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West meets East: Seabird migration, ocean-basin weather systems and trans-Atlantic population connections

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Key words: trans-Atlantic migration strategies; population connectivity; northern gannet; North Atlantic weather systems; geo-location loggers; species radiation

Abstract

Banding and geo-locator data reveal two fundamentally different migration strategies and the first round-trip trans-Atlantic migrations by the largest North Atlantic seabird. Analysis of extensive North American and European banding records of northern gannets (*Morus bassanus*) document movements of post-breeding adults and juveniles from the western to the eastern Atlantic but not the reverse. Geo-location logger equipped adults from the easternmost Canadian colonies exploited ocean-scale weather systems to make remarkably rapid 4 – 5 day crossings, covering 550 – 1300 km/day and engaging in uncharacteristic nocturnal flight. Western Atlantic migrants over-wintered in the same productive West African upwelling system as gannets from eastern Atlantic populations. These movements demonstrate previously unknown population connectivity and shed light on trans-Atlantic phylogeographic radiations.

INTRODUCTION

Many seabird species cross vast ocean expanses to reach distant shelf-edge, coastal and pelagic wintering areas (Harrison 1983; Nelson 2002). To facilitate long-distance movements, seabirds often exploit large-scale atmospheric systems (Weimerskirch *et al.* 2002; Murray *et al.* 2003) and exhibit intra-specific differences in migration and winter strategies (González-Solís *et al.* 2007). Migration decisions are vital for energy efficiency and rapid crossing of "desert zones" of low productivity (Murray *et al.* 2003).

Conventional band recovery analyses have provided broad-scale assessments of migration and wintering areas. More recently, bird-borne devices have generated novel insights into seabird migration (Croxall *et al.* 2005; Shaffer *et al.* 2006). Combining banding and device analyses can yield essential information about movement ecology needed for habitat and population conservation (González-Solís *et al.* 2007).

Here, we document the first round-trip trans-Atlantic gannet migrations, their facilitation by ocean-basin atmospheric features, and their regional and colony specificity that determine population connectivity and radiation.

MATERIALS AND METHODS

Study Sites - Research was conducted at Bonaventure Island (48°29'N, 64°09'W, Québec); and Cape St. Mary's (46°49'N, 54°49'W) and Funk Island (49°45'N, 53°11'W), Newfoundland, Canada.

Bands - The North American banding database yielded 13,494 banding records and 844 known-location recoveries as of 17 Jan 2006. Winter (16 Sept - 15 May; n = 442) recovery ages were categorized as "immature" (< 5 years), "adult" (≥ 5 years), or "unknown".

Devices - Two geo-location loggers were used: Geo-LT (14 x 45 mm, earth & Oceans, Kiel, Germany) and LTD 2400 (11 x 32 mm, Lotek Wireless, St. John's, NL, Canada) weighing (including attachment) 16.2 g and 8.8 g in air, respectively (< 1% adult mass). Geo-LTs recorded light level every 30 s and temperature every 120 s; light data were processed (MultiTrace, Jensen Software Systems) producing daily position estimates (Hill 1994). LTD 2400s sampled light every 60 s, temperature and pressure every 32 s; position estimates were computed by internal logger software. Latitude error can be more than double longitude error (Teo *et al.* 2004; Shaffer *et al.* 2005) and light-based latitude estimates cannot be obtained during solar equinoxes. We improved light-based latitude estimates by reconciling logger-measured sea surface temperatures (SSTs) with remotely-sensed satellite SSTs (Teo *et al.* 2004), likely halving mean latitude errors (Shaffer *et al.* 2005).

Deployments - 46 gannets (31 Bonaventure Island, 14 Funk Island, 1 Cape St. Mary's) carried loggers (38 with Geo-LTs, 6 with LTD 2400s, 2 with both) during the 2004/2005 and/or 2005/2006 non-breeding seasons. Adults attending large chicks were captured at nests near (to reduce disturbance) but not on (to avoid young inexperienced breeders) colony peripheries (Nelson 2002). Loggers retrieved during subsequent breeding seasons provided 38 datasets (28 Bonaventure Island, 9 Funk Island, 1 Cape St. Mary's). Animals were cared for following guidelines of the Canadian Council on Animal Care.

Weather - Timing and routes of trans-Atlantic migrations were compared with daily weather system and winds from the National Oceanic and Atmospheric Administration (NOAA) Earth Systems Research Laboratory website (www.cdc.noaa.gov/Composites/Day).

Analyses – Numbers of banded and logger-equipped birds making trans-Atlantic transits from Newfoundland versus Bonaventure Island colonies were compared using Fisher exact tests ($\alpha = 0.05$). Similarly, we compared trans-Atlantic crossings of banded birds from North American and European colonies. Logger temperature data distinguished flight versus non-flight in computing trans-Atlantic flight times (Shaffer et al. 2005). Periods when light level was below device measurement threshold were considered night. Device effects were assessed by comparing pre- with post-tracking masses ($n = 8$), and return and breeding rates with survival and fecundity (Mowbray 2002).

RESULTS

Band Recoveries – 98% of winter recoveries of North American bands were in North America; 2% (9/442; 3 adults, 6 immatures) were in the eastern Atlantic. Newfoundland gannets (3 adults, 5 immatures) were recovered in Iceland, Ireland, Portugal, Morocco and Canary Islands; a single Bonaventure Island immature was recovered in Spain (Table 1; electronic supplementary material, figure S1). Significantly more Newfoundland than Bonaventure Island gannets crossed the Atlantic (all ages: 14.9%, 8/54 versus 0.3%, 1/385, $p < 0.0001$; adults only: 13.6%, 3/22 versus 0/118, $p = 0.0034$; table 1).

About 4.5 times more gannets have been banded in Europe than in North America (Wanless 2002; table 1), yet no European recovery exists for the western Atlantic. The difference in Atlantic crossings by North American (9/844) versus European (0/3218) gannets is highly significant ($p < 0.0001$).

Geo-location loggers - Equipped gannets from North America displayed two different migration/overwinter strategies. Thirty-six of 38 birds migrated south, wintering along the eastern U.S. coast and Gulf of Mexico (electronic supplementary material, figure S2). Single gannets from Cape St. Mary's (bird C) and Funk Island (bird F) undertook previously undescribed round-trip trans-Atlantic migrations to the western African coast (figure 1).

Both birds departed Canadian shelf waters within a day of each other in late October 2005, crossing the Atlantic in just 4 – 5 days, traveling straight-line distances of 3,400 - 3,500 km (mean: 850 km/day; table 2). Migration initiations and progressions were synchronized with broad-scale weather systems. Gannets 'rode' favorable tailwinds south of a massive Atlantic-crossing low-pressure system (figure 2). Bird C took a northerly route to coastal Spain, then moved south to its core wintering area off West

Africa within a few days (figure 1a). Bird F took a direct route to the Canary Islands reaching the same wintering area at about the same time (figure 1b). Both gannets flew considerably at night, mostly > 1 hour after dusk or before dawn. The moon, between third quarter and new, provided little nocturnal light.

Return spring migration timing and routes differed between birds (electronic supplementary material, figure S3 and S4). Bird C retraced its route, re-crossing the Atlantic in early April in 5 days, averaging 815 km/day while bird F made a 13-day transit beginning mid-February, averaging 370 km/day (table 2). Both employed less nocturnal flight than in fall (mean: 0.4 hr/night each versus spring mean: 3.1 and 2.4 hr/night respectively), occurring mostly within 1 hr of daylight. Bird F displayed similar timing and trajectory when wintering off West Africa again the following year (Fifield & Montevecchi, unpubl. data).

Concurring with banding results, 2/10 gannets from Newfoundland made trans-Atlantic migrations versus 0/28 from Bonaventure Island. This difference, constrained by sample sizes, approached significance (p = 0.0640).

Device Effects - Forty-two of 46 (91 %) equipped birds were recaptured (44 were seen) the following year and 41 of 42 had an egg or chick. Mean body masses (n = 8) were comparable before (3025g, range: 2725 – 3225g) and after (3046g, range: 2730 – 3355g) overwintering. Some legs had superficial calluses due to attachments.

DISCUSSION

Population Interactions and Origins. Gannets are continental shelf inhabitants that breed on both sides of the North Atlantic and in Iceland, but the species' geographic radiations and population connectivity are unresolved. Most recoveries of North American bands come from North America, yet nine banded gannets (8 from Newfoundland) made cross-ocean transits. It is impossible to determine whether these birds were undertaking intentional migrations or were simply "lost".

Our geo-locator documented round-trip trans-Atlantic migrations resolve this uncertainty and further demonstrate that cross-ocean migrants originated from the easternmost North American colonies in Newfoundland. West African wintering area occupation overlapped spatially and temporally with eastern Atlantic gannets (Nelson 2002; Wanless 2002; Kubetzki, Garthe, Mendel, Crane and Furness, unpubl.). This could result from recent or ongoing population exchanges between Newfoundland and the Old World (electronic supplementary material, figure S5).

The eastern Atlantic has 6 times more colonies (35 versus 6) and 3.5 times more gannets (350,000 versus 100,000 pairs) than the west (Chardine 2000, pers. comm.; Nelson 2002). This, combined with the retreat of the Wisconsin glaciation 10,000 yr BP, suggests that gannets radiated from east to west, like other seabirds (Montevecchi *et al.* 1987; Robertson 2002). Paradoxically, Atlantic crossing is unrecorded in eastern Atlantic gannets despite ~ 4.5 times more bandings (> 60,000 bands, > 3,200 recoveries; table 1; Nelson 2002; Wanless 2002). Genetic analyses could help resolve population structure and radiations (Friesen *et al.* 2007).

Migration and Weather – Most gannets make coastal shelf migrations (Nelson 2002; Mowbray 2002), but our results indicate a second trans-Atlantic strategy undertaken by a segment of the easternmost North American population. Presumably constrained by poor food availability in the deep central ocean, trans-Atlantic migration seems risky, necessitating precise and rapid execution. This strategy, perhaps influenced by a retained predisposition to return to West Africa, could be maintained by wintering in an extremely productive coastal upwelling (Camphuysen & van der Meer 2005).

Ocean-crossing gannets are likely dependant on "finer tuned" migratory initiations than shelf edge conspecifics. These long-distance migrants enhance flight performance by "waiting" for favorable conditions (Murray *et al.* 2003), exhibiting synchronous weather-induced transits involving nocturnal flight (Shaffer *et al.* 2006; González-Solís *et al.* 2007). Ocean transits are aided by regular movements of "weather bridges" across the North Atlantic.

Device Effects – Geo-locators likely did not cause significant negative effects; body mass did not differ before and after deployments and return and recapture, and breeding rates were comparable to gannet survival and fecundity (Nelson 2002; Mowbray 2002).

Conclusion – We demonstrate two very different migration and over-winter strategies employed by North American gannets. Trans-Atlantic migrants used ocean-basin weather systems to make transits. Trans-ocean migrations by western (and not eastern) Atlantic birds suggests species radiation from Europe. Resolution of Northern Gannet population connectivity and radiation would be facilitated by tracking more migrants, especially from Iceland and by investigating population genetics (e.g. Gómez-Dias & González-Solís 2007).

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Table 1. Comparison of domestic and trans-Atlantic northern gannet (*Morus bassanus*) winter band recoveries and round-trip migrations, summarized by colony, region, continent and age.

Banding or Deployment	**Bands**						**Geolocation Loggers Over-winter Location**		
		All Winter Recoveries		**Trans-Atlantic Recoveries**					
Location	**Banded**	**Adult**	**All Ages**	**Immature**	**Adult**	**All Ages**	**Intra-Continental**	**Trans-Atlantic**	**All**
North America									
Newfoundland									
Funk Is.	2,853	20	52	5	3	8	8	1	9
Cape St. Mary's	42	1	1	0	0	0	0	1	1
Baccalieu Is.	27	1	1	0	0	0	0	0	0
Newfoundland Total	2,922	22	54	5	3	8	8	2	10
Gulf of St. Lawrence									
Bonaventure Is.	10,465	118	385	1	0	1	28	0	28
Other[*]	107	0	3	0	0	0	0	0	0
N. American Total	13, 494	140	442	6	3	9	36	2	38
Europe									
Bass Rock, Scotland							22	0	22
European Total	62,328	3218[†]		0	0	0	22	0	22

[*] "Other" refers to gannets banded along the eastern North American coast, colony of origin unknown.
[†] Includes recoveries throughout year.

Table 2. Trans-Atlantic migration flight parameters for geo-location logger-equipped northern gannets (*Morus bassanus*). Birds F's spring crossing is divided into two parts comparing favorable (1st 3 days) and unfavorable (next 10 days) winds.

	Crossing Dates	No. Days	Total Distance (km)	Mean (range) daily transit rate (km/day)*	Total flight time (h)	Mean (range) daily flight time† (h)	Total night flight (h)	Mean (range) nightly flight time (h)	Mean (range) daylight (h)
Fall									
Bird C	26 - 30 Oct 2005	5	3500	850 (650 - 1000)	54.4	10.9 (7.2 - 13.3)	12.3	3.1 (1.8 - 4.6)	10.9 (10.1 - 11.3)
Bird F	27 - 30 Oct 2005	4	3400	855 (550 - 1300)	43.6	10.9 (6.4 - 13.7)	7.1	2.4 (0.6 - 3.6)	10.9 (10.7 - 11.3)
Spring									
Bird C	4 - 8 Apr 2006	5	3260	815 (200 - 1100)	59.1	11.8 (7.9 - 13.7)	1.7	0.4 (0 - 0.8)	14.5 (14.1 - 14.8)
Bird F	1st 3 days: 18 - 20 Feb 2006	3	1820	607 (250 - 820)	37.6	12.5 (10.0 - 14.5)	2.9	1.0 (0.1 - 2.0)	12.3 (11.9 - 12.5)
Bird F	Next 10 days: 21 Feb - 2 Mar 2006	10	2630	292 (20 - 550)	86.6	8.7 (3.1 - 12.3)	2.3	0.23 (0 - 0.8)	11.8 (11.0 - 12.2)
Bird F	Overall	13	4450	370 (20 - 820)	124.2	9.6 (3.1 - 14.5)	5.2	0.4 (0 - 2.0)	11.9 (11.0 - 12.5)

* Minimum distance traveled based on straight-line distances between daily positions.

† Including night flight.

Figure 1. Round trip migrations of northern gannets (*Morus bassanus*) from (a) Cape St. Mary's and (b) Funk Island. Daily positions are color coded by month.

Figure 2. Weather and wind (red arrows) assisting fall trans-Atlantic migrations of northern gannets (Morus bassanus) from Funk Island (squares) and Cape St. Mary's (triangles). Arrow length is proportional to wind speed.

References

Camphuysen CJ and van der Meer J. (2005). Wintering seabirds in West Africa: foraging hotspots off Western Sahara and Mauritania driven by upwelling and fisheries. *Afr. J. Mar. Sci.,* **27**, 427-437.

Chardine JW. (2000). Census of northern gannet colonies in the Atlantic region in 1999. Can Wildl Serv Tech Rep Ser, No. 361, Candian Wildlife Service, Ottawa.

Croxall JP, Silk JR, Phillips RA, Afanasyev V and Briggs DR. (2005). Global circumnavigations: tracking year-round ranges of nonbreeding albatrosses. *Science,* **307**, 249-250.

Friesen VL, Burg TM and Mccoy KD. (2007). Mechanisms of population differentiation in seabirds. *Molecular Ecology,* **16**, 1765-1785.

Gómez-Dias E and González-Solís J. (2007). Geographic assignment of seabirds to origin: combining morphologic, genetic and biogeochemical analyses. *Ecol. Appl.,* **17**, 1484-1498.

González-Solís J, Croxall JP, Oro D and Ruiz X. (2007). Trans-equatorial migration and mixing in the wintering areas of a pelagic seabird. *Front. Ecol. Env.,* **5**, 297-301.

Harrison P. (1983). *Seabirds: an identification guide*. Houghton Mifflin Co., Boston, MA.

Hill RD. (1994). Theory of geolocation by light levels. In: *Elephant Seals: Population Ecology, Behaviour and Physiology* (eds. Le Boeuf B.J. & Laws R.M.) University of California Press, Berkeley, CA, pp. 227-236.

Montevecchi WA, Cairns DK, Burger AE, Elliot RD and Wells JL. (1987). The status of black-headed gulls *Larus ridibundus* in Newfoundland and Labrador. *American Birds,* **41**, 197-203.

Mowbray TB. (2002). Northern Gannet (*Morus bassanus*). *In* The Birds of North America, No. 693, The Academy of Natural Sciences, Philadelphia, PA.

Murray MD, Nicholls DG, Butcher E and Moors PJ. (2003). How wandering albatrosses use weather systems to fly long distances. 2. The use of eastward-moving cold fronts from Antarctic lows to travel across the Indian Ocean. *Emu,* **103**, 59-65.

Nelson B. (2002). *The Atlantic Gannet*. Felix Books, Norfolk UK.

Robertson GJ. (2002). Current status of the Manx shearwater (*Puffinus puffinus*) colony on Middle Lawn Island, Newfoundland. *Northeast. Nat.,* **9**, 317-324.

Shaffer SA, Tremblay Y, Awkerman JA, Henry RW, Teo SLH, Anderson DJ, Croll DA, Block BA and Costa DP. (2005). Comparison of light- and SST-based geolocation with satellite telemetry in free-ranging albatrosses. *Mar. Biol.,* **147**, 833-843.

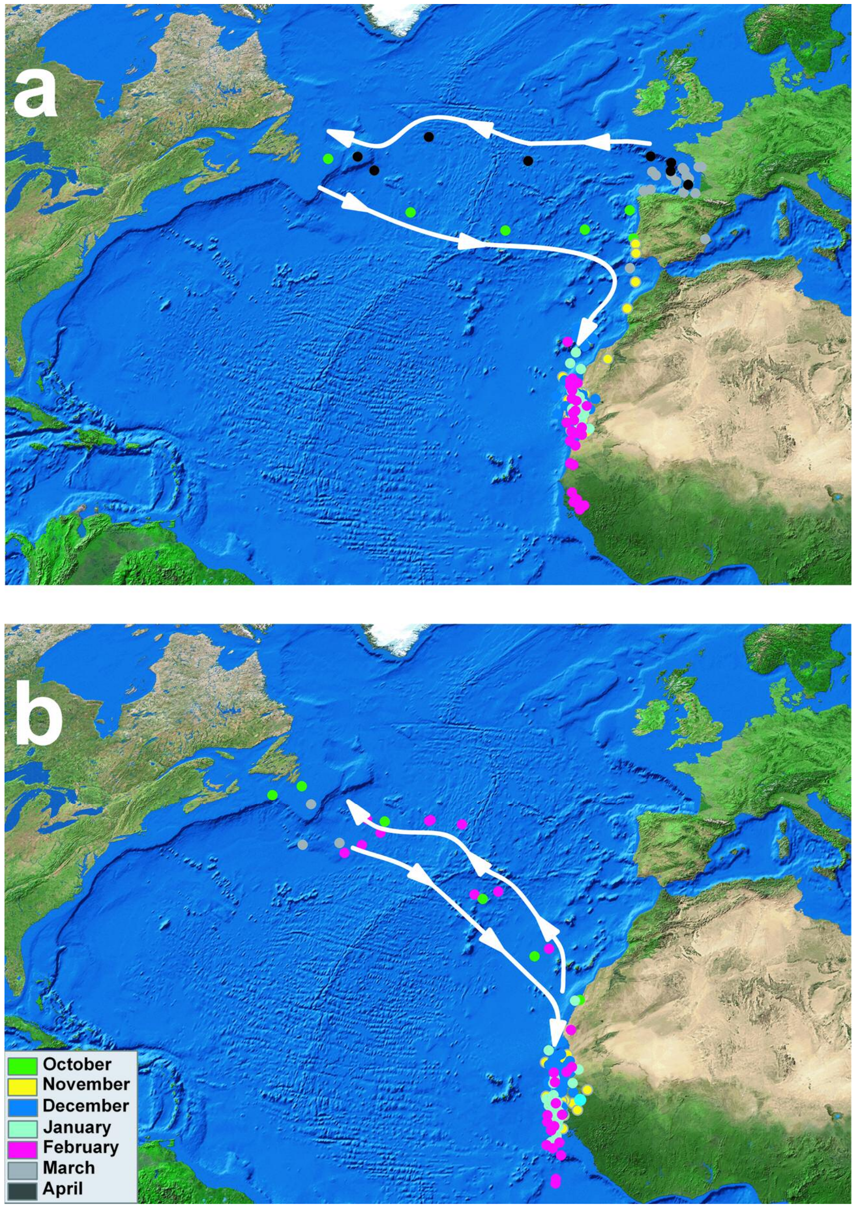
Shaffer SA, Tremblay Y, Weimerskirch H, Scott D, Thompson DR, Sagar PM, Moler H, Taylor GA, Foley DG, Block BA and Costa DP. (2006). Migratory shearwaters integrate oceanic resources across the Pacific in an endless summer. *P. Nat. Acad. Sci.,* **103**, 12799-12802.

Teo SLH, Boustany A, Blackwell SB, Walli A, Weng KC and Block BA. (2004). Validation of geolocation estimates based on light level and sea surface temperature from electronic tags. *Mar. Ecol. Prog. Ser.,* **283**, 81-93.

Wanless S. (2002). Northern gannet *Morus bassanus*. In: *The Migration Atlas: Movements of the Birds of Britain and Ireland* (eds. Wernham C.V., Toms M., Marchant J., Clarck J., Siriwardena G. & Baillie S.) Poyser, London, pp. 130-132.

Weimerskirch H, Guionnet T, Martin J, Shaffer SA and Costa DP. (2002). Fast and fuel-efficient? Optimal use of wind by flying albatrosses. *Proc. R. Soc. B,* **267**, 1869-1874.

Short Title: Trans-Atlantic Population Linkage



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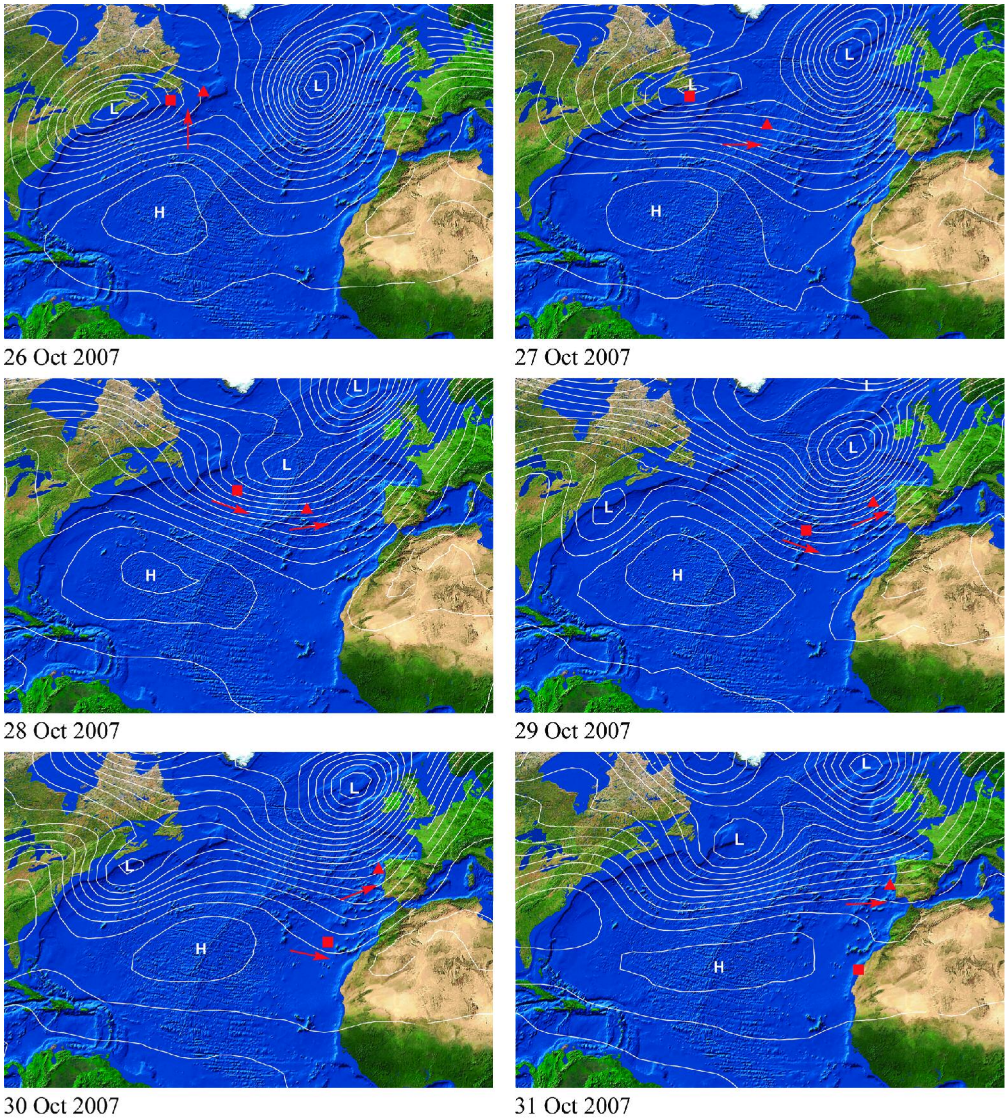

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