3,218) gannets is remarkable (Fisher exact test, $P < 0.0001$).

The rate of trans-Atlantic recoveries differed between birds originating from Bonaventure Island and colonies in Newfoundland (Funk Island, Cape St. Mary's, and Baccalieu Island). Trans-Atlantic birds accounted for 7.2% (8 of 111) of the band recoveries from Newfoundland colonies (adults and immatures combined), which was significantly greater than the 0.1% (1 of 714) of the Bonaventure Island recoveries (Fisher exact test, $P < 0.0001$; Table 7). Considering only adults, trans-Atlantic recoveries accounted for 6.1% (3 of 49) of Newfoundland recoveries,

TABLE 6. Location, age, and date of trans-Atlantic band recoveries of Northern Gannets banded at North American colonies (see Fig. 18).

Colony	Band number	Banding date	Recovery age	Recovery date	Recovery location
Funk Island	0638-73740 ^a	Aug 1984	Adult ^b	May 1991	Iceland
	0748-54713	Aug 1988	Adult ^c	Feb 1994	Iceland
	0748-54848 ^a	Aug 1988	Adult ^d	Nov 1988	Morocco
	0638-73634 ^a	Aug 1984	Immature	Mar 1988	Ireland
	0678-27286	Aug 1979	Immature	Nov 1979	Portugal
	0638-73693 ^a	Aug 1984	Immature	Nov 1984	Portugal
	0678-27313 ^a	Aug 1979	Immature	Oct 1979	Madeira
Bonaventure Island	0748-05814	Aug 1986	Immature	Sep 1986	Morocco
	0508-00379 ^a	Sep 1967	Immature	Nov 1970	Spain

^aDetails reported in Gaston et al. (2008).^bBanded as an immature.^cBanding age: "after hatch year."^dBanded as an adult.

TABLE 7. Comparison of North American and trans-Atlantic Northern Gannet band recoveries and round-trip migrations based on geolocators, summarized by colony, region, continent, and age.

Location	Bands									
	Banded	Recoveries			Trans-Atlantic recoveries			Geolocators Overwinter area		
		Adult	Imma- ture	All ages	Imma- ture	Adult	All ages	Non-trans- Atlantic	Trans- Atlantic	All
North America										
Newfoundland										
Funk Island	2,877	46	60	106	5	3	8	8	1	9
Cape St. Mary's	108	1	0	1	0	0	0	3	1	4
Baccalieu Island	45	2	2	4	0	0	0	4	1	5
Newfoundland total	3,030	49	62	111	5	3	8	15	3	18
Gulf of St. Lawrence										
Bonaventure Island	10,809	265	449	714	1	0	1	28	0	28
Other ^a	107	1	6	7	0	0	0	-	-	-
North American total	13,946	315	517	832	6	3	9	43	3	46
Europe										
France, Norway, United Kingdom ^b										
European total	62,328	-	-	3,218	0	0	0	106	0	106

^aGannets banded along the east coast of North American, colony of origin unknown.^bSource: Fort et al. 2012, Stauss et al. 2012.

compared with zero of the 265 recoveries from Bonaventure Island (Fisher exact test, $P = 0.004$).

Trans-Atlantic wintering areas from geolocators.—Remarkably, three geocator-equipped gannets ($n = 4$ trips), one from each of the Newfoundland colonies, displayed a radically different migration and overwinter strategy than those wintering in North America. These birds, one from Cape St. Mary's (80182, sex unknown, hereafter "bird 82"), one from Funk Island (80185, female, hereafter "bird 85") and one from Baccalieu Island (16295, sex

unknown, hereafter "bird 95"), undertook previously undescribed round-trip trans-Atlantic migrations to the west coast of Africa (Fig. 19 and Table 7). The birds spent the winter over the narrow continental shelf along the coasts of Western Sahara, Mauritania, and Senegal in the Canary Current. Winter centroids were 4,267, 4,343, and 4,320 km from their respective breeding colonies, exceeding the distances of all birds wintering in North America. Interestingly, bird 85 was tracked again during the following year, when it again wintered off the coast of West



FIG. 18. Banding and recovery locations of Northern Gannets banded in North America and recovered in the eastern Atlantic Ocean (based on Gaston et al. 2008; for details, see Table 6).

Africa, where its winter centroid was 4,335 km from the colony (the other two birds were not tracked again). Home-range and core-range sizes (home: 171,200–309,800 km²; core: 38,000–57,800 km²) were comparable but on the low end of the range sizes for their North American wintering counterparts (Table 8).

The frequency of the two migration strategies (North American vs. trans-Atlantic) in geolocator-equipped birds differed among North American colonies. Three of 18 breeding gannets from Newfoundland colonies made round-trip trans-Atlantic migrations, whereas none of the 28 birds from Bonaventure Island did so (Table 7). This difference in the frequencies, although constrained by limited sample size, approached significance (Fisher exact test, $P = 0.07$).

Trans-Atlantic timing and movement.—In 2005, bird 82 and bird 85 departed their colonies (separated by 350 km) 9 days apart in October and remained on the Grand Bank until the last week of October. They then departed Canadian shelf waters within a day of one another on 26–27 October (Fig. 19 and Table 8). Over the next 5 days, both birds crossed the North Atlantic, traveling distances of about 3,600 to 3,800 km. Bird 82 took a northerly route to reach coastal Spain, traveling at a speed of 717 km day⁻¹, and then, within a few days, moved south to arrive at its wintering area off Western Sahara by 6 November (Fig. 19A). Bird 85 took a more direct route via the Canary Islands, averaging 762 km day⁻¹ to reach the coast of Western Sahara by 1 November 2005, where it stopped until early January before moving

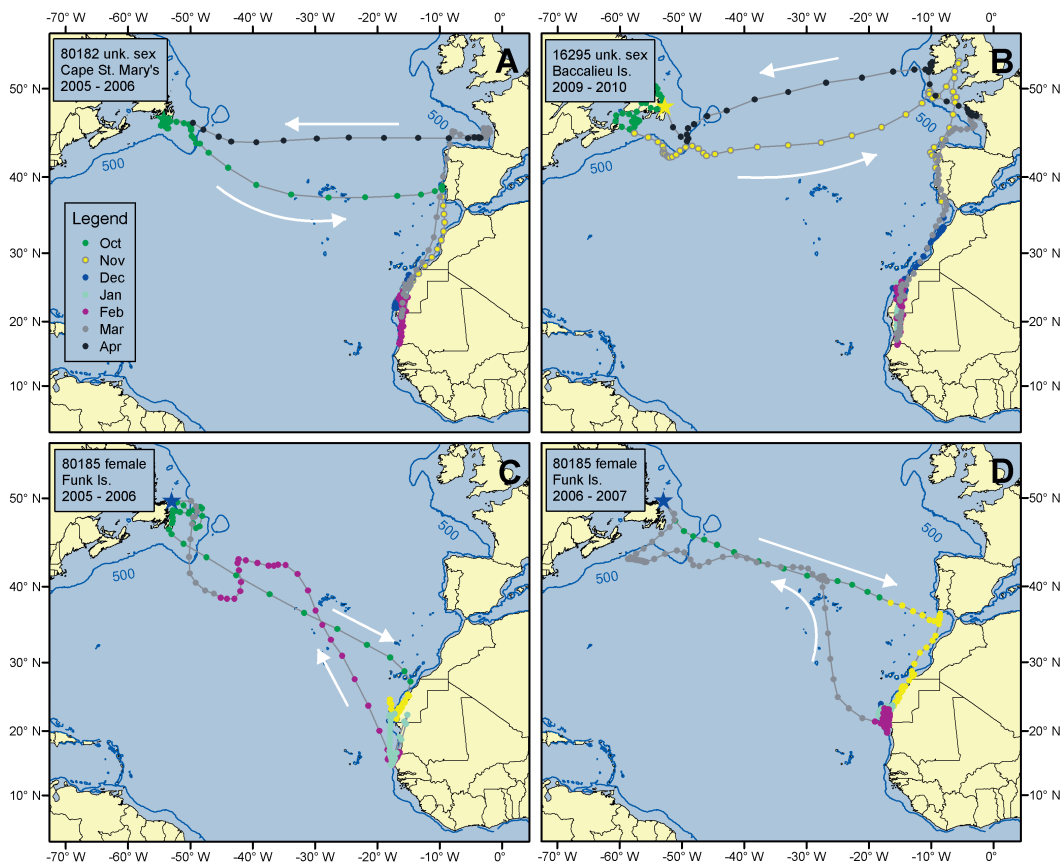


FIG. 19. Tracks of trans-Atlantic migration and wintering on the coast of western Africa by three Northern Gannets breeding at (A) Cape St. Mary's (bird 82; 2005–2006), (B) Baccalieu Island (bird 95; 2009–2010), (C) Funk Island (bird 85; 2005–2006), and (D) the same bird from Funk Island in 2006–2007. Dots represent bird positions (2 day^{-1}).

south to spend the rest of the winter off the coast of Senegal (Fig. 19C).

Timing and routes of return spring migration differed between these two birds. In mid-March 2006, bird 82 retraced its route northward, spending late March in the Bay of Biscay, and on 4 April it departed on its trans-Atlantic journey (Fig. 19A). Its route took it ≤ 800 km north of its eastward autumn crossing, recrossing the North Atlantic in 5 days, at a speed of 679 km day^{-1} , to arrive on the Canadian shelf waters by 8 April 2006 (Table 8). By contrast, bird 85 initiated its return much earlier, on 17 February 2006. It made good progress for the first 5 days but then progressed slowly for the next 9 days on a more circuitous route, to reach Canadian shelf waters on 3 March 2006 (Fig. 19C). Overall, it covered

5,409 km on its 15-day crossing, averaging 361 km day^{-1} (Table 8).

In 2006–2007, bird 85 departed the colony on 24 October and departed Canadian shelf waters on 26 October, one day earlier than in the previous year (Fig. 19D). It took a more northerly route than in 2005 and reached coastal waters off southwestern Portugal after covering 3,502 km in 9 days at a speed of 389 km day^{-1} , about half its speed in the previous year. It then proceeded south along the African coast, to reach its winter area by 16 November (Table 8). Remarkably, it remained on the winter grounds only 1 day longer than in the previous year. Its return migration, beginning on 1 March 2007, was the longest of any trans-Atlantic trip (16 days), and the only one to feature a stopover. After leav-

TABLE 8. Migration parameters and winter range sizes of North American breeding Northern Gannets wintering on the west African coast.

	Bird 82 Cape St. Mary's 2005–2006	Bird 85 Funk Island 2005–2006	Bird 85 Funk Island 2006–2007	Bird 95 Baccalieu Island 2009–2010
Fall				
Start date	6 Oct	15 Oct	24 Oct	17 Oct
Begin Atlantic crossing	26 Oct	27 Oct	26 Oct	8 Nov
End Atlantic crossing	30 Oct	1 Nov	3 Nov	15 Nov
Duration Atlantic crossing	5	5	9	7
Distance Atlantic crossing	3,586	3,810	3,502	3,322
Speed Atlantic crossing (km day ⁻¹)	717	762	389	475
Stopover Atlantic crossing	0	0	0	0
End date	6 Nov	5 Nov	16 Nov	9 Dec
Duration (days)	31	22	23	54
Stopovers (days)	14	6	2	17
Distance (km)	6,343	6,347	5,899	10,145
Speed (km day ⁻¹)	205	289	256	188
Winter				
Home range size (km ²)	171,200	226,000	213,600	309,800
Core range size (km ²)	38,000	39,700	57,500	48,300
Days in winter area	127	104	105	94
Spring				
Start date	13 Mar	17 Feb	1 Mar	14 Mar
Begin Atlantic crossing	4 Apr	17 Feb	1 Mar	9 Apr
End Atlantic crossing	8 Apr	03 Mar	16 Mar	13 Apr
Duration Atlantic crossing	5	15	16	4.5
Distance Atlantic crossing	3,397	5,409	4,587	2,758
Speed Atlantic crossing (km day ⁻¹)	679	361	287	613
Stopover Atlantic crossing	0	0	0	4
End date	9 Apr	7 Mar	29 Mar	17 Apr
Duration (days)	28	18	28	34
Stopovers (days)	9	3	10	12
Distance (km)	7,435	6,016	6,392	7,584
Speed (km day ⁻¹)	266	334	229	223

ing the African coast, it proceeded almost due north until intersecting its fall route north of the Azores, where it paused for 4 days. On 10 March 2007, it departed the stopover area for the final 9 days of the journey, to reach the Canadian shelf by 13 April, covering 4,587 km across the Atlantic at an overall speed of 229 km day⁻¹.

In comparison to the first year, bird 85 spent part of the winter farther north and did not venture south to the Senegal coast in the second year. This contributed to its fairly large distance between winter centroids of 295 km. Likewise, core ranges did not overlap and home-range overlaps were relatively low (year 1 on year 2: 21%; year 2 on year 1: 22%).

The final trans-Atlantic migrating gannet, bird 95, departed Canadian shelf waters on 8 November 2009 (Fig. 19B) following a similar (though more northerly) fall migration route

as bird 82, to reach the continental shelf waters of the Celtic Sea in 7 days, covering 3,322 km at a speed of 475 km day⁻¹ (Table 8). On arrival in European waters, it made a brief sojourn to the Irish Sea, near the gannet colonies at Great Saltee and Grasholm, before following the coast south to reach its winter area by 9 December. In spring, it retraced its route north, making brief stops in the Bay of Biscay and off the southwest coast of Ireland near colonies at Little Skellig and Bull Rock. It departed the Irish coast on 9 April and recrossed the North Atlantic via a direct route, covering 2,758 km in just 4.5 days at a speed of 613 km day⁻¹.

The dates of colony departure for trans-Atlantic migrants were within the range of those for North American wintering birds from the same colony in the same year. Bird 82 was the only bird tracked from Cape St. Mary's in 2005–2006

and had a departure date that was 3 days earlier than other Newfoundland (i.e., Funk Island) gannets. In comparison to fall, spring migration duration was shorter, faster, with fewer stop-over days for all migrations except for bird 85's repeat migration of 2006–2007, which was characterized by a slow return with stops in the central Atlantic and eastern Scotian Shelf (Fig. 19D).

Integration of bands and geolocators.—Both recoveries (all nonbreeding) and geolocator records indicated that ~60% of gannets wintered in the NE zone in North America, but the proportions in the other zones differed (Fisher exact test, $P = 0.016$; Tables 2 and 3). About one-third of band recoveries occurred in the SE zone, compared with only 10% of geolocator-equipped birds with centroids in this zone. Only 6% of adult band recoveries versus 28% of geolocator-equipped wintering birds occurred in the GoMex zone (also see Montevecchi et al. 2011). Similar patterns were evident when Bonaventure Island and Funk Island were examined individually, but band-recovery sample sizes were low, and the differences could not be established statistically (Bonaventure Island: Fisher exact test, $P = 0.18$; Funk Island: Fisher exact test, $P = 0.10$; Tables 2 and 3). Further, the tendency for Funk Island geolocator-equipped gannets to remain farther north within the NE zone than Bonaventure Island birds was not apparent in band recoveries. Because only a single band recovery came from a known-sex bird, no meaningful sex comparison could be made between bands and geolocators. Both technologies indicated trans-Atlantic crossing, although only geolocators clearly showed round-trip migrations. In concurrence with banding results, the proportions of trans-Atlantic crossing birds was higher for Newfoundland colonies than for Bonaventure Island. Speeds of gannet migration estimated from bands (fall: 24–32 km day⁻¹, spring: 56–112 km day⁻¹; Gaston et al. 2008) were considerably slower than North American migration speeds indicated by geolocators (fall: 110 ± 20 km day⁻¹, spring: 164 ± 72 km day⁻¹).

DISCUSSION

Device effects.—The mass of the tiny geolocator devices was a much smaller proportion of the gannet's adult body mass (0.1–0.5%) than the commonly accepted limit of 1–3% (Phillips et al.

2003); thus, it is unlikely that the devices' weight affected the birds. Body mass did not differ before deployments and after return and recapture. Return rates for equipped gannets (95.8%) were comparable to adult gannet survival (>94%; Mowbray 2002, Nelson 2002). No ill effects were found when gannets carried these (Kubetzki et al. 2009) or larger and heavier devices (Lewis et al. 2002, Garthe et al. 2007a, b). Further, no significant effects were found for loggers of similar size on much smaller Cory's Shearwaters (Iguar et al. 2005). Therefore, we assume that information from geolocators reflects normal behavior, with the caveat that it is probably biased toward successful, high-quality individuals.

Winter areas and connectivity.—At the global scale, gannets displayed strong connectivity: the majority of sampled North American breeders wintered within North America. Yet three individuals, one from each Newfoundland colony, displayed a radically different strategy and crossed the Atlantic Ocean to winter on the coast of Africa. At the continental level, the tracked gannet population as a whole displayed weak connectivity by wintering across a broad geographic range in North America while favoring a number of distinct winter areas and hotspots. Most individuals did not wander widely but instead remained within relatively small, discrete winter ranges. Range sizes did not show a detectable difference between sexes or destinations, and the difference in range size between Bonaventure Island and Funk Island in 2005–2006 was an artifact of extremely large ranges for two birds from Bonaventure Island and probably does not represent an ecological difference in the winter ranges of gannets from these two colonies.

As in Europe (Fort et al. 2012), North American gannets wintered across a broad latitudinal range and were concentrated in regions typified by widely divergent thermal regimes, indicating a lack of habitat specialization. Similarly, Australasian Gannets wintered at a variety of locations in Australian and Tasmanian coastal waters (Ismar et al. 2011).

The hotspots in the Gulf of Maine, from Long Island to Chesapeake Bay, and in the Gulf of Mexico may reflect the distribution of prey. Notable concentrations of gannets are known near the mouths of major bays along the eastern and Gulf coasts of the United States (i.e., Chesapeake, Delaware, Onslow, and Mobile).

Little detailed information exists regarding gannets' winter diet, though in North America they are known to forage on a variety of schooling fish, including menhaden (*Brevoortia* spp.; Mowbray 2002) and croakers (*Sciaena* spp.). Similar to Capelin (*Mallotus villosus*), which are consumed during the breeding season (Montevecchi et al. 2009), menhaden support a diverse food web of piscivorous fish, seabirds, and marine mammals (Carscadden and Nakashima 1997, Franklin 2007). Like capelin, menhaden exhibit a complex cycle of population fluctuations and are the target of the second-largest commercial fishery (by weight) in the United States (Pritchard 2008). On the Atlantic coast, large stocks of menhaden previously occurred in the Gulf of Maine but were overfished for the reduction industry (i.e., for the production of fish meal, oil, and fertilizer; Franklin 2007). Nonetheless, industrially fished stocks still occur along the mid-Atlantic coast from Cape Cod to Cape Hatteras. This area is also a winter hotspot for bluefin tuna, whose main prey is menhaden (Wilson et al. 2005). The largest remaining menhaden stocks in the northern Gulf of Mexico are the target of the largest and most recently developed industrial fishery (Franklin 2007, Vaughan et al. 2007). Gannets (and their congeners) are attracted to pelagic forage fish and also to discards from fisheries (Garthe et al. 2007b, Käkälä et al. 2007, Pichegru et al. 2007, Montevecchi et al. 2009, Bicknell et al. 2013, Kai et al. 2013, Votier et al. 2013). Thus, the apparent increase in gannets in the Gulf of Mexico could result from a combination of a relative decline in menhaden stocks on the Atlantic coast in comparison to the Gulf of Mexico and increased fish discards in the Gulf (Franklin 2007). In this case, the observed weak connectivity in North American winter distribution could simply be a function of available resources, essentially an ideal free distribution on a large scale (Fretwell and Lucas 1970). Geolocator-equipped gannets breeding at Bass Rock, Scotland, wintered in one of four distinct areas, and a similar southerly shift in distribution toward the West African coast (compared with banding records) was associated with both the availability of pelagic fish in a highly productive upwelling system (Wynn and Kniefelkamp 2004) and discards from intensely prosecuted fisheries that have increased during recent decades (Camphuysen and van der Meer 2005). Likewise, recent distributional

shifts in Cape Gannets breeding in Africa have been associated with changes in prey distribution and fishing effort (Crawford et al. 2007, Pichegru et al. 2009, Kai et al. 2013). Similarly, White-chinned Petrels (*Procellaria aequinoctialis*) wintered in discrete regions with differing depths and thermal characteristics, with the relative abundance of prey determining distribution (Phillips et al. 2006). The availability of prey most likely had a strong influence on determining gannet distribution and the within-year fidelity to such small discrete core areas (that could be crossed in a few hours of flight in most cases) implies the existence of predictable prey at this scale. Studies focused on winter diets—employing tracking and intrinsic markers (e.g., stable isotopes and fatty acid signatures) and relating habitat selection with food availability (Wakefield et al. 2009)—could help further elucidate the mechanisms responsible for changes in gannet distribution on both sides of the Atlantic Ocean (Kubetzki et al. 2009).

A number of gannets that wintered in the NE zone also made excursions into the neighboring SE zone (or vice versa) to varying extents, with one bird having a winter range that covered most of the NE zone in one year and all of the NE and SE zones combined in the next. However, no bird in either the NE zone or the SE zone ventured into the Gulf of Mexico (or vice versa), which indicates that the choice between the northeast and southeast may be more plastic than the choice between these areas and the Gulf of Mexico or that longer-distance migrants have more discrete target areas. And, of course, the geographic separation between the NE and SE zones is much less distinct than the limits of the GoMex zone.

The previously published contention that the Florida coast is the main wintering area for gannets in North America, based on band returns of all ages combined (Nelson 2002), was not substantiated by band or geolocator analyses. The adult band returns analyzed here indicated roughly equal importance for the NE and SE zones. Further, only seven migrations by five individuals terminated in the SE zone, which suggests that it is a less frequent destination. Yet this zone had the greatest number of year-round band returns, mostly from immature birds (Nelson 2002, Gaston et al. 2008). It may be that this area is favored by immature birds (from which most recoveries come), thus

biasing the comparison. High proportions of immature and juvenile gannets occur in the Gulf of Mexico (Nelson 2002, Montevvecchi et al. 2011), so some of these birds in the southeast may have been in transit; immatures, especially juveniles, also experience high mortality, especially during their first migrations (Wanless et al. 2006). This area also has extensive human-frequented beach habitat where carcasses are more likely to be detected than in other areas. Alternatively, the large number of band returns (primarily from dead gannets) and the low number of geolocator-equipped birds wintering in the southeast could indicate that this is a poor-quality area. Indeed, several mass die-offs of gannets and other species have occurred in the SE zone in recent decades (Lee 2009; B. Monk pers. comm.). Likewise, male Great Cormorants wintering at intermediate distances had lower fitness than those wintering closer to or farther from the colony (Bregnballe et al. 2006), and a similar (unexplained) mechanism could also be responsible for the paucity of gannets wintering in the SE zone.

Most geolocator-equipped birds (62%) wintered in the NE zone, remaining relatively close to the breeding grounds. This preponderance of birds in the NE zone may indicate that birds choose to go only as far as necessary to find adequate resources for winter survival (Gauthreaux 1982). The large percentage (28%) of adult geolocator-equipped gannets wintering in the Gulf of Mexico was also unexpected, because band recoveries indicated that a very small proportion of the adult population wintered there. These differences are indicative of biases in band recoveries, and recovered birds in the NE and SE zones could have been in transit to or from other regions. Alternatively, this may herald a recent shift in winter distribution, because most band returns (1930s–2010) predate geolocator tracking (2004–2010). Small winter ranges make gannets vulnerable to mortality from regional or localized events, and the extent of the oil from the 2010 *Deepwater Horizon* spill in the Gulf of Mexico overlapped all or part of the home range of most geolocator-equipped birds wintering there. The increasing number of adult gannets wintering in the Gulf of Mexico raises considerable concern for direct and indirect mortality from the ongoing effects of that spill (Montevvecchi et al. 2011).

When comparing colonies, small sample sizes make it difficult to draw firm conclusions from the band-recovery results, especially for Funk Island recoveries during winter. However, banded birds appeared to display a lack of population structuring. Recoveries from Funk Island and Bonaventure Island occurred in all three zones during both the nonbreeding and winter seasons, with the exception of an absence of Funk Island recoveries in the Gulf of Mexico during winter. Geolocator evidence indicates slightly stronger population structuring. The four breeding populations (Bonaventure Island, Funk Island, Cape St. Mary's, and Baccalieu Island) overlapped during winter in North America to a large extent. Yet birds from Newfoundland colonies wintered only in the nearest and the most distant zones, avoiding the southeast, which hints that Newfoundland birds may employ either short (northeast) or long (Gulf of Mexico or Africa) migration strategies. Likewise, gannets from a Norwegian colony exhibited a bimodal strategy, wintering either close to the colony in northern Europe or in Africa (Fort et al. 2012), and Black-legged Kittiwakes (*Rissa tridactyla*) breeding in Scotland wintered either in the eastern or the western Atlantic (Bogdanova et al. 2011). This result is at odds with the adult banding data, possibly indicating that the adult Funk Island winter band recoveries in the SE zone were from birds in transit to or from the Gulf of Mexico. Alternatively, the lack of geolocator-tracked gannets from Newfoundland wintering in the SE zone may simply be due to small sample size. In the NE zone, Funk Island gannets (from colder-water breeding environments) tended to winter farther north within the zone than those from Bonaventure Island. However, winter ranges for Baccalieu Island gannets did overlap those of Bonaventure Island gannets. These distribution patterns indicate some degree of winter habitat partitioning between colonies, but the observed distribution is limited by the small sample size of both bands and geolocators from Newfoundland gannets.

Northern Gannets from five breeding colonies in Europe showed a propensity to migrate a similar maximum (straight-line) distance from the colony (about 3,550–4,000 km), thus displaying oriented chain migration (Fort et al. 2012). That distance is broadly similar to the maximum in the present study (4,000–5,000 km, including

trans-Atlantic migrants), which supports the idea that an upper limit on migration distance may exist. Cory's Shearwaters from three breeding populations showed preferences among wintering areas while exhibiting considerable overlap among populations (González-Solís et al. 2007). African Cape Gannets breeding and foraging in two distinct upwelling systems wintered in different areas but, unlike Northern Gannets, they did not undertake long-range migrations, instead remaining in the same habitat year round (Jaquemet and McQuaid 2008). Common Murres (*Uria aalge*) and Thick-billed Murres (*U. lomvia*) from different Canadian colonies overlapped broadly on winter grounds, but Common Murres converged in areas of higher risk from hydrocarbon extraction and shipping, underscoring the importance of understanding species-specific dispersal patterns (McFarlane Tranquilla et al. 2013). Similar patterns were seen in Dovekies (*Alle alle*), with some overlap among colonies but also some differences, resulting in differing levels of risk (Fort et al. 2013a). Several other species of mostly procellariiforms use multiple, distinct wintering areas (e.g., Weimerskirch and Wilson 2000; Croxall et al. 2005; Phillips et al. 2005, 2006, 2008; Shaffer et al. 2006; Hatch et al. 2010; Yamamoto et al. 2010; Bogdanova et al. 2011; Catry et al. 2013), but most studies have focused on single colonies, so few data are available with which to compare population structuring during winter.

Intriguingly, almost two-thirds (64%) of known-sex birds that were equipped with geolocators were males. Bird captures occurred at several locations within each colony and at varying times during the day. This suggests that males spend more time chick-guarding than females during the day (when there is more aggression and disturbance at the nest site), although females are reported to have significantly longer brooding shifts (Mowbray 2002). Alternatively, if a pair was in attendance when investigators attempted captures, the less aggressive females may have departed (which seemed to be the case in a few instances in the field), biasing the sex ratio of the sample. Nonetheless, contrary to expectation, no evidence was detected of males wintering closer to the breeding colonies than females. The winter ranges of male and female geocator-equipped birds overlapped completely. Only one band recovery included sex, so this shed no further light. Differential distance

migration, in order to evolve, normally requires a higher cost for migrating farther and an isolating mechanism between the sexes. Three main hypotheses have been developed to account for the isolating mechanism: differential cold-weather resistance due to sexual dimorphism allowing one sex to winter farther north (body-size hypothesis); competitive exclusion due to social dominance (dominance hypothesis), and pressure for one sex to arrive at the breeding areas earlier (arrival-time hypothesis; Cristol et al. 1999). Gannets are sexually monomorphic and are likely equally suited to survive winter conditions throughout their range. Also, there is no evidence of a sex bias in interference competition in gannets (Lewis et al. 2002) as in, for example, giant petrels (*Macronetes* spp.), in which males exclude females at carrion (González-Solís et al. 2008). Male gannets are reported to arrive earlier at the colony than females in order to defend nest sites (Nelson 2006). If this is true, it is not due to wintering closer, as predicted by the arrival-time hypothesis. Instead, males would simply need to leave winter areas before females or travel faster to arrive earlier at the colony. This also did not occur, so there may also be little incremental cost for migrating long distances along a productive continental shelf, precluding selection for differential migration. No evidence of sexual segregation in wintering area was found in gannets breeding at Grasholm, Wales (Stauss et al. 2012). Although female gannets from Bass Rock, Scotland, wintered farther from the breeding colony on average, the difference was not statistically significant (Kubetzki et al. 2009). Several large, sexually dimorphic albatrosses and giant petrels showed weak differences in nonbreeding-season $\delta^{13}\text{C}$ (but not in $\delta^{15}\text{N}$), indicating differences in distribution (likely due to niche specialization) but a lack of dominance exclusion, leading to similar trophic levels (Phillips et al. 2009). It is possible that gannets displayed fine-scale spatial segregation and/or niche specialization. More accurate tracking methods and/or biochemical assays of gannet feathers grown during winter are needed to address questions of fine-scale spatial segregation and niche specialization (Furness et al. 2006).

Winter-site fidelity.—The present study is one of only two that have reported winter-site fidelity in a non-procellariiform pelagic seabird (Frederiksen et al. 2002). On a global scale, all

birds wintered on the same side of the Atlantic Ocean in successive years while, on a regional scale, all birds returned to the same oceanographic zone and had median intercentroid distances of only 87 km between years. There was also considerable overlap at the scale of individual ranges. Most home ranges had overlap indices >50%, and core ranges overlapped by >30%. These findings indicate a remarkable tendency to return to a spatially restricted area in consecutive years. For many species, fidelity to the breeding area is markedly greater than fidelity to the winter grounds, whereas in other species the opposite is true (Newton 2008). Like most colonial seabirds, gannets are highly faithful to their breeding colony and to an individual nest site. This behavior has evolved to take advantage of predictable prey aggregations within foraging range during the breeding season. Likewise, winter-site fidelity on the scale observed in this study has likely evolved to take advantage of spatially predictable, seasonally variable prey and habitat (Mueller and Fagan 2008). Gannets exhibited colony-based differences in fidelity to distinct foraging areas during the breeding season that were mediated by differing prey predictability within foraging range of the colony (Hamer et al. 2001, Garthe et al. 2007a). No colony-based differences in winter-site fidelity rates were found in this study, likely because birds from different colonies overlapped in their wintering areas to some extent or because prey availability did not differ substantially between areas. Likewise, no sex-based differences in winter-site fidelity were observed, although these findings are not surprising given the small number ($n = 16$) of consecutively tracked birds.

Winter-site fidelity is being reported from a small but growing number of seabird species. Surprisingly, winter-site fidelity in the Wandering Albatross (*Diomedea exulans*) was established by repeat sighting of banded birds (Weimerskirch and Wilson 2000) on their wintering grounds. Cory's Shearwaters had intercentroid distances in repeat years ($1,901 \pm 2,886$ km) that differed significantly from that expected by chance (Dias et al. 2010). Repeat-year inter-centroid distances of gannets were also significantly closer than expected by chance and were more than an order of magnitude closer than those of the shearwaters. Gray-headed Albatrosses (*Thalassarche chrysostoma*)

showed consistency in choice of staging areas and in timing and routes of circumnavigations (Croxall et al. 2005), whereas a single White-chinned Petrel tracked in successive years inhabited the same areas of the Patagonian Shelf and Humboldt Current (Phillips et al. 2006). Black-browed Albatrosses displayed fidelity to widely separated winter areas and exhibited correlated centers of activity within those areas in consecutive years, prompting the authors to suggest that fidelity might be common in albatrosses (Phillips et al. 2005). Although some Cory's Shearwaters switched sites between years, others displayed high site fidelity (Dias et al. 2010). Winter-site fidelity may well be common in seabirds in general, as it is among sea-ducks (Robertson and Cooke 1999).

At least three hypotheses have been proposed to explain winter-site fidelity. The local-knowledge hypothesis posits that return to the same area in subsequent years confers an advantage through knowledge of localized prey resources, predator distribution and behavior, and location of conspecifics. For a highly mobile apex predator like the gannet, the location of predictable prey may be the most important of these for increased winter survival and body condition that carries over proximately into the next breeding season and, ultimately, to fitness (Marra et al. 1998, Furness et al. 2006, Norris and Marra 2007, Sorensen et al. 2009). Predictable aggregations of once hyperabundant prey (e.g., menhaden) in the Gulf of Maine, Chesapeake Bay, and Gulf of Mexico likely influenced the evolution of this trait. The small core (and home) ranges of most gannets imply intensive knowledge of prey distribution, supporting this hypothesis. Two alternative hypotheses explaining winter-site fidelity appear to be less suited to gannets. The genetic hypothesis requires that individuals consistently select a winter site in order to maintain an optimal level of inbreeding (Greenwood 1987, Robertson et al. 2000). This hypothesis is appropriate for waterfowl that pair on their winter grounds, but it lacks explanatory power for gannets that are not known to do so. Likewise, the social-cohesion hypothesis, whereby site fidelity allows family groups to stay together and/or pairs to reunite, appears to be inappropriate for gannets. Juvenile gannets depart their breeding colonies independent of adults and are not known to remain in family groups at sea, and although nothing is known

of pair behavior during winter, the single pair in this study did not winter together. However, if reuniting on the wintering grounds strengthened the pair bond, this could translate into greater fitness because Australasian gannets that retain their mates across years have higher reproductive success (Ismar et al. 2010b).

Marine pollution, fishery interactions, and climate change have the potential to bring about substantial changes in prey predictability and habitat quality in a relatively short time frame. Gannets exhibit considerable plasticity in prey species and foraging range in response to oceanographic changes at their breeding colonies (Garthe et al. 2007b, Montevecchi et al. 2009, Pettex et al. 2012), but the ability of gannets to respond through plasticity in winter-site fidelity on an appropriate spatial and temporal scale is unknown. In this context, the process whereby an immature gannet eventually settles on a consistent winter site may have long-term implications. Is the location of the winter site inherited? Do juveniles randomly follow groups of conspecific adults to a winter site and, having wintered there successfully once, simply return to this familiar territory in successive years (often bypassing perfectly suitable habitat en route)? The resolution of these questions has important implications for gannet (and many other species') conservation and evolution, and will require synoptic tracking of parents and offspring.

Migration timing.—There was remarkable synchrony in colony departure and arrival timing, the overall range in each being similar at 26 and 29 days, respectively. The maximum departure and arrival ranges for specific colonies in specific years were 19 and 18 days, respectively. Gannets breeding at Bass Rock were slightly more variable in initiating migration, with a range spanning almost 1 month (Kubetzki et al. 2009). To a large extent, the timing of chick fledging, mediated through growth and development, likely determines colony departure date for adults. This is corroborated by the fact that failed breeders and nonbreeders typically depart earlier than breeders (Nelson 2002). Indeed, some gannets occupied northern waters well into December, indicating that prey is still available and temperatures adequate long after fledging has occurred. Likewise, Cory's Shearwaters (Cathy et al. 2013) and Black-legged Kittiwakes (Bogdanova et al. 2011) departed earlier after failed breeding.

The date of colony arrival was similar to those previously published (Mowbray 2002) for North American colonies, yet, contrary to those of colonies in the eastern Atlantic, there was no indication of later breeding compared with past decades (Wanless et al. 2008). The benefits of early arrival on the breeding grounds are well known (Kokko 1999, Drent et al. 2006). Early arrival accrues fitness benefits because reproductive success decreases with increasing breeding date in most (Drent et al. 2003) but not all (Phillips et al. 2005) avian species, including gannets (Nelson 2002). However, arriving too early incurs the cost of a mismatch between arrival timing and availability of resources for survival (Bêty et al. 2004, Gaston et al. 2009). Most birds (including some seabirds; Bond and Diamond 2010) employ a combined capital and income breeding strategy (Drent et al. 2006), and sufficient accumulation of nutrients for egg formation must occur during and/or after migration to the breeding colony. Thus, females should aim to arrive as early as possible (but not too early) with excess energy reserves to produce superior eggs (Drent et al. 2006). Males, by contrast, may be under pressure for early-season establishment of a territory (Nelson 1978). These pressures produce a race for optimal early arrival on the breeding grounds. Yet synchronized arrival and breeding may be more important than early arrival in colonial species. Indeed, food supplementation successfully advanced laying date in 70% ($n = 46$) of experiments involving solitary nesting species, compared with only 27% ($n = 11$) of experiments with colonial breeders (reviewed in Nager 2006). In Common Murres, earlier breeding was favored in general, but either early or late deviation from mean laying date resulted in reduced success (Hatchwell 1991, Reed et al. 2009).

Arrival synchrony within individual pairs of colonial breeders is likely important. Individual gannet pairs form at the colony and may rely on specific relative individual migratory schedules to synchronize their yearly reunion (Gunnarsson et al. 2004), renew the pair bond, and provide for timely onset of breeding. Indeed, it may be that initial pairing of young breeders is mediated by similar individual migratory schedules that brought them to the colony at the same time in the first place (Gunnarsson et al. 2004). Therefore, synchronous arrival would seem to

be of utmost importance in this and other seabirds (Phillips et al. 2005, 2006; Catry et al. 2009). Predation may be the largest source of mortality for some seabird species, and synchronous arrival and breeding provides predation dilution through predator swamping (Hatchwell 1991, Reed et al. 2006). Although overall predation rates of adult and young gannets and their eggs are low (Mowbray 2002), gulls (*Larus* spp.), Bald Eagles (*Haliaeetus leucocephalus*), and foxes (*Vulpes* spp.) do occur (in at least some years) at all gannet colonies in our study (e.g., Burke et al. 2011).

Role of winter destination.—Gannets traveling to the NE zone departed later than those destined for the SE zone, but no difference was detected in departures for other zones. Northeast-bound birds also had the greatest variation, including the earliest and latest recorded departure dates. Similar to gannets, Streaked Shearwaters (*Calonectris leucomelas*) also displayed differences in departure date depending on destination (Yamamoto et al. 2010). Shearwaters taking a coastal route from the breeding colony in Japan to the closest wintering area in the South China Sea departed later and took longer to reach their destination than those crossing the open west-central Pacific to winter off northern New Guinea and in the Arafura Sea. Yamamoto et al. (2010) hypothesized that this difference was due to the productivity of the waters encountered en route; birds going farther crossed less productive waters and therefore crossed quickly. The routes to all gannet winter zones overlapped, but there may have been differences in the quality of each winter area. With the NE zone's proximity and very productive hotspots for wintering, perhaps the timing of departure is not as critical as for the SE zone.

Colony arrival date did not show a detectable difference for migrations initiated from the different wintering zones. Instead, birds wintering in more distant areas departed earlier in order to arrive at the colony in relative synchrony. The range in departure dates from the earliest start date in the Gulf of Mexico to the latest departure from the Gulf of Maine was 62 days, or ~4 days per degree latitude. Birds have endogenous control cycles for molt, gonad development, and migration (Gwinner 1986, Newton 2008), and these rhythms interact with photoperiod to control migration timing. Subsequently, secondary environmental factors such as weather

and food supply allow fine tuning of migratory timing, potentially en route. For birds that winter in a single hemisphere and away from the equator, latitude is encoded in photoperiod, allowing birds from the same breeding populations to synchronize their arrival. Arrival timing of gannets breeding at Bass Rock showed little variation for birds returning from different sections of the eastern Atlantic and Mediterranean (Kubetzki et al. 2009). Arrival timing of Streaked Shearwaters (Yamamoto et al. 2010), Black-browed Albatrosses (Phillips et al. 2005), and Black-tailed Godwits (*Limosa limosa*; Gunnarsson et al. 2006) also did not differ by distance to wintering grounds. But not all colonially breeding seabirds arrive in synchrony. Great Cormorants that wintered close (<300 km) to the breeding colony in Denmark returned 2–3 weeks earlier than those farther away (Bregnballe et al. 2006). For cormorants that wintered 301–2,500 km away, arrival date was only weakly related to distance from the colony, which the authors hypothesize is due to more distant birds initiating migration earlier and joining up with intermediate-distance birds en route. The spring return route of gannets migrating from the most distant wintering areas in North America takes them through the nearer wintering zones, where they almost certainly join (or perhaps trigger) local birds in migration.

Colony and year influenced departure and arrival timing. Bonaventure Island birds departed earlier during fall 2005 than during 2004, and they returned to the colony later in the following spring (2006) than Funk Island birds that year. In 2007, Funk Island birds returned to the colony even earlier. Gannets are synchronous breeders, and departure date is constrained by chick fledging (up to a certain limit). Chick growth and development are affected by a variety of factors, including environmental conditions and food availability, which may be linked to colony arrival in spring, which itself may be affected by conditions during the previous winter and during spring migration (Norris 2005, Sorensen et al. 2009). Therefore, it is not surprising that local conditions could dictate colony- and year-specific departure timing. European colonies cover a broad range of latitudes, and there is a latitudinal gradient in the arrival date for these sites due to the temporal progression of hospitable conditions during spring (Wanless et al. 2008). Arrival dates at United Kingdom

colonies at higher latitudes than Newfoundland are also much earlier, emphasizing the role of oceanography.

Females departed the colony 5 days earlier, on average, than males. This could be an adaptation to equalize energy expenditure, because females feed chicks more than males late in the breeding season (Montevecchi and Porter 1980). Streaked Shearwater females fed chicks more frequently than males and also departed the colony 5 days earlier, ostensibly to satisfy a greater need to recover body condition before migration (Yamamoto et al. 2010). Despite the fact that female Black-browed Albatrosses provisioned chicks less, they too departed earlier than males, perhaps because the larger males were more capable of provisioning chicks and the females' early departure reflects equalization of investment relative to body size (Phillips et al. 2005).

Alternatively, the male gannets' later departure may be socially mediated. Male gannets defend territories against potential usurpers throughout the breeding season (Nelson 2002), and perhaps their attendance at the nest site after female departure assists in establishing continued site ownership that carries over into the next breeding season (Nelson 2002, Drent et al. 2003). Male and female Manx Shearwaters (*Puffinus puffinus*) showed no detectable difference in departure dates, though departure was defined as the exit from a 500-km buffer surrounding the colony (Guilford et al. 2009). This definition could have masked actual sexually divergent colony departure, which was followed by a period of residency near the colony (similar to Streaked Shearwaters; Yamamoto et al. 2010) before departing. Many gannets also remained in the colony area before departing on migration; when colony departure was defined as the exit from a 300-km colony buffer, no sex-based difference in departure date was detectable.

Contrary to expectation, males and females did not display a detectable difference in date of return to the colony, although the male of the only tracked pair arrived three days before the female. It is believed that males arrive earlier at the colony in order to establish territories (Nelson 2006). Arrival of male Australasian Gannets preceded that of females (Ismar et al. 2010b), and male Black-browed Albatrosses also arrived 4–5 days earlier than females, a result attributed to their greater role in nest

acquisition and defense (Phillips et al. 2005). However, earlier male arrival at the colony may not be a prerequisite for male-biased territory establishment and reclamation. Female gannets could arrive at the same time or even first, and defend territories or wait in the colony. Alternatively, females could play a role in territory establishment. Sexes arrive synchronously in Manx Shearwaters (Guilford et al. 2009), Sooty Shearwaters (*Puffinus griseus*; Hedd et al. 2012), and Streaked Shearwaters (Yamamoto et al. 2010), but these species subsequently depart for a prelaying exodus. It may be that the arrival timing of individual pairs was more finely tuned than in the population as a whole, with males of each pair arriving before females. Black-tailed Godwits retain mates by arriving within ~3 days of one another (Gunnarsson et al. 2004), which could be the result of strong individual migration schedules that caused these birds to arrive in synchrony and pair in the first place (Battley 2006). Examination of the arrival-time data for gannets showed that many birds stayed for a short period (<1 day) on their first visit to the colony and departed for a variable number of days before arriving again, their attendance becoming more regular as time passed. For females, these visits could correspond to checking to see whether their partner has established the territory. An analysis of the timing, number, and length of early-season colony visits by males and females might shed more light. Tracking of both members of mated pairs over several breeding seasons would address this question.

Migratory distance and duration showed considerable individual variability even within birds destined for the same wintering zone. The overall distance covered between colony departure and arrival on the winter grounds varied by an order of magnitude (1,304–13,584 km), and duration by almost a factor of five (12–110 days). The greatest variation in distance and duration occurred in migrations to the NE zone. This was driven largely by the fact that some (but not all) of these birds had extensive stopovers immediately following colony departure or upon reaching the American coast at Cape Cod, where small daily distances during many days of circuitous travel accrued to large total distances.

One gannet also undertook a visit to the Labrador Shelf early in migration, and although

gannets are not abundant in this area, they are known to occur on the shelf and in the Labrador Sea (Fifield et al. 2009). Direct-route migration distances of gannets breeding at Bass Rock (343–4,654 km; Kubetzki et al. 2009) were similar to those for North American birds (about 1,000–4,000 km). The primary difference was that some Bass Rock gannets remained in the North Sea very close to the colony during winter, which is not tenable for North American gannets because of weather and ice. Maximum migration distances for gannets from European colonies were remarkably similar (3,000–3,900 km; Fort et al. 2012) and comparable to those for birds wintering in North America (~4,000 km), which supports the theory of oriented chain migration in gannets (Fort et al. 2012).

The speed of migration was highly variable between individuals (mean: 136 km day⁻¹, range: 71–486 km day⁻¹) and was in the middle to high theoretical range for birds of this size (Hedenström and Ålerstam 1998). Surprisingly, male spring migration speed was slower than for females (though this difference was not significant), in contrast to the expectation that males would migrate faster to arrive earlier at the colony. Fall migration speed did not show a detectable dependence upon departure date, which suggests that the timing of arrival on the winter grounds was not critical and that there was no penalty for departing late from the colony.

Despite individual variation, winter destination had a significant effect on speed in fall but not in spring. In fall, migration speed was significantly faster to the more distant regions (southeast and Gulf of Mexico) than to the northeast. This was due to the effect of long stopover periods for many northeast-bound birds, resulting in lower overall speeds rather than a difference in daily travel speed per se. In spring, migration speeds from each zone were more similar, although the fastest speeds were recorded by birds from the northeast. These migrations were relatively short (in distance and time), possibly indicating that such high speeds could not be maintained for long periods, likely because of the high cost of flight in gannets (Birt-Friesen et al. 1989, Hedenström and Ålerstam 1998).

Migration speed for North American gannets (median: 120 km day⁻¹) was slower than that (250–450 km day⁻¹) for gannets breeding at Bass Rock (Kubetzki et al. 2009). This is likely due to the difference in how speeds were cal-

culated. The speeds reported in Kubetzki et al. (2009) (for birds migrating to the most distant, African coastal wintering area) were based on the portion of the migration with the highest rate of change in latitude. They did not include stopover days near the colony (immediately after departure) or along the African coast before entering the (kernel-defined) winter area (Kubetzki et al. 2009). Australasian Gannets that migrated from New Zealand to Australia exhibited similar speeds ranging from 125–350 km day⁻¹ while covering about 2,300–5,000 km on migration (Ismar et al. 2011).

Gannet migration speeds and distances were slower and shorter than those for most other long-distance migrating seabirds that have been tracked to date. Black-browed Albatrosses covered ~5,000 km from South Georgia Island to the Benguela Current in 3 to 6 days at speeds of about 800–1,770 km day⁻¹. Gray-headed Albatrosses can reach speeds of 750–950 km day⁻¹ (Croxall et al. 2005), whereas female White-chinned Petrels covered 4,850–8,560 km at 310–610 km day⁻¹ during their prelaying exodus (Phillips et al. 2006). Sooty Shearwaters migrating in the Pacific Ocean used prevailing winds to cover 536–910 km day⁻¹ (Shaffer et al. 2006), whereas Arctic Terns in the Atlantic Ocean covered 20,070–27,790 km at speeds of 390–670 km day⁻¹ (Egevang et al. 2010). In contrast to gannets, these studies involved birds crossing large ocean basins with, in many cases, the assistance of wind. Further, all these species (excluding the tern) are procellariiforms, which use less costly gliding flight and, thus, can be expected to have higher flight speeds and migration distances than gannets (Hedenström and Ålerstam 1998).

Migration speeds of North American gannets ascertained using geolocators were much higher than those reported in banding studies (Gaston et al. 2008). A similar result was found for gannets breeding at Bass Rock (Wernham et al. 2002, Kubetzki et al. 2009). The determination of speed of migration from banding records is complex and fraught with assumptions (Wernham et al. 2002), and therefore this disparity should not be very surprising. Published speeds of migration based on banding data should be treated with caution, and updated by tracking studies whenever possible.

Stopovers.—All birds used stopover days during fall and spring migrations. This suggests that breaking the migration into periods of directed

travel punctuated by more stationary periods is important for gannets. Yet there was large variation in the number of stopover days used, and seven birds had only 0.5 stopover days in spring. There were no detectable differences in the number of stopover days used between sexes, colonies, or years. Gannet stopover locations were not distributed randomly, but instead were aggregated at several hotspots. A few of these highly productive hotspots coincided with areas of intense overwinter use, particularly in the Gulf of Maine, from Long Island to Chesapeake Bay and, to a lesser extent, along the coasts of South Carolina and Georgia. Although vacated during winter, a small area on the eastern Scotian Shelf in the vicinity of Sable Island and The Gully (the largest marine canyon in eastern North America) was used extensively in fall and, to a lesser extent, in spring. This region at the edge of the continental shelf is highly productive as a result of physical forcing that drives upwelling of nutrients. The Gully is a nationally and globally recognized area that contains a rich diversity of species and habitats and is a Marine Protected Area. Several gannets had extensive stopovers in off-shelf oceanic regions east and south of the Grand Bank (more so in fall than in spring), as did many satellite-tracked juvenile gannets (Montevecchi et al. 2012), which suggests that this deep-water region is a productive and important part of the gannet migration cycle for both age groups. Intriguingly, during spring migration, the temperature data indicated that several gannets spent one or more nights on land in the vicinity of Sable Island, suggesting that they roosted on this island. Such terrestrial roosting has not previously been reported for migrating gannets.

The number of stopover days varied by wintering area, although not in the manner expected in fall. It was expected that more stopover days would be required to reach more distant wintering areas. However, the number of stopover days during fall migration for birds targeting the Gulf of Mexico was not significantly different than that for gannets wintering in the NE zone, and migrations to both zones had significantly more stopover days than migrations to the SE zone. However, there was no detectable difference in number of stopover days per day of migration between the winter zones, which suggests that there was no difference in the daily cost of migration to each area. Instead, the

difference in the number of stopover days was due to the difference in the duration (and speed) of migration to each zone.

Although stopover days appear to be important and increase with distance traveled, there was extensive individual variability. Variability was greatest for birds en route to the Gulf of Mexico (followed closely by migrations to the NE zone), with these birds having both the lowest and highest numbers of stopover days. For example, one bird from Funk Island made an essentially continuous migration to the Gulf of Mexico involving only two stopover days. Several birds had protracted periods of stopover, immediately after leaving the colony, in the Gulf of St. Lawrence and Laurentian Channel and on the southern Grand Bank and Scotian Shelf, lasting well into December. Many birds wintering in the NE zone differed from those in the other two zones in the way they used stopover days. Birds traveling to the other zones typically had periods of direct migration punctuated by stopovers at several locations, including the Scotian Shelf, Chesapeake Bay, and the coasts of North Carolina and Georgia. Although some birds traveling to the NE zone had similar patterns, many did not. Many birds traveling to the NE zone initiated essentially direct migrations (with or without stopovers on the Scotian Shelf) across the eastern Gulf of Maine to intersect the American coast around Cape Cod. These birds subsequently drifted slowly, with much circuitous routing (i.e., most days classified as stopover), southward toward their winter home-range areas. Therefore, many of the "stopover" days for NE-zone migrants were really part of a slow drift more akin to dispersal than to true migration. Although there was considerable individual variability, these observations, along with the fact that migrations to the Gulf of Mexico were faster, indicate that, in general, migration timing to the NE zone was less critical than migration timing to the SE or GoMex zone.

Very few seabird-tracking studies have addressed stopover or staging areas directly. Some Bass Rock gannets moved to the North Sea and Norwegian Sea for a few days to a few weeks before continuing their fall migration, and this behavior did not differ by winter destination (Kubetzki et al. 2009). Likewise, in spring, most birds migrated to areas north of the colony before returning to breed (Kubetzki et al. 2009).

All Manx Shearwaters tracked from the United Kingdom to South America made stopovers involving both sexes with roughly equal frequency between the outgoing and return migrations (Guilford et al. 2009). These stopovers were associated with behavior that was similar to foraging, and Guilford et al. (2009) concluded that they likely serve the same refueling function as they do in landbirds. Sooty Shearwaters migrating from the Northern Hemisphere to breeding grounds in the Falkland Islands used a highly productive major terminal stopover site before returning to the colony (Hedd et al. 2012). Curiously, Sooty Shearwaters in the Pacific (Shaffer et al. 2006) and Streaked Shearwaters (Yamamoto et al. 2010) did not display stopover behavior during long-distance migration. Yet Cory's Shearwater (Dias et al. 2010) and other seabird species as diverse as Black-browed Albatross (Phillips et al. 2005), Bugio Petrel (*Pterodroma deserta*; Ramírez et al. 2013), Arctic Tern (Egevang et al. 2010), and Little Gull (*Hydrocoloeus minutus*; Bellerby et al. 2000) have done so. This implies that the use of stopovers is a flexible trait among (and perhaps within) seabird species and that much remains to be discovered about the reasons underlying these differences.

Migration consistency.—Several aspects of timing and movement were highly consistent for repeat migrations. There was no detectable difference in the values of all parameters between years. This suggests a lack of wholesale shifts in the timing of migration and use of stopovers between years. High repeatability was apparent in some, but not all, parameters. In fall, migration duration, distance, and arrival date on the winter grounds showed significant repeatability within individuals across years, as did the departure date from the wintering area and the duration and distance of spring migration. Given that gannets displayed strong winter-site fidelity, it is not surprising that the duration and distance of fall migration were more consistent within individuals than between them. Yet tracked gannets were individually consistent in the date of arrival on the winter grounds, even though their departure from the colony was not. This suggests that gannets have individual schedules for the duration and distance of migration and for the timing of arrival on the winter grounds. Likewise, the repeatability of spring departure date supports the

idea that gannets have an endogenous seasonal rhythm that is likely triggered by photoperiod. The significant repeatability of these parameters implies that they have a genetic component. By contrast, the initiation date, number of stopover days, and speed of fall migrations did not show detectably significant repeatability, nor did the number of stopover days, speed, and date of arrival in spring. This implies that these factors have a greater environmental component that determines their timing and magnitude. For example, the date of fall migration initiation is likely constrained by chick development. The number of stopover days and speed of migration are likely strongly affected by conditions encountered during the journey. Poor weather and strong headwinds would decrease migration speed and require more frequent stopovers to replenish energy reserves at sites where productivity and interference competition from conspecifics could combine to determine the length of stopover. The timing of arrival in spring may be affected by local conditions near the colony (Frederiksen et al. 2004, Bregnballe et al. 2006). It is therefore intriguing that consistency in arrival timing was found for Bonaventure Island (but not for Funk Island) when colonies were considered separately. However, these results should be viewed cautiously because sample sizes were small (especially at Funk Island) and only 2 consecutive years were considered.

Only a relatively small number of studies have reported on migration timing in seabirds, and even fewer have tracked the same individuals more than once. Fewer still report on the full suite of migration timing parameters presented here. A variety of descriptive (Phillips et al. 2006) and statistical procedures have been used to assess interannual consistency in migration timing, including correlation (Phillips et al. 2005), paired *t*-test, and repeatability (Catry et al. 1999, Battley 2006, Dias et al. 2010, Lourenço et al. 2011). Although these all measure consistency in some way, there are subtle differences between them, making comparisons between studies potentially problematic. For example, paired *t*-tests determine whether, in the population as a whole, the mean of the individual differences between two measurements of a migration timing variable is significantly different from zero. But this is not the same as repeatability, which measures whether an animal is

more (or less) variable in its behavior than the variability in that behavior in the population as a whole. Attention must therefore be paid to how consistency is measured when comparing studies.

Phillips et al. (2005) reported remarkable inter-annual consistency in migration timing parameters for Black-browed Albatrosses, except for the date of colony departure, which, as in gannets, was determined by breeding status and failure date. They found significant correlations in date of winter area departure, duration of migration, and arrival near the colony, but no consistency in use of staging (i.e., stopover) areas, and concluded that consistency in migration timing may imply a major genetic component of control in individuals. Phillips et al. (2005) also hypothesized that albatrosses must have an endogenous timer (*sensu* Gwinner 1986) cued by environmental factors such as photoperiod. Dias et al. (2010) tracked Cory's Shearwaters to the same (or different) winter locations in multiple years and found consistency (repeatability >0.51) in the timing of departure and arrival from both nesting and wintering areas, but they did not find consistency in the use of stopover sites. Bar-tailed Godwits (*L. lapponica*) also displayed strong repeatability ($r = 0.83$) in adult departure date from the wintering area (Battley 2006). Repeatability of departure date in immatures was slightly less ($r = 0.77$), implying optimal departure date refined with age. Black-tailed Godwits exhibited repeatable departure from staging areas and arrival on breeding grounds (Lourenço et al. 2011). Passerines have shown significant repeatability ($r = 0.39$) for fall departure date in Eurasian Blackcaps (*Sylvia atricapilla*; Pulido et al. 2001) and spring arrival in Barn Swallows (*Hirundo rustica*; $r = 0.51$; Møller 2001). These results are consistent with those for gannets, with the exception that gannets did not display detectable repeatability in colony return dates. This difference is expected, given the distinct selective pressures affecting each group (Hatchwell 1991, Drent et al. 2006, Reed et al. 2009). The consistency in arrival date for Black-browed Albatrosses (Phillips et al. 2005) and the repeatability of Cory's Shearwater arrival dates (Dias et al. 2010) were both for individuals from the same colony. When gannet colonies were considered separately, Bonaventure Island birds displayed repeatability in colony arrival date, though this

was not detected for Funk Island birds; sample size was small at Funk Island ($n = 6$), so conclusions are difficult to draw. Procellariiforms have a mating system that involves a prelaying exodus, and the effect of this behavior on relative arrival repeatability in comparison to other seabird taxa is unknown. Finally, although repeatability is often interpreted as an upper limit on heritability (Falconer 1981), this study and most others cited above were conducted in only 2 or 3 successive years. Yet repeatability over more than 2 years can decline rapidly. Catry et al. (1999) showed that both simulated and measured repeatability of laying date in Great Skuas (*Stercorarius skua*) declined to almost zero when a lag as small as 5 years was considered. They hypothesized that both age-related effects and environmentally induced changes in the ranking of plastic phenotypes may be responsible and concluded that "most traits of interest cannot be permanent in a variable environment." Continued and repeated long-term tracking of gannet migrations will address the extent of consistency in their consistency.

Fall versus spring migration.—In comparison to fall, spring migrations were shorter in time and distance and executed with an average of 1.5× greater speed, using fewer stopover days. Similarly, Gaston et al. (2008) reported spring speeds 2–4 times faster than fall speeds based on band returns. In fall, birds are freed from the constraints of central-place foraging and have many months before they are due back at the colony; thus, they may not be under pressure to migrate at maximum speed (Newton 2008). With several highly productive stopover areas to choose from along the route, the timing of movement is less constrained in fall than in spring (McNamara et al. 1998). This also implies that the timing of arrival on the winter grounds is not critical and, thus, that food supplies are relatively predictable in wintering areas. By contrast, in spring, gannets are constrained to arrive early enough, and in synchrony, at the colony to secure their territories and commence breeding in the relatively brief summer season. Given that their arrival typically precedes that of abundant prey and good-weather days (Nelson 2002), the increase in migration speed with departure date (contra that for passerines; Newton 2008) suggests that birds wait as long as possible on productive winter or stopover areas to maximize energy intake.

Gannets used fewer stopover days during spring migration, further confirming the urgency of spring migration. Nonetheless, the number of stopover days per day of migration was not detectably different in fall, indicating physiological constraints on the rate of migration imposed by the rate of energy intake (Hedenström and Alerstam 1998, Weber et al. 1998). By contrast, gannets breeding at Bass Rock had spring migrations that were about as long as those in fall, though no detailed analysis of timing has been conducted in those birds (Kubetzki et al. 2009); and two of three Australasian Gannets had more protracted and spatially variable prebreeding (spring) as opposed to postbreeding (fall) migrations (Ismar et al. 2011). Although Black-browed Albatrosses that left their wintering area late traveled more slowly and at higher latitudes than earlier birds, they compensated by using fewer stopovers (Phillips et al. 2005). In one study of Cory's Shearwater (González-Solís et al. 2007), spring migration durations (23 ± 7 days) were slightly longer than fall migrations (19 ± 10 days) although the ranges overlapped completely; whereas Dias et al. (2010) reported that spring migration (~ 3 weeks) was shorter than fall migration (36 days). By contrast, spring migrations were significantly longer than fall migrations for male Manx Shearwaters and slightly shorter for females (Guilford et al. 2009). But the routes of fall and spring migration are different in the studies of procellariiforms, making comparisons of timing with gannets problematic. Further detailed analysis of spring and fall migration timing in gannets (particularly in Europe) and in their congeners and other seabirds will shed more light on these patterns.

Trans-Atlantic migration.—Northern Gannets breed throughout the North Atlantic Ocean, and questions about the species' geographic radiations, large-scale population interactions, and connectivity are unresolved (Nelson 2002). Our study is the first to describe a normally continental shelf-slope migrant seabird with two divergent migration strategies, and one of a very few studies that involve such differing strategy rates for two populations that breed in relative proximity: the Bonaventure Island population remaining entirely in North American waters, and the Newfoundland population employing a dual strategy. Further, the larger European

population does not show any evidence of making the reciprocal trans-Atlantic migration.

During winter, some seabirds range widely (Weimerskirch and Wilson 2000, Croxall et al. 2005, Shaffer et al. 2006), and some occasionally stray, particularly immature birds. Nine banded Northern Gannets were documented to cross the Atlantic Ocean in this study, and the details for only six of these were previously published (Gaston et al. 2008). Trans-oceanic band recoveries have been almost exclusively from Newfoundland gannets, mostly immatures. The one-off nature of band returns made it impossible to determine whether trans-Atlantic banded gannets were undertaking intentional migrations, but these were considered likely to be accidental, one-way crossings at best (Nelson 2002, Gaston et al. 2008). Thus, the discovery of trans-Atlantic round-trip migration and wintering off the coast of Africa by three geolocator-equipped breeding adults, one from each of three Newfoundland colonies, was surprising. Trans-Atlantic migrations involved birds in multiple years and from multiple colonies, and for the only bird tracked again, the same route was repeated. These tracks and movements indicate that trans-Atlantic migration is a deliberate tactic. Although sample size is small, it implies the likely regular use of a radically different migratory tactic by a small segment of the Newfoundland population.

The Northern Gannet's two congeners are also capable of long-distance, trans-oceanic movements. Both adult and immature Australasian Gannets disperse $\sim 2,500$ km across the Tasman Sea to winter on the east coast of Australia (Ismar et al. 2010a, 2011). One Australasian Gannet crossed the Indian Ocean and settled in an African Cape Gannet colony (Dyer 1995), whereas another ventured to Brazil (Nelson 2006). Likewise, a Cape Gannet mated with an Australasian Gannet at a colony in Australia (Nelson 2006), and an adult accounted for the first Pacific Ocean record in Peru (García-Godos 2002). During August 2010, two sightings of Northern Gannets were made from research vessels in the Arctic Ocean off the Alaskan coast (Alaska 200 Club 2011), and during April–September 2012, a northern gannet took up residence on the cliffs of the Farallon Islands off San Francisco Bay (see <http://losfara-lones.blogspot.ca/>). One explanation is that the gannet(s) ventured through the opening waters

of the Northern Sea Route and may have originated either from colonies in Newfoundland or North Norway. Thus, although trans-oceanic journeys are rare for adult gannets, it is clear that the capability to do so is well represented in the genus.

Colony departure dates of trans-Atlantic migrants were similar to those for other birds from the same colony (or region) in the same year, further emphasizing that this parameter does not depend on winter destination, but is instead determined by conditions at the colony. Spring departure dates from the African coast were similar to departure dates for North American gannets, though later than those for Bass Rock gannets wintering in the same area (Kubetzki et al. 2009). Colony arrival dates for three of four trans-Atlantic migrations fell within the range of their North American wintering conspecifics for a given colony and year, which suggests that trans-Atlantic migrants are under the same selective pressures for synchronous arrival at the colony, rather than synchronous departure from the wintering area. However, contrary to the other trans-Atlantic migrants, female bird 85's spring colony arrival was not synchronized with other Funk Island birds tracked the same year. Bird 85 had the earliest winter-area departure date of any bird in 2006 and the second-earliest in 2007 and arrived at the colony 3–4 weeks in advance of any other tracked bird in both years. The consistency of this gannet's routing and early arrival, and the fact that its date of African-coast departure was more similar to the departure dates of Bass Rock gannets, hints at a close genetic linkage between some trans-Atlantic North American migrants and European gannets.

Migration distances, durations, and numbers of stopover days were similar to those of birds wintering in the Gulf of Mexico and of North American migrants in general. However, trans-Atlantic migrants exhibited much higher average flight speeds ($188\text{--}762\text{ km day}^{-1}$) than their North American wintering counterparts ($71\text{--}486\text{ km day}^{-1}$). Gannet positions were smoothed using a 2.5-day sliding window filter that diluted the large daily displacements during trans-Atlantic portions of the migration, particularly at the start and end of crossing, with the smaller displacements over continental shelves. An examination of daily longitudinal shifts of unsmoothed positions during crossing revealed

that gannets may have actually reached speeds of up to $\sim 1,200\text{ km day}^{-1}$. These speeds rival or exceed those of Gray-headed Albatrosses ($750\text{--}950\text{ km day}^{-1}$; Croxall et al. 2005), White-chinned Petrels ($310\text{--}610\text{ km day}^{-1}$; Phillips et al. 2006), Sooty Shearwaters ($534\text{--}996\text{ km day}^{-1}$; Shaffer et al. 2006, Hedd et al. 2012), Arctic Terns ($390\text{--}670\text{ km day}^{-1}$; Egevang et al. 2010), and Bar-tailed Godwits ($800\text{--}900\text{ km day}^{-1}$; Gill et al. 2009) crossing large ocean basins.

The trans-Atlantic strategy carries different risks and benefits compared with wintering in North America, although the net effect on fitness may be similar (Garthe et al. 2012, Alves et al. 2013). Normally coastal-shelf migrants, gannets are presumably constrained by poor food availability in the deep central ocean, making ocean-crossing risky and necessitating precise and rapid execution. Streaked Shearwaters migrated faster over the low-productivity south-central Pacific, en route to seas off northern New Guinea, than birds from the same colony migrating over relatively productive coastal waters to the South China Sea (Yamamoto et al. 2010). However, recent tracking studies of Arctic Terns (Egevang et al. 2010), Cory's Shearwaters (Magalhães et al. 2008), Sooty Shearwaters (Hedd et al. 2012), Great Skuas (Sittler et al. 2011), Bugio Petrels (Ramírez et al. 2013), and even Thick-billed Murre (Gaston et al. 2011) indicate stopovers for considerable periods near the Mid-Atlantic Ridge, where prey is presumably more abundant as a result of upwelling. A gannet in the present study spent ~ 5 days in this area on its return journey from Africa (Fig. 19), and one satellite-tracked juvenile spent weeks in the mid-Atlantic before returning to the North American coastal shelf (W. A. Montevecchi et al. unpubl. data).

The wintering area of the gannets that made trans-Atlantic crossings from Newfoundland overlapped both spatially and temporally with that of gannets from eastern Atlantic colonies (Nelson 2002, Wanless 2002, Kubetzki et al. 2009, Fort et al. 2012, Stauss et al. 2012) and other seabirds (Furness et al. 2006, González-Solís et al. 2007). The 75% kernel winter ranges of gannets from Bass Rock, Scotland (Kubetzki et al. 2009), were intermediate in size between the core (50%) and home (95%) ranges of the birds in the present study, indicating a similar pattern of space use. This part of the Canary Current system is extremely productive, and its upwelling has been characterized as the "most

intense and persistent in the western Palearctic" (Wynn and Knefelkamp 2004). Such a migration strategy could be maintained by the benefits of wintering in this region (Garthe et al. 2012), especially given that gannets and other seabirds scavenge discards from fisheries that target key avian prey, including sardines (*Sardinella* spp.) and European Pilchards (*Sardina pilchardus*) (Camphuysen and van der Meer 2005, Alves et al. 2013, Kai et al. 2013).

Compared with the western Atlantic population, the eastern Atlantic has more than 6× more colonies and 3.5× more gannets (Nelson 2006). These circumstances and the retreat of the North American Wisconsin glaciation ~10,000 years ago suggest that gannet colonies radiated from east to west, similar to other North Atlantic seabirds, including Manx Shearwaters (Robertson 2002) and Black-headed Gulls (*Larus ridibundus*; Montevecchi et al. 1987). In this regard, it is paradoxical that trans-Atlantic movement has never been recorded in eastern Atlantic gannets, despite the fact that >60,000 birds have been banded there, almost 5× more than in North America (Wanless 2002). A single gannet banded in Iceland was recovered in northwest Greenland (Petersen 1998, cited in Wanless 2002), and seven have been recovered in Europe (Wanless 2002). Further, none of the 106 geolocator-equipped adult gannets tracked from Europe crossed the Atlantic (Kubetzki et al. 2009, Fort et al. 2012, Stauss et al. 2012), although nine of these wintered in the same area off West Africa as the trans-Atlantic migrants from Newfoundland. Other avian species that have colonized the New World through trans-Atlantic crossings, such as Northern Wheatears (*Oenanthe oenanthe*), Common Ringed Plovers (*Charadrius hiaticula*), and Red Knots (*Calidris canutus islandica*), continue to retrace their ancestral routes of radiation during migration (Sutherland 1998, Newton 2008, Bairlein et al. 2012). The higher rate of Atlantic Ocean crossing by birds from Newfoundland colonies (versus Bonaventure Island) and the overlap in winter with European gannets could reflect a retained genetic predisposition for returning to coastal West Africa in winter. Such a migratory behavior could result from more recent or ongoing trans-Atlantic population exchanges between Newfoundland and the eastern Atlantic population. Further, it is intriguing that the only three known North American Great Black-backed

Gulls (*Larus marinus*) to have undertaken trans-Atlantic migrations were hatched and banded in eastern Newfoundland, whereas no trans-Atlantic migration has been detected for birds breeding to the west of Newfoundland; and similar to gannets, no European-banded Great Black-backed Gull has been recovered in North America (Wille et al. 2011), again underscoring the need to understand how genetic and environmental factors interact to affect migration, and the need to investigate and compare migratory patterns between parents and offspring.

Two such divergent migratory programs rarely coexist in a single population (Newton 2008). The occurrence of multiple migration strategies to such broadly disjunct winter areas within the same seabird populations (particularly from the same colony) has only rarely been reported (although this is increasing with the proliferation of tracking studies). Black-legged Kittiwakes breeding in Scotland wintered either in the eastern Atlantic and North Sea (predominantly successful breeders) or in the western Atlantic (dominated by failed breeders), crossing the ocean in as little as 8 days (Bogdanova et al. 2011). In Cory's Shearwater, failed breeders were less likely to migrate long distances (Cтры et al. 2013). Bugio Petrels breeding in the Madeira archipelago migrated to one of five wintering areas in the North and South Atlantic (Ramírez et al. 2013). South Polar Skuas (*Catharacta maccormicki*) breeding in the South Shetland Islands showed fidelity to wintering areas in the North Pacific Ocean, North Atlantic Ocean, and the Southern Hemisphere (Kopp et al. 2011). Black-browed Albatrosses breeding in South Georgia have three wintering areas, two of which are each used by only 3% of the population (Phillips et al. 2005). Most birds wintered in the Benguela Current system, and one wintered in the southwest Atlantic and another off southeastern Australia. On the basis of breeding success and migration timing, the authors concluded that the more distant wintering areas were in no way suboptimal and that the choice of destination likely had a major genetic component. Gray-headed Albatrosses displayed three distinct migratory strategies, one of which involved global circumnavigation (Croxall et al. 2005). Cory's Shearwaters breeding in the Azores, the Canary Islands, and the Mediterranean showed colony-based preferences for one of three major wintering sites, two

in Africa and one in South America, but there was substantial mixing (González-Solís et al. 2007). More than half of the Cory's Shearwaters breeding at Selvagem Grande Island off the northwest coast of Africa wintered in the Benguela Current, while the rest were distributed among five other wintering areas, including the northwest Atlantic and the Brazilian, South Central Atlantic, Canary, and Agulhas currents (Dias et al. 2010). Streaked Shearwaters breeding in Japan wintered in three separate regions, although these were not as widely separated as the gannets' North American and African destinations (Yamamoto et al. 2010). Sooty Shearwaters breeding at two colonies in New Zealand followed similar migratory routes across the equator and overlapped in one of three distinct winter regions in the North Pacific (Shaffer et al. 2006). These examples involve mostly procellariiform species, which, in contrast to gannets, regularly perform long-distance migration and/or foraging trips that cross ocean basins.

Gannets are not known to form pair bonds on the wintering grounds, so this migratory connection may not imply large-scale gene flow between eastern and western Atlantic populations. On the other hand, because gannets, like shearwaters (González-Solís et al. 2007), migrate in groups, it is possible that inexperienced, immature birds could follow older, more experienced conspecifics during return migration and begin breeding at colonies on the opposite side of the Atlantic Ocean from which they were hatched. In this light, the recovery of an adult Newfoundland-banded Northern Gannet in Iceland during the breeding season (Table 6) is consistent with cross-oceanic gene flow.

Ecological, evolutionary, and conservation implications.—The ecology and evolution of wintering strategies and the selective pressures that shape them, both proximally and ultimately, form a complex web of interaction. The degree of population structure or connectivity during winter is a direct result of (and an input into) this interplay. An important ecological advantage of weak connectivity or population structuring is that it allows more efficient exploitation of available food resources, when birds spread out over a broad winter range. Such a pattern also limits excessive competition (Salomonsen 1955) and prey disturbance (Camphuysen 2011) that could occur if all gannets wintered in the NE zone, as

close to the colony as possible. This lack of strong population structuring in tracked gannets suggests that birds from any one breeding population experience a variety of areas and selective pressures during winter, which implies that, in evolutionary terms, any adaptive variation in different breeding populations must be due to selective pressures that act during the breeding season (e.g., Garthe et al. 2007a). The degree of gene flow among breeding populations will influence the extent to which such variation can develop. Gannets display strong natal philopatry, and adults rarely switch colonies (Nelson 2002), although it has occurred, particularly after colony collapse (Barrett 2008); thus, there appears to be little opportunity for gene flow, as conditions favor local adaptation. This can cause severe population crashes if long-term foraging conditions within range of the colony deteriorate and birds lack the flexibility to move the colony to a better location (Pichegru et al. 2010). Yet dispersal to nonnatal colonies occurs occasionally (Nelson 2002), working to counteract local adaptation. Furthermore, natal dispersal could have a complex relationship with migratory behavior, depending on the extent of genetic and environmental influences on the transmission of migratory traits across generations (Webster and Marra 2005). More research is needed to unravel the relative contributions of genetics and environment in determining migration and winter location.

Weak connectivity implies substantial genetic variation for wintering area and a lack of strong local adaptation to particular wintering sites (Webster and Marra 2005). Local adaptation may be advantageous when prey resources are predictable (Weimerskirch 2007), particularly during breeding, when adult gannets are limited to central-place foraging (Hamer et al. 2007, Pettex et al. 2010). Strong local adaptation to winter areas might, however, be detrimental to survival in the face of dynamic and stochastic ocean conditions. Thus, weak connectivity is associated with better adaptability to changes in winter conditions in the population as a whole (Webster et al. 2002). During breeding, Northern Gannets show considerable flexibility in foraging behavior associated with variations in oceanographically driven prey fields (Hamer et al. 2007, Montevecchi et al. 2009, Garthe et al. 2011), so it is expected that they could also use such flexibility to their advantage over the

more extensive spatial and temporal scale of migration and wintering. If conditions become unfavorable enough to affect survival in one part of the winter range, the population as a whole could suffer reduced losses if there is substantial behavioral flexibility and/or genetic variation for winter location (Berthold 1996).

Weak connectivity has positive and negative implications for gannet conservation. On the positive side, widespread mixing of populations across a large geographic area reduces the risk that any one threat will significantly affect a single breeding population or the species as a whole. Even if a nonlocalized threat such as climate change affects gannets' winter survival in some regions, the gannets' broad winter latitudinal range could help to mitigate serious population-level effects, presuming that the extent of change differs in different wintering regions. However, population overlap in winter results in a broader geographic range of effect from such threats. The *Deepwater Horizon* explosion and blowout in the Gulf of Mexico during 2010, mass die-offs in the SE zone (and in Chesapeake Bay), and interactions with planned wind-farm developments near Chesapeake and Delaware Bays can carry over across seasons to affect distant and broadly separated breeding populations (Montevecchi et al. 2011). This complicates the assessment and response to such threats, which often require monitoring and interaction with birds on the breeding grounds. The cost and logistical constraints involved in carrying out this work at multiple colonies is thus magnified. Furthermore, such a year-round distribution across multiple national and state or provincial (and departmental) jurisdictions complicates the coordination of response, reserve network design (Norris et al. 2006), and planning for effective conservation (Ramírez et al. 2013). Even broad geographic distribution is no guarantee against some threats. The majority of tracked gannets wintered in relative proximity to the outflow of one or more large river systems (e.g., the Hudson and Mississippi Rivers, and the Delaware and Chesapeake Bay estuary systems), and these rivers are the source of considerable contaminants that could threaten gannets (Rattner and McGowan 2007). Thus, although gannets display broad geographic distribution, they may have a narrow distribution on the "contaminant landscape," putting the entire North American population at risk.

The consistency and repeatability of migration timing in tracked gannets implies that these are characteristics of individuals and under genetic control (Berthold 2001). If climate change alters the timing of prey availability at stopover sites or at the breeding grounds, a mismatch could occur between the timing of events in wintering and breeding areas, possibly resulting in suboptimal arrival timing and reduced fitness (Both and Visser 2001, Durant et al. 2007, Bauer et al. 2008). Climate change is likely to vary by latitude, thereby affecting birds returning to colonies at different latitudes differently. Birds wintering far from the breeding grounds have evolved departure timing based on endogenous rhythms that are fine tuned by environmental cues, allowing them to arrive when environmental conditions are appropriate on the breeding grounds. But climate change may decouple this timing linkage, causing a mismatch in timing of migration for more distant migrants. Further, climate change may decouple the relationship between climate indices that birds also use to time their migration (Frederiksen et al. 2004, Senner 2012), and the extent of this decoupling may vary by wintering area. Birds wintering closer to the breeding grounds have the opportunity to sample local environmental conditions and may arrive at a better time (Bregnballe et al. 2006).

The date of breeding has been getting later for gannets in the eastern Atlantic (Wanless et al. 2008), but no difference in timing was detected for North American gannets in our study. Even if the lay date for North American gannets were to become later, the gannets' current migration schedule would, at first, not seem to be problematic; they would still arrive in plenty of time to breed. But if prey becomes unavailable early in spring because of timing effects of climate change (Walther et al. 2002), then birds that arrive with current scheduling could pay a survival penalty (Drent et al. 2003). Moreover, if the spring peak in food availability were to become earlier (Gaston et al. 2009), gannets might be constrained to suboptimal arrival by inflexible migration timing (Both and Visser 2001).

The ability of gannets to adapt to an altered environment will depend on the level of genetic variation or behavioral plasticity in timing (Pulido 2007). Artificial selection can quickly alter the timing of migration. In an artificial selection experiment in which later onset of

migration was selected for (simulating natural selection), Eurasian Blackcaps breeding in Germany changed their timing by one week in just two generations (Pulido et al. 2001). The *K*-selected life history of gannets and other seabirds dictates that adaptation will be slow (Dias et al. 2010). Even if natural selection could act as quickly as observed in artificial selection experiments, gannets may not be able to respond quickly enough because of their long generation time. The ability to respond plastically and the rate of response will depend on the extent to which migration timing and winter-site choice are fixed (Catry et al. 1999). Flexibility in wintering site (Dias et al. 2010) and migration timing (Frederiksen et al. 2004) has been observed in other seabirds. The gannets' ability to evolve or adapt will determine the extent to which they are winners or losers in a changing environment (Hamer 2010).

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