**Trans-Atlantic migration by post-breeding puffins: a strategy to exploit a temporarily abundant food resource?**

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**Abstract**

The distribution of Atlantic puffins (*Fratercula arctica*) from southwest Ireland was investigated using geolocation loggers between the 2010 and 2011 breeding seasons. All tracked birds travelled rapidly west into the north Atlantic at the end of the breeding season in August, with the majority undertaking trans-Atlantic trips from Ireland to Newfoundland. The furthest distance from the colony reached by each bird was not influenced by body mass or sex, and was achieved in approximately 20 days. By October, all birds had moved back to the mid Atlantic where they remained resident until returning to the breeding colony. The most parsimonious explanation for the rapid, directed long-distance migration is that birds exploit the seasonally high abundance of spawning capelin *Mallotus villosus* off the Canadian coast, which is also utilised by large populations of North American seabirds at this time. Once this short-term prey resource has diminished, the tracked puffins moved back towards the northeast Atlantic. A relationship between relative abundance of puffins and zooplankton was found in all winter months, but after correcting for spatial autocorrelation, was only significant in November and January. Nevertheless, these results suggest a potential switch in diet from mainly fish in the early winter, to zooplankton. This study suggests that puffins from southwest Ireland have a long-distance migration strategy that is rare in breeding birds from the UK, and identifies a key non-breeding destination for puffins from Ireland. This has implications for the susceptibility of different breeding populations to the effects of possible climatic or oceanographic change.

Keywords: Atlantic puffin; *Fratercula arctica*; geolocation; migration; plankton density

**Introduction**

Most seabirds undertake long migrations following the breeding season. This behaviour is thought to be an adaptive strategy to avoid seasonal deterioration in climate or increasing scarcity of resources around colonies at the end of the breeding season ([Newton 2010](#_ENREF_37)). However, considerable energy is required to travel large distances, and migrating birds often need to transit through unproductive areas to reach their main nonbreeding grounds ([Mackley et al. 2010](#_ENREF_29); [Landers et al. 2011](#_ENREF_25)).

The Atlantic puffin *Fratercula arctica* is a common, pursuit-diving seabird which breeds on coastal cliffs and islands in the North Atlantic, but is entirely pelagic during the nonbreeding period. Puffins have a small wing area relative to body weight that has been suggested to be a compromise between aerial flight and underwater maneuverability ([Wilson et al. 1992](#_ENREF_54)), although Storer ([Storer 1960](#_ENREF_49)) suggests that small wings evolved to be efficient for high speed, long distance flight rather than for use underwater. As a result, puffins have one of the highest energetic costs of flight across a range of bird groups ([Vandenabeele et al. 2012](#_ENREF_52)), with an estimated flap-rate of 300-400 beats per minute ([Meinertzhagen 1955](#_ENREF_32)). Despite this, young birds from British and Irish colonies may travel extensively throughout the north Atlantic as evidenced by ring recoveries off Newfoundland ([Lyngs 2003](#_ENREF_28)). Furthermore, the results of two recent studies using geolocation technology show that adult Atlantic puffins disperse widely during the non-breeding period ([Harris et al. 2010](#_ENREF_19); [Guilford et al. 2011](#_ENREF_16)). Many birds in these two studies dispersed into the Atlantic after the breeding season, with little evidence that they were targeting particular areas. An “exploration-refinement” hypothesis for puffin migration has been suggested ([Guilford et al. 2011](#_ENREF_16)), describing a reliance by pre-breeding puffins on large-scale exploratory movements, which become refined into an individual migratory route and set of destinations through learning. This was considered to be the most likely explanation for the high consistency among years in the migratory route and destination of individual puffins ([Guilford et al. 2011](#_ENREF_16)), as recorded in other marine migrants ([Broderick et al. 2007](#_ENREF_4); [Jorgensen et al. 2010](#_ENREF_23)). The degree of plasticity in migratory behavior affects the ability to adapt to environmental change ([Dias et al. 2011](#_ENREF_10)). Despite the limited annual variation in the migratory routes of individual puffins, and the fact that detailed data on individual puffin migrations has only recently become available, a recent change in the distribution of adult puffins outside the breeding season from a major North Sea colony has already been documented ([Harris et al. 2010](#_ENREF_19)).

In Ireland, breeding puffins are concentrated on the west and southwest coasts ([Mitchell et al. 2004](#_ENREF_33)). Little is known about the non-breeding distribution of most seabirds from Ireland, which are at the westerly extremes of the European breeding ranges. Without this information, it is impossible to predict the impacts of fluctuations in resource availability resulting from environmental change or over-fishing. The objectives of this study were to determine the winter distribution and possible environmental drivers of the seasonal shift in distribution of puffins breeding in southwest Ireland.

**Methods**

Twenty-four adult birds were captured and tagged towards the end of the breeding season (24-26th July) in 2010 on Skellig Michael, Co. Kerry, Ireland (51.77**°**N, 10.54**°**W, Fig. 1). Birds were captured during late chick-rearing using purse nets at burrow entrances on return to the colony. Birds were weighed and fitted with a British Antarctic Survey Mk18 geolocator device attached to a coloured Darvic ring fitted to the tarsus. Each device measured approximately 15x10x6mm and weighed 1.5g. Total deployment weight (device plus leg ring and cable tie attachment) was 2.8g, representing approximately 0.7% of average body mass. Breast feathers were sampled for genetic identification of sex before the birds were returned to their burrows. Logistical constraints limited access to the island for tag recovery to two weekends in early and late July 2011 to recover instrumented birds.

Data were downloaded from retrieved loggers, decompressed and processed using TransEdit and Locator in the BASTrak software suite (British Antarctic Survey, Cambridge). Light level data were processed using a sun elevation angle of -4.5, based on calibration data from loggers at a fixed location. During processing, dawn and dusk transitions were filtered according to a minimum dark period of 4 hours. Any transitions with obvious interruptions to light curves were noted, and the resulting locations checked visually and excluded from analyses as appropriate. Location estimates occurring within 2-3 weeks either side of the vernal equinox that were clearly affected by inaccuracy of latitude estimation were removed from the analysis (although longitude information was retained), as were locations representing movements of more than 500km day-1. Accuracy of validated locations is in the region of ±200km ([Phillips et al. 2004](#_ENREF_39)). Date of departure from the colony and onset of migration was considered to be the date that birds were last recorded within 500km of the colony given the accuracy of geolocation estimates and since it was apparent from the data that some birds spent a period of days at sea before returning briefly to the colony before migration. The terminus of directed westerly migration was identified by visual inspection. The distance travelled west on the outward (postbreeding) migration was the great-circle distance between the breeding colony and the mean latitude and longitude of the eight most westerly, validated locations (to account for variability in position error). The relationship between distance travelled west and body mass was examined using linear regression, while the relationship between distance travelled and gender was examined using a Mann-Whitney U test.

Non-breeding distributions of the tracked birds were examined in relation to potential prey availability. Data on zooplankton abundance were from the Continuous Plankton Recorder (CPR) survey for 1985-2010, and obtained from the Sir Alistair Hardy Foundation for Ocean Science (SAHFOS). The CPR is an upper layer plankton sampler towed behind vessels of opportunity along regular shipping routes. The device filters seawater at a depth of 7–9m on a moving band of silk. The silk is divided into samples, with each sample representing approximately 10 nautical miles of towing and 3m3 of filtered seawater, and effectively captures relative abundance of zooplankton ([Richardson et al. 2006](#_ENREF_44)). Copepod abundance in many parts of the North Atlantic has declined over the past 40 years, indicating geographical shifts in plankton communities ([Pitois and Fox 2006](#_ENREF_41)). Given these changes and the high spatial and temporal variability in sampling effort, only records from 1990 to 2010 (the most recent available data) were used to identify areas of persistently high zooplankton abundance.

Dietary information from puffins suggests consumption of large zooplankton species, including euphausiids and amphipods over 12mm in size ([Falk et al. 1992](#_ENREF_13); [Hedd et al. 2010](#_ENREF_22)). Data on large zooplankton (euphausiids, gammarids, hyperiids, decapod larvae, siphonophores, chaetognaths, salps, mysids, cephalopod larvae, and fish larvae) were therefore selected from the CPR data for analysis. Abundance (individuals per m3) of all large zooplankton species combined, as well as separately for euphausiids given their prevalence in CPR data, was mapped using Inverse Distance Weighted (IDW) interpolation on a 1**°** grid which is roughly comparable to the accuracy of the GLS positions (Phillips et al. 2004), using a node search radius of 3**°**. Puffin densities in each cell within a 1**°**x1**°** grid across the North Atlantic were estimated for each month from August to February as the number of individual positions recorded in that cell. In each month, the relationship between relative bird density and zooplankton abundance was investigated using Dutilleul’s modified T-test ([Dutilleul 1993](#_ENREF_12)) to account for spatial autocorrelation using the freely available PASSaGE 2.0 software ([Rosenberg and Anderson 2011](#_ENREF_45)). This method reduces the degrees of freedom in proportion to the degree of spatial autocorrelation in the data ([Haining 1991](#_ENREF_18)).

Monthly average and long-term (1981-2010) monthly average zonal (east-west direction) wind velocity at a 2.5**°** resolution data were obtained from the [National Oceanic & Atmospheric Administration](http://www.noaa.gov/) (NOAA) Physical Sciences Division ([http://www.esrl.noaa.gov/psd/data/gridded/data.ncep.reanalysis.derived.surface.html)](http://www.esrl.noaa.gov/psd/%20/data/gridded/data.ncep.reanalysis.derived.surface.html)) to determine whether there was a relationship with wind speed and direction and the timing and bearing of outward migration routes taken by tracked birds.

**Results**

Ten birds were successfully recaptured at the colony one year after deployment. A further five individuals were observed at the colony that evaded recapture. The colony is located on a UNESCO world heritage site, and restoration works on a monastic wall resulted in the burrows of four tagged birds being built over between deployment and recovery of the devices. These birds were not resighted in the colony the following year. This and the limited time available in the colony for recapture (2 weekends in early and late July 2011) resulted in an overall resighting rate of only 62.5%. A summary of bird metrics and details of migration is given in Table I. Data were available for 4 females, 5 males, and 1 bird of unknown sex (the feather sample did not yield enough genetic material for reliable sexing).

All tagged birds commenced a directed westerly migration at the end of the breeding season. Six birds (3 males, 3 females) travelled from southwest Ireland across the North Atlantic to the coast of Canada, typically taking approximately 20 days to make the journey and spending 15-42 days in waters off Newfoundland or the Labrador shelf. The remaining four birds migrated as far as waters off southern Greenland. Although there was considerable variation among birds in the extent of the initial outward migration and subsequent movement patterns, all spent the majority of the winter months in the central Atlantic Ocean southeast of Greenland, moving closer to Ireland in spring months. This is consistent with the timing of breeding birds returning to the colony to excavate burrows and (re)establish pair bonds. One bird (17817) spent 1-2 months in the Mediterranean Sea in January/February before returning to the colony (Fig 2).

The prevailing winds during the month of August 2010, when puffins departed the colony, were westerlies, indicating that the tracked puffins were largely travelling into headwinds. This was consistent wit the long-term (1981-2010) monthly average winds for August (Figs 3 a,b). The distance migrated west from the colony (to the average of the 8 most westerly, reliable fixes), ranged from 1722-3165km (mean 2537 ± 506km). There was no significant effect of bird mass (F1,9 = 0.68, P= 0.435) or sex (W=24, P=0.391) on the distance travelled west during the initial outward journey from the breeding colony.

Despite interpolating the zooplankton densities using a 3-degree search radius, some areas of the North Atlantic were un-sampled or poorly represented as CPR sampling effort is largely opportunistic. There was significant spatial autocorrelation in the data on puffin relative abundance in all months (Morans I statistic, P<0.01 in all months), violating the assumption of independence of residuals and leading to increased chance of Type I error. We therefore used Dutilleul’s modified T-test, which takes into account spatial autocorrelation, to test for significance of the correlation using 5 equidistant classes. After accounting for spatial autocorrelation, the correlations that remained significant were those between abundance of puffins and that of large zooplankton and euphausiids in November, and of euphausiids only in January (Table II).

**Discussion**

All tracked Atlantic puffins undertook rapid, directed westerly migration into the Atlantic Ocean at the beginning of the non-breeding period, departing the colony between the 29th July and 14th August. Most puffins have left British colonies by the middle of August, with the main exodus from the intensively monitored colony on the Isle of May typically occurring within the first week of August ([Harris and Wanless 2011](#_ENREF_21)). Six of the 10 birds travelled to the east Canadian coast where they remained throughout August and September, while the remaining four birds travelled as far west as the southern tip of Greenland.

Those puffins from Ireland that have travelled as far as the Newfoundland/Labrador area were therefore feeding in the same area (and presumably on the same food) as North American puffins, of which there are an estimated 350,000-400,000 breeding pairs ([Lowther et al. 2002](#_ENREF_27)). Baillie & Jones ([2004](#_ENREF_1)) report median fledging dates for puffins on the Gannet Islands, Labrador, between 1981 and 1998 as 9-21 September, while Lowther et al. ([2002](#_ENREF_27)) report fledging from mid-August to early September, indicating that North American puffins are still provisioning chicks until this time. Despite having undertaken such a long journey, the puffins tracked in this study did not spend long periods off the east coast of Canada, remaining there for 15-42 days before returning eastwards. The reason why residency times off Canada were so short is unclear, although it is likely to be related to availability of prey resources. Optimal foraging theory suggests that some individuals may exploit new areas or prey that are further afield, when doing so outweighs the energetic costs of movement ([Pyke 1978](#_ENREF_42)). During the early post-breeding period zooplankton abundance was generally patchy, and large zooplankton were uncommon off Newfoundland (unpublished data).

However, a seasonally abundant prey species off the Canadian coast is capelin, a small, pelagic schooling fish. Adult fish range in size from 12-23cm, and at maturity, schools of adults migrate to spawn on Newfoundland beaches and demersal sites ([Davoren et al. 2006](#_ENREF_7)). Recent studies in the northwest Atlantic show that spawning of capelin is now c. 4 weeks later than in the 1980s, with arrival ranging from 12 June to 23 August ([Regular et al. 2009](#_ENREF_43)), and an increased tendency towards demersal spawning ([Davoren et al. 2008](#_ENREF_6)). Eggs deposited on shallow beach sediment typically emerge 10-12 days later ([Nakashima and Wheeler 2002](#_ENREF_36)), while colder temperatures at depths associated with demersal spawning prolong larval development and result in later emergence ([DFO 2011](#_ENREF_9)). Larvae exit the sediment and are carried out of bays in large numbers by surface currents. Therefore, the period throughout August-September coincides with high local abundances of both spawning capelin and emerging larvae.Capelin features heavily in the diet of Atlantic puffins rearing chicks in Newfoundland during August and early September ([Lowther et al. 2002](#_ENREF_27)), and there is a strong correlation between the abundance of puffins and capelin in inshore waters at this time of year ([Piatt 1990](#_ENREF_40)). Large numbers of other capelin predators, including common *Uria aalge* and Brunnich’s guillemots *U. lomvia* (both local birds and migrants from further north) also use the waters off Labrador and the Grand Banks, as do nonbreeding kittiwakes *Rissa tridactyla* ([González-Solís et al. 2011](#_ENREF_15)) and great skuas *Stercorarius skua* from the east Atlantic ([Magnusdottir et al. 2012](#_ENREF_30)).

The mean calorific density of adult capelin in August-October varies from 5.3 – 8.3 kJ/g wet mass ([Barrett et al. 1987](#_ENREF_2); [Øyan and Anker-Nilssen 1996](#_ENREF_38)). By comparison, most zooplankton species, which dominate puffin diet elsewhere during the winter months ([Falk et al. 1992](#_ENREF_13); [Hedd et al. 2010](#_ENREF_22)) are much smaller and less energy-rich. Mean energy densities of amphipods, euphausiids, cnidarians, and cephalopods from the north Atlantic are 5.44, 3.4, 0.7, and 4.4kJ/g wet mass respectively, and the overall mean for crustacean zooplankton is c. 1.6kJ/g wet mass ([Steimle and Terranova 1985](#_ENREF_48); [Spitz et al. 2010](#_ENREF_47)). Atlantic puffins have a reported daily requirement of 1065kJ/day ([Lilliendahl and Solmundsson 1997](#_ENREF_26)). Presumably, meeting this requirement through consumption of capelin, which are comparatively large (spawning males average 183mm, 42.1g; spawning females 158mm, 20-29g) and energy-rich ([Montevecchi and Piatt 1984](#_ENREF_35)), would result in a higher rate of energy intake than foraging on even high calorific content zooplankton prey such as copepods, euphausiids, mysids and chaetognaths ([Davis 1993](#_ENREF_5)), which are comparatively small, and would require additional foraging effort even if highly aggregated.

Considerable time from October onwards, presumably after the abundance of capelin off Newfoundland had declined, was spent in a broad area to the southeast of Greenland that has recently been recognized as a pelagic seabird biodiversity hotspot ([Boertmann 2011](#_ENREF_3); [Wakefield et al. 2011](#_ENREF_53); [Montevecchi et al. 2012](#_ENREF_34)). Hedd et al. ([2010](#_ENREF_22)) showed that the winter diet of Atlantic puffins was dominated by zooplankton, and despite there being relatively few areas of high zooplankton abundance (unpublished data) in the area, a significant correlation was found between relative puffin density and zooplankton abundance in November and January. Puffin distribution correlated best with that of a single prey group, euphausiids, which is also consistent with other studies linking seabird distribution to zooplankton prey. A positive correlation between little auks (*Alle alle*) and large copepod *Calanus finmarchicus* densities was found in the North Atlantic ([2012](#_ENREF_14)), and it has been suggested that seabird distributions are more likely to reflect those of one or more key taxa rather than all types of zooplankton ([Sydeman et al. 2010](#_ENREF_50)). The lack of a strong correlation between puffin and zooplankton abundance in other months may be due to annual or seasonal changes in distribution of puffins or plankton. Plankton data were averaged over 20 years, whereas the puffin tracking data were from just one year, and both distributions will to some degree vary as a consequence of climatic or oceanographic changes ([Pitois and Fox 2006](#_ENREF_41)). Alternatively, the synchronous moult of their primary feathers during the winter renders puffins flightless for a period of weeks ([Harris and Wanless 2011](#_ENREF_21)), and may reduce their ability to track prey patches, or they may actively avoid areas with high plankton densities during this time if these attract generalist predators such as great skuas and sharks.

While strong winds have been known to divert migrating birds off-course, and wrecks of larger alcids have been recorded ([Underwood and Stowe 1984](#_ENREF_51); [McFarlane Tranquilla et al. 2010](#_ENREF_31)), the puffins tracked in this study were clearly not blown from Ireland to Newfoundland. The observed westerly migration was against prevailing winds, so presumably, high abundances of capelin provide a rich source of energy that outweighs the energetic cost of such a long migration. Long-distance migrations by birds taking advantage of highly seasonal food availability have also been observed in shearwaters ([Shaffer et al. 2006](#_ENREF_46); [Guilford et al. 2009](#_ENREF_17)). While multi-year data are not currently available for Irish populations, a remarkable degree of repeatability in the direction and extent of migration in puffins tagged on Skomer has been reported ([2011](#_ENREF_16)). Puffins from Ireland that visited the eastern Canadian coast as pre-breeders ([ring recoveries of young birds from British colonies off Newfoundland have been noted, Lyngs 2003](#_ENREF_28)), would presumably have experienced high foraging success on capelin, and be likely to return there as adults. The rapid and directed movement of puffins tracked from southwest Ireland is consistent with the “exploration-refinement” hypothesis for migration, where puffins rely on a system of large-scale exploratory movements during the prebreeding years, which become refined into an individual migratory route and set of destinations ([Guilford et al. 2011](#_ENREF_16)).

Delays in the timing of arrival of capelin in inshore waters has led to delayed breeding chronology in common guillemots ([Davoren and Montevecchi 2003](#_ENREF_8); [Regular et al. 2009](#_ENREF_43)). The median lay date of Atlantic puffins in a Maine study population was 15th - 21st June in 1985 ([Kress and Nettleship 1988](#_ENREF_24)), so the majority of broods would therefore be expected to fledge by mid-August. It seems that there has also been a shift in breeding chronology of puffins in the west Atlantic over the past 2 decades, with puffins now rearing chicks into early September ([Lowther et al. 2002](#_ENREF_27)), mirroring the later spawning of capelin. Long time-series of breeding data from the 1980s and 1990s from St Kilda ([Harris et al. 1998](#_ENREF_20)) and Norway ([Durant et al. 2004](#_ENREF_11)) suggest that in the east Atlantic there has not been any systematic shift in timing of breeding; hence, if post-breeding migration of Irish puffins is motivated by capelin, it seems likely that it is a recent phenomenon.

A long-distance migration to avail of abundant capelin may put post-breeding puffins from Ireland at risk, as fidelity to non-breeding destinations in seabirds is usually high ([but see Dias et al. 2011](#_ENREF_10)). Large declines in capelin abundance off Labrador and Newfoundland have been noted, with the 2010 estimate of abundance from spring acoustic surveys being about 10% of 2007-2009 values and 1% of historical levels ([DFO 2011](#_ENREF_9)). Our results have identified a key non-breeding destination for migrating puffins, and suggest that reliable prey aggregations are important. However, this study also highlights the need for multi-year data to determine if puffins breeding at the western edge of the European range exhibit sufficient plasticity in migration strategies to adequately respond to environmental change.

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**Figure legends**

Fig. 1 Location and relative size of Atlantic Puffin colonies in UK and Ireland. Data from Seabird 2000 census data available from http://jncc.defra.gov.uk/. Only colonies with >50 breeding birds are shown. Yellow stars denote the location of previous tagging studies in the UK (Skomer and the Isle of May), and the present study, highlighting the more westerly location of Skellig Michael, southwest Ireland.

Fig. 2. Mean monthly (Aug 2010 – Feb 2011) positions of individual Atlantic Puffins tracked from southwest Ireland using geolocators during the non-breeding period. 0 denotes colony start/end point with all other numbers denoting month (1=January).

Fig. 3. Zonal (east-west) wind speeds (m/s). A) August 2010, showing that migrating puffins were flying into headwinds, and B) Long-term average (1981-2010) for August. Positive values (red spectrum) indicate winds in an easterly direction, while negative values (blue spectrum) represent winds in a westerly direction.

**Tables**

Table I. Details of deployments.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Bird ID** | **Sex** | **Weight (g)** | **Colony departure date** | **Trans-Atlantic migration?** | **End of westerly migration** | **Residency off Newfoundland/Labrador (days)** |
| 17713 | F | 345 | 7 Aug 2010 | Y | 28/08/2010 | 24 |
| 17715 | ? | 370 | 14 Aug 2010 | N | 30/08/2010 |  |
| 17717 | M | 405 | 29 Jul 2010 | N | 14/08/2010 |  |
| 17718 | M | 385 | 29 Jul 2010 | Y | 20/08/2010 | 42 |
| 17803 | M | 385 | 12 Aug 2010 | Y | 31/08/2010 | 24 |
| 17804 | F | 370 | 1 Aug 2010 | Y | 19/08/2010 | 35 |
| 17809 | M | 410 | 17 Aug 2010 | Y | 01/09/2010 | 25 |
| 17812 | F | 360 | 1 Aug 2010 | Y | 30/08/2010 | 15 |
| 17816 | M | 390 | 13 Aug 2010 | N | 31/08/2010 |  |
| 17817 | F | 390 | 5 Aug 2010 | N | 30/08/2010 |  |

Table II. Correlations between relative puffin density and zooplankton abundance during the non-breeding period (August-February). Bold indicates P values that were statistically significant according to Dutilleul’s modified T-test accounting for spatial autocorrelation.

|  |  |  |  |
| --- | --- | --- | --- |
| **Month** | **Correlation** | **Uncorrected P** | **Modified T-test P** |
| ***All large zooplankton*** | | | |
| Aug | 0.08 | 0.011 | 0.18 |
| Sep | 0.16 | 0.002 | 0.12 |
| Oct | 0.05 | 0.142 | 0.52 |
| Nov | 0.16 | 0.0001 | **0.03** |
| Dec | 0.06 | 0.121 | 0.6 |
| Jan | 0.09 | 0.02 | 0.12 |
| Feb | -0.12 | 0.0007 | 0.17 |
| ***Euphausiids only*** | | | |
| Aug | 0.11 | 0.0005 | 0.13 |
| Sep | 0.14 | 0.005 | 0.18 |
| Oct | 0.09 | 0.007 | 0.27 |
| Nov | 0.2 | 0.0001 | **0.003** |
| Dec | -0.04 | 0.269 | 0.65 |
| Jan | 0.09 | 0.02 | **0.02** |
| Feb | -0.06 | 0.06 | 0.32 |