**ORIGINAL PAPER**

# Did the animal move? A cross-wavelet approach to geolocation data reveals year-round whereabouts of a resident seabird

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## Abstract

Considerable progress in our understanding of long-distance migration has been achieved thanks to the use of small geolocator devices (GLS). The tracking of resident or short-distance migrant animals remains however challenging because geolocation errors are substantial and difficult to estimate. This study aims to examine the sex-specific marine space uses of a resident tropical seabird, the masked booby (*Sula dactylatra*), during its full annual life cycle at the Fernando de Noronha archipelago (Brazil). Masked boobies ($n = 31$) tagged with GLS recording light intensity, seawater immersion, and water temperature showed a resident behaviour over their entire annual cycle. A wavelet analysis of GLS data revealed oscillatory patterns of inferred longitude correlated with changes in immersion frequency. This synchronicity demonstrated that birds traveled away and back from the colony on consecutive trips of short length ($\sim$ 2–4 days) and short range ($\sim$ 100–300 km) eastward of the colony. Duration and range of trips depended on the sex of the individual and on the time of the year. Trip duration increased gradually from the end of the breeding period to the post-breeding period, probably due to the release of the central-place breeding constraints. During the pre-breeding period, females had farther ranges eastward and spent more time in water than males. Despite inherent limits of light-based geolocation, this study demonstrates the relevance of synchronicity analysis of GLS data for investigating year-round movements of resident or short-distance migrants.

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## Introduction

Animals move to feed, to find mates, to avoid risks such as predation or adverse climatic conditions, or to locate breeding areas, within the range of their motion and navigation abilities (Bowler and Benton 2005; Nathan et al. 2008). Birds in particular, including seabirds, have great mobility and navigation skills. Many migratory birds travel over long distances, occupy distant areas at different seasons, and return repeatedly to the same localities from year to year (Egevang et al. 2010; González-Solís et al. 2007; Shaffer et al. 2006; Stenhouse et al. 2012; Weimerskirch and Wilson 2000; Wilson et al. 1998). Other seabirds can in contrast be referred to resident (or sedentary) when their distribution and center of distribution remain more or less the same all year round, and from year to year (Newton 2008; Schacter and Jones 2018).

Resident behaviour might be explained by a reliable supply of food available locally all year, and/or by territorial advantages to regular year-round visits to their breeding site (Newton 2008). This behaviour might therefore be related to an energy-saving strategy, where birds avoid metabolic

costs associated with migration and prefer to spend energy in remaining in seasonally less favorable habitats (Garthe et al. 2012). In particular, numerous tropical seabirds such as petrels, shearwaters, tropicbirds, boobies and noddies are classed as resident species (Ballance et al. 2006; Diamond 1978). Seasonality is indeed generally less pronounced and food resources have smoother variation in tropical areas than in temperate and polar regions (Ashmole 1971; Longhurst and Pauly 1987).

Migration may have evolutionary consequences at the species level, as it increases the probability of encountering individuals from other populations and, consequently, of gene flow. Being resident can therefore have important consequences on gene flow disruption between populations and on population genetic structures (Friesen et al. 2007), which in the end conditions the evolutionary resources populations may rely on in changing environments. Resident behaviour is thus of great interest for future investigations into the topic of population resilience. Current knowledge of seabird residency is however mainly based on direct observations (Jaquemet et al. 2004; Olson et al. 2001), and to our knowledge few studies have aimed at confirming or elucidating year-round behaviour of a resident seabird using tracking devices (Schacter and Jones 2018).

Masked booby (*Sula dactylatra*) is a pan-tropical seabird found in every ocean on or off nearly every coast except the eastern Atlantic, northern Indian Ocean and the central-eastern Pacific (Nelson 2005). This species has been the subject of a relatively large number of movement-based studies during breeding period (Lerma et al. 2020; Wilkinson et al. 2020). Yet, the movements of masked boobies during the non-breeding period remain unclear. Adults would stay in the vicinity of the colony and would eventually disperse widely (thousands of km from the colony), while post-breeders return back to the colony intermittently (Del Hoyo et al. 1992; Nelson 2005). Apart from the uncertainties related to the post-breeding whereabouts of masked boobies, other questions remain, particularly concerning their reversed sexual dimorphism (hereafter RSD, when females are heavier and larger than males). Several studies have expected sex-related differences in the foraging strategies of masked boobies, assuming that the challenges related to foraging in tropical ecosystems characterized by low productivity presumably exert strong selection pressure on body size differences of tropical seabird species (Lewis et al. 2005; Weimerskirch et al. 2009). Some studies suggested a higher foraging effort by females (Weimerskirch et al. 2009), however most of them did not demonstrate differences between sexes in foraging trips (Poli et al. 2017; Sommerfeld et al. 2013; Young et al. 2010).

Accurately tracking year-round resident seabirds such as masked boobies is yet challenging. Due to attachment and power limitations, the use of tracking devices such as GPS loggers and Argos transmitters is often limited to short time periods (from hours to months) (Ropert-Coudert et al. 2004; Wakefield et al. 2009; Wilson et al. 2002). Light-level data loggers or global location sensors (GLS) remain the preferred option for studying seabird spatial behaviour perennially since they are small enough to be attached on a plastic ring, energy-efficient when deployed for up to several years, and associated with reduced costs. Positions can be inferred from light data with an analysis of twilights derived from high-frequency light intensity records (Hill 1994; Lisovski et al. 2019). However, light signals may be subject to errors due to physical features (e.g., shade from vegetation or animal body covering the device), weather (e.g., cloud cover), and animal behaviour (individuals nesting in burrows or being sat on the logger). As a consequence, positions derived from light records are less precise than positions estimated from GPS (Ekstrom 2007; Lisovski et al. 2012; Phillips et al. 2004). Latitude error is for example highest during the equinoxes and close to the equator (Hill 1994). GLS and associated analytical methods are for these reasons particularly relevant for elucidating migratory movements, as well as for movements that are in the order of magnitude of geolocation errors (e.g., $65 \pm 54$ km in longitude and $347 \pm 462$ km in latitude, as estimated in our study; Fig. 1a). In the latter case, the stumbling block remains in distinguishing movements from geolocation error to detect animal movements.

Many GLS also record external data such as saltwater immersion and sea surface temperature, which is crucial for improving geolocation estimations and/or interpreting GLS data (Guilford et al. 2009; Merkel et al. 2016). To identify whether oscillatory patterns of location inferred for GLS-tagged resident seabirds represent real movement, a solution would be to study its synchronicity to external data. For example, if a measure of animal behaviour supposedly independent of geolocation error (e.g., saltwater immersion frequency) correlate with changes in location, this would be evidence that movements are real, and not a consequence of GLS location error. Wavelet analysis provides appropriate tools for comparing the frequency contents of time-series and drawing conclusions about series' synchronicity at certain periods and across certain ranges of time. It has been widely used in ecology (e.g., Bertrand et al. 2008; Cazelles et al. 2008; Fablet et al. 2013; Jenouvrier et al. 2005) since this method is highly appropriate to analyze periodic patterns in biological time series that are often noisy, non-linear and non-stationary, such as in GLS data (Cazelles and Stone 2003).

In this study, we use GLS to understand year-round at-sea movements of the masked booby. The goal is to elucidate the post-breeding movements of masked boobies and sex-specific non-breeding behaviours, and to demonstrate the relevance of wavelet analysis as an analysis tool for GLS data derived from short-migrants or resident species.
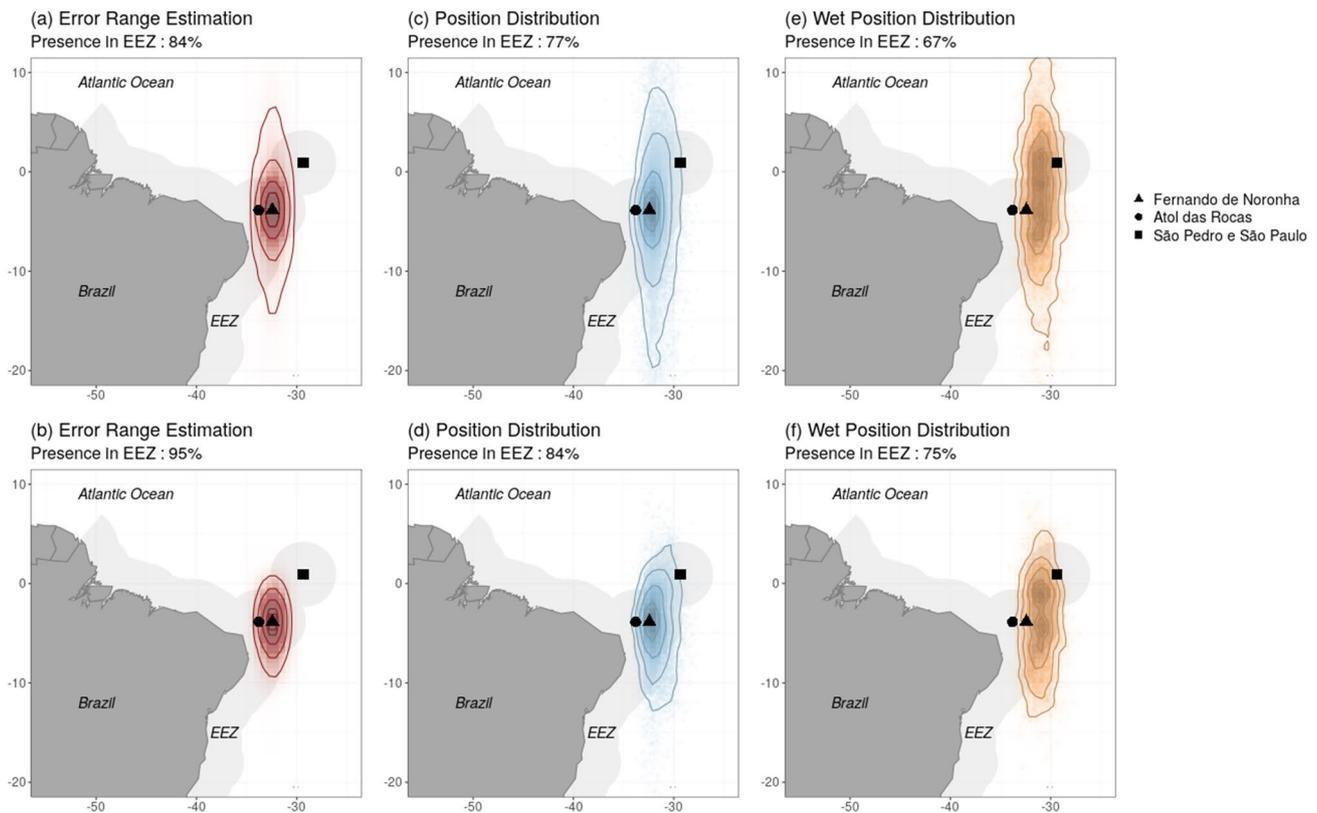
**Fig. 1** Maps of geolocation error (**a**, **d**) represent the geographical error range estimation of a GLS fixed at Fernando de Noronha (FdN), Brazil, based on the error structure presented in Fig. 2. Position distributions (**b**, **e**) have been estimated using observed data from all GLSs. Wet position distributions (**c**, **f**) correspond to positions where the mean proportion of time spent on water is above 75%. In (**a**–**c**) all positions have been used, in (**d**) positions whose satellital SST dif- fered by more than 0.5 °C from FdN's SST were removed, while in (**e**, **f**) only positions whose temperature deviation (sensor observation vs satellital observation) ranges within − 0.25 °C and + 1.5 °C were used. Contours correspond to confidence intervals of 10, 25, 50, 75, and 90%. Black points refer to main islands around FdN. EEZ stands for the Exclusive Economic Zone

## Material and methods

### Study site

Fernando de Noronha (hereafter FdN, 03°50′ S, 32°25′ W) is an offshore archipelago (21 islands and islets, 18.2 km²) lying at 360 km east from the mainland city of Natal, Brazil. FdN is a clear priority for biodiversity conservation at the Brazilian federal state level (through the Ministry of Environment, ICMBio) and scientific data are critical for improving the design of conservation policies. This archi- pelago hosts the largest number of breeding seabird spe- cies in Brazil, with eleven species reported to breed there (Mancini et al. 2016). To elucidate the year-round where- abouts of masked boobies breeding on the archipelago, fieldwork was conducted on one of the secondary islets, Meio island, which hosts one of the main masked booby breeding colony with 388 active nests (i.e., with eggs

or chicks) censused in April 2018 (Antas 1991, authors unpublished data).

### GLS data analysis

#### GLS deployment

Breeding adults raising two to seven weeks old chicks were caught on 4–6 May 2017 and fitted with GLS attached to a plastic ring. In total, 34 individuals were caught (16 females and 18 males) and 2 types of GLS were deployed (*n* = 20 MK3006 and *n* = 14 MK3005 models both from Biotrack Ltd., Wareham, UK). GLS weighted 2.5 g and were fixed to the plastic ring (2 g) with cable ties, the entire equipment corresponding to less than 0.4% of the body mass. All log- gers recorded daylight level intensity, saltwater immersion (i.e., activity data) and sea surface temperature data.

Loggers measured daylight level intensity every 60 s and recorded the maximum light intensity for each 10 min for

MK3006 and each 5 min for MK3005. They measured wet/dry status based on conductivity measurement. For MK3006 wet/dry status was sampled every 3 s and the sum of immersion events for each 10 min received a score between 0 and 200 (wet; immersion data > 0) and was stored. Temperature was recorded after 20 first minutes continuously wet, temperature wet timer reset anytime the device goes dry for > 3 s. For MK3005, wet/dry status was sampled every 3 s and the sum of wet/dry duration was stored. Temperature was recorded after 25 min continuously wet, temperature wet timer reset anytime device went dry for > 6 s.

## Light-based geolocation

Twilight times (i.e., sunrise and sunset) were determined using an arbitrary light intensity threshold of 2.5. A good choice for light threshold is often the lowest value that is consistently above any noise in the nighttime light levels (Pollet et al. 2014). The selection of the threshold was performed through the existing R library TwGeos (Lisovski et al. 2016). *In situ* calibration was done following Lisovski et al. (2019) recommendations. Relying on our knowledge of the phenology of masked boobies based on in situ observations, we assumed that birds stayed at their breeding place at least from 10 May 2017 to 15 June 2017. A sun elevation angle was computed for each tag using the Hill-Ekstrom calibration (i.e., minimization of latitude error variance), and used for the estimation of birds' geographic positions over the whole deployment. This was performed through the existing R library SGAT (Wotherspoon et al. 2016). Light-based geolocation using the threshold method provides one position from two consecutive twilights (i.e., two positions per day). We assigned to each position a mean temperature and the proportion of time in water calculated between two twilights.

For each individual, we evaluated the deviation between all observed twilight times and theoretical twilight at FdN with respect to the calibrated sun elevations (Fig. 2a, c, e). The OSTIA global sea surface temperature (SST) reprocessed product[1] provided by the Copernicus Marine Service was also used to compute the deviation between mean temperature recorded by the tags and the SST gathered from satellite observations at FdN (Fig. 2b, d, f).

## Position distributions and map of geolocation errors

The impact of measurement errors on geolocation estimates was illustrated by maps of geolocation error (Fig. 1a, b). These maps were estimated by sampling positions likely to be observed from a fixed GLS at FdN and by applying

a two-dimensional Kernel Density Estimation (KDE) with grid of mesh 0.5° and a bandwidth of 2°. In our case, a twilight error structure was defined by fitting a gamma distribution on all twilight times deviation estimated during the calibration period (Fig. 2a). Twilight time observations were then simulated and used to estimate geolocations. Estimated positions whose satellite-based SST deviated over 0.5 °C from FdN's SST were removed (Fig. 1b), based on the theoretical sensor accuracy given by the archival tag provider (Biotrack Ltd., Wareham, UK).

Position distributions were estimated by applying a two-dimensional KDE on observed positions from all GLSs with same parameters (Fig. 1c–f). A temperature error structure was arbitrary defined using a uniform distribution on all temperature deviation estimated during calibration period (Fig. 2b). Such distribution was then used to remove positions whose deviation between sensor-derived temperature and satellital SST was unlikely (Fig. 1d–f). Percentage of presence, defined as the proportion of positions laying within the Exclusive Economic Zone (EEZ), was also computed. Bhattacharyya coefficient was used for estimating quantitatively the dissimilarities between these distributions.

## Cross-wavelet analysis

Wavelet analysis consists in a local scale decomposition of a signal through the computation of the wavelet coefficient:

$$W_y(a, \tau) = \int_{-\infty}^{+\infty} y(t)\Psi_{a,\tau}(t), \tag{1}$$

where $\Psi_{a,\tau}$ is the mother wavelet in its conjugate form, $\tau$ represents time, and $a$ is the scale of the wavelet (Fig. 3). The wavelet coefficient represents the contribution of a scale $a$ (i.e., the time periods on vertical axis in Figs. 3 and 4) in the observed signal at time $\tau$ (i.e. the absolute time on horizontal axis in Figs. 3 and 4). In other words, the more the signal $y(t)$ at time has a pattern with the same period as $\Psi_{a,\tau}$, the higher is $W_y(a, \tau)$. In practice, the Morlet wavelet is the most widely used mother wave, and is known for performing a good trade-off between temporal and scale resolutions (Torrence and Compo 1998).

The cross-wavelet transform of two time series $x(t)$ and $y(t)$, with respective wavelet transforms $W_x$ and $W_y$ is defined by:

$$W_{x,y}(a, \tau) = \frac{1}{\tau}.W_x(a, \tau).W_y(a, \tau). \tag{2}$$

The evaluation of the statistical significance of power cross-wavelet coefficients is then critical for interpreting them correctly (Cazelles et al. 2014; Rouyer et al. 2008). The
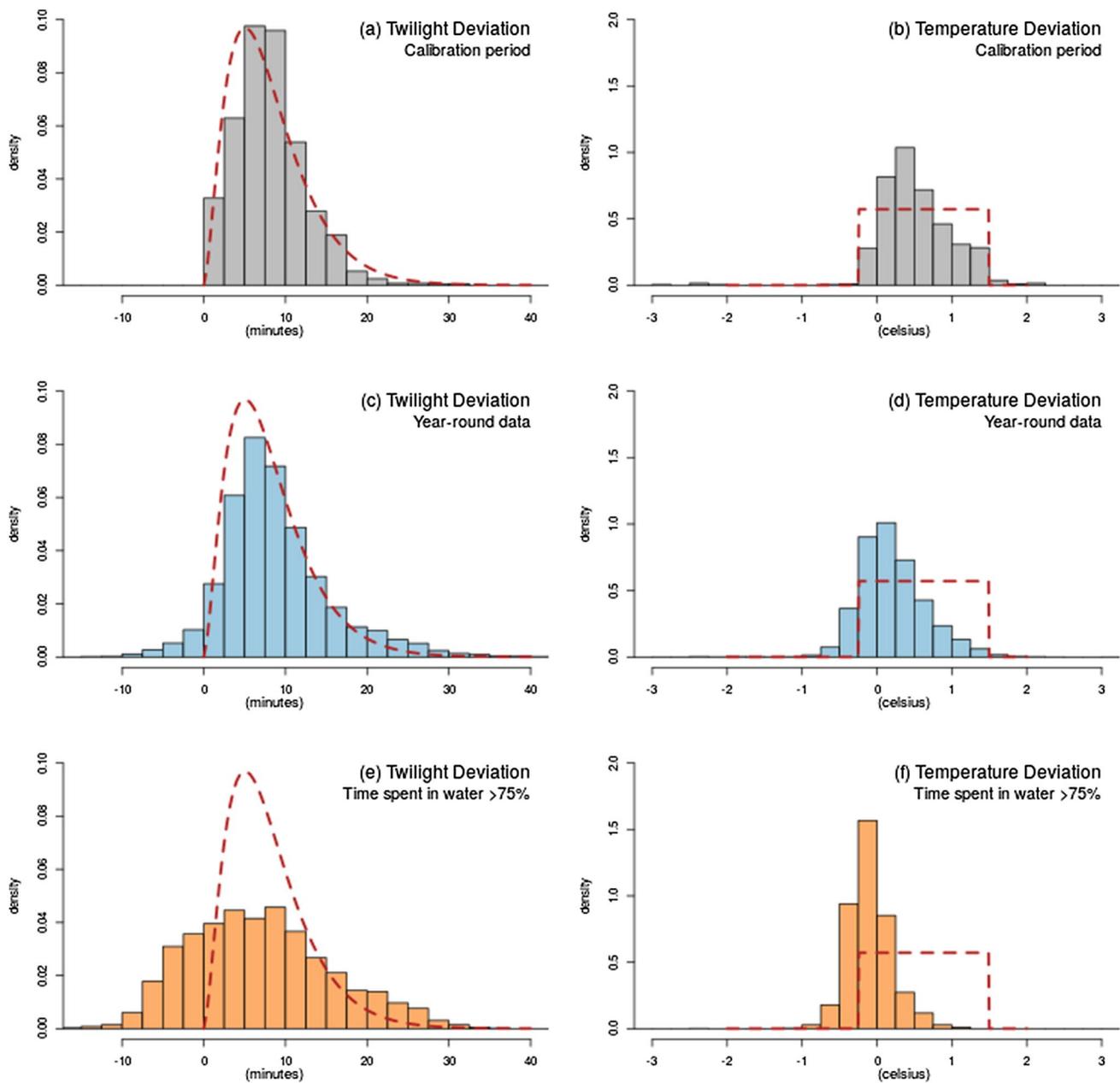
**Fig. 2** Twilight times and temperature deviation at Fernando de Noronha. Grey histograms consider the calibration period only (10 May 2017–15 June 2017). Blue histograms consider all deployment period (05 May 2017–24 April 2018). Orange histograms consider periods where the mean saltwater immersion time is above 75%. Red-dotted curves correspond to the error structure used in Fig. 1

significance test involves a null hypothesis of "no joint periodicity", and performs simulations of random time series to estimate the cross-wavelet coefficients range under the null hypothesis. By fixing a level of significance, it is therefore possible to determine statistically significant correlation between the two observed time-series.

In our study, we evaluate cross-wavelet coefficient with the time-series of mean time in saltwater immersion, and longitude, since longitude is more accurately estimated than latitude (Hill 1994). Thus, as a null hypothesis we simulated time-series by random sampling longitude and mean time in saltwater immersion. More precisely, we sampled for each calendar
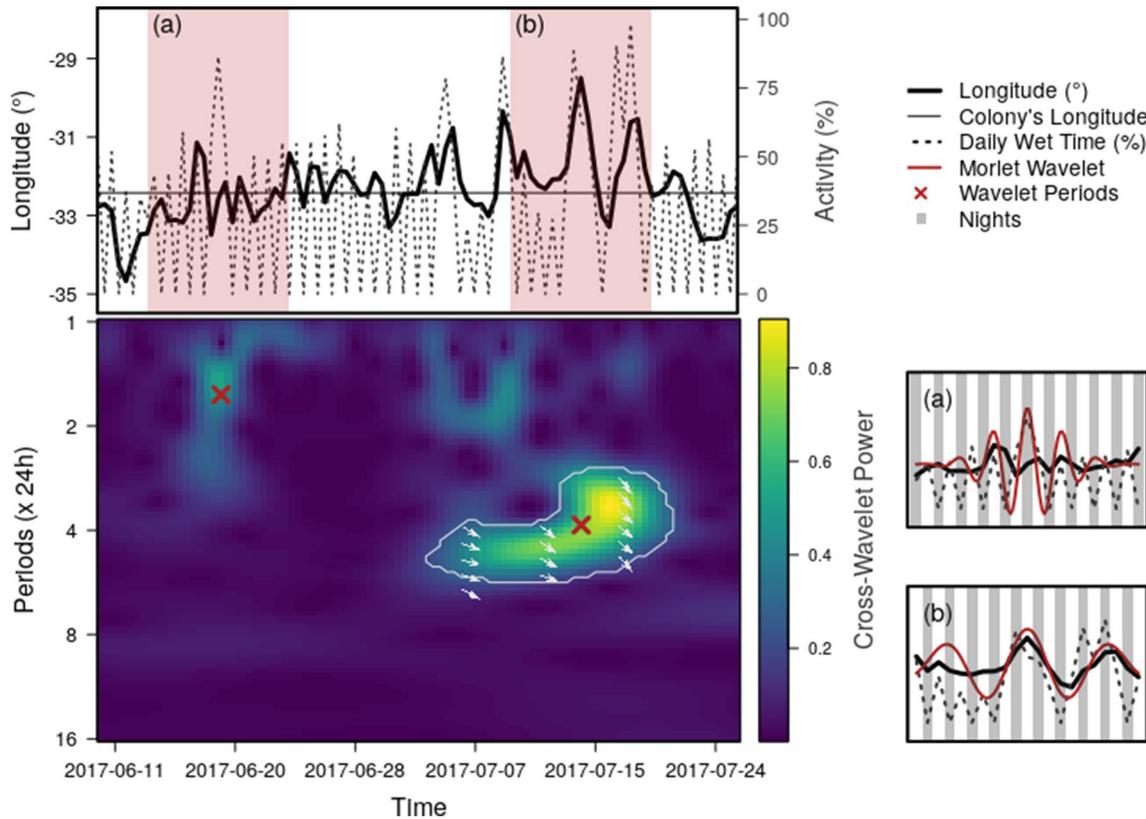
**Fig. 3** Illustration of the cross-walelet theory based on GLS time-series derived from one individual and the associated cross-wavelet power matrix. The upper plot is longitude and saltwater immersion time-series. The bottom plot is the cross-wavelet power coefficient matrix. In such matrix, each power coefficient depends on one specific pair time/scale. The two plots on the right (**a**, **b**), illustrate how to compute such coefficients for the time/scale pairs marked with red crosses. In both cases, black lines consist in raw time-series for distinct time-windows, red lines show the Morlet wavelet with associated period, and grey rectangles show nights. Finally, coefficient matrix with significant synchronicity ($p < 0.01$; lower left panel) are contoured with white lines, and white arrows illustrate the difference of phases between these synchronized time-series. Arrows pointing to the right (respectively left) indicate that the two series are in phase (respectively anti-phase)

day one daylight and one night data point (i.e., longitude and corresponding time in water). Analysis were conducted with the help of the WaveletComp R library (Rosch and Schmidbauer 2018).

## Results

### Light-based geolocation

GLS were recovered ($n = 31$ loggers, i.e., 91% recovery rate) during the following breeding season during the second half of April 2018, and the light-based geolocation approach revealed that no masked booby had shown any migratory or wide-range movement (Fig. 1c, d). Indeed, 84% of the estimated positions laid within EEZ after filtering positions based on satellital sea surface temperature data (Fig. 1d). The estimation of twilight deviations between observed and expected times at FdN over a year-round deployment did not differ much from deviations estimated during the calibration period (Fig. 2a, c). The estimation of global error twilight structure lead to a gamma distribution of scale 2.66 and rate 0.32, which corresponds to detection of dawn and dusk with about 10

**Fig. 4** Averaged cross-wavelet matrixes of longitude and activity time-series based on the analysis of all GLSs over the whole deployment for females (*n* = 14; F) and males (*n* = 17; M). White lines contour the time/period pairs where at least one individual has shown significant joint-periodicity between the two time-series. White arrows illustrate the difference of phases between the two time-series (see Fig. 3 for further explanations). The white area corresponds to the cone of influence (sensu Cazelles et al. 2008). The different stages of the phenology of masked boobies are indicated for Fernando de Noronha (center panel), Brazil, based on in situ observations. Lower panel show the averaged power over the three respective time-windows: **a** early chick-rearing, **b** late chick-rearing to post-breeding and **c** pre-breeding periods. Individual analysis are available on a GitHub repository (AmedeeRoy/WaveLightGLS)
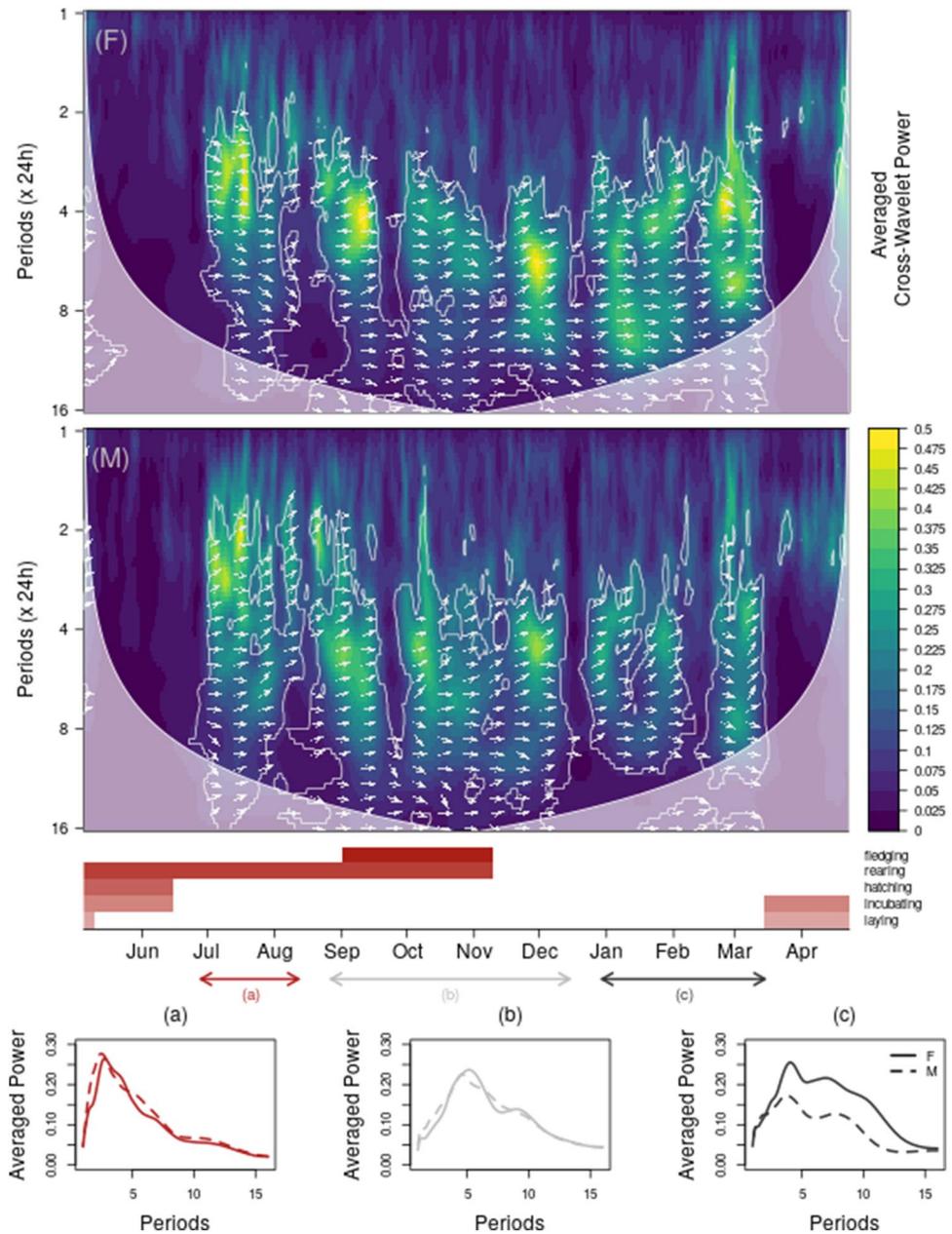


min deviation in average and 20 min in worst cases, while maximal deviations over the whole deployment were about 30 min. SST measured by GLS over the whole deployment mainly deviated between − 1 °C and + 1.5 °C from satellital temperature at FdN (Fig. 2b). Yet, during calibration period, GLS-derived temperature records of SST were in average 0.52 °C higher than temperature at FdN derived from satellital data (Fig. 2b).

The twilight detection error structures fixed during calibration (Fig. 2a) lead to geolocation errors of around 65 ± 54 km in longitude and 347 ± 462 km in latitude (Fig. 1a). When filtering positions whose satellital SST deviated from FdN satellital SST more than 0.5 °C, errors in latitude were

reduced to 198 ± 168 km (Fig. 1b). Positions distributions were very similar to these geolocation errors when comparing respectively without and with filtering coordinates related to temperature data (Bhattacharyya coefficient of 0.95 and 0.92, respectively) (Fig. 1a–d). However, important deviations in twilight times occurred when masked boobies spent more than 75% of the time in water between two consecutive twilights (Fig. 2e), and were associated with a slight deviation eastward in the position distribution (Fig. 1e, f) and with temperature measurement up to 1 °C lower than FdN's SST (Fig. 2f).

## Wavelet analysis

The cross-wavelet analysis revealed local significant joint-periodicities (i.e., synchrony) between longitude and salt-water immersion time-series for every individual ($p <$ 0.01). This synchronicity appeared for different couple of specific periods and times and they are discernable in matrixes of cross-wavelet power coefficients (Fig. 3). The average matrixes of cross-wavelet power coefficient for all individuals show global patterns of joint synchronicity, and a strong relationship with the phenology of masked boobies (Fig. 4). Periods with almost no significant periodicity occurred mostly between March and July which correspond to the first stage of the breeding period (i.e., incubation: laying to hatching). In contrast, from July to March, which corresponds to the last stage of the breeding season until the end of the non-breeding season, significant joint-periodicity can be observed for both females and males. During this period, eastward movement (longitude increasing) corresponded to an increase of time spent on water and, equally, westward movement (longitude decreasing) corresponded to a decrease of proportion of time spent on water. These joint-periodicities occurred mainly for periods of 2–8 days, with a modal period that increases from 2 days in July to 5 days in November. Specific periods could also be observed where all birds seemed to stop showing joint-periodicity such as in the end of September or in mid-December. Differences by sex appeared when breeding is over, i.e., after fledging with higher power coefficient for females (Fig. 4).

These joint-periodicity illustrated that the tagged birds traveled way and back from the colony on consecutive trips of short length with (∼ 2–4 days) to the east of the colony, with length and range depending on the sex and on the time of the year (Figs. 4 and 5). Trips had increasing average duration from the end of the breeding season to the pre-breeding period (Fig. 4) and associated increasing range (Fig. 5). In particular, during the pre-breeding period (January–March), females travelled significantly further to the east (Welch Two Sample $t$-test: $p < 0.001$) and spent more time in water than males (Fig. 5).

## Discussion

### GLS data and resident behaviour

Data from 31 GLS showed that masked boobies from FdN archipelago stayed in the vicinity of their breeding site both during breeding and non-breeding seasons. The cross-wavelet analysis revealed their short round trip of few days eastward to their breeding site.

GLS data have been only rarely used to demonstrate resident behaviour (Schacter and Jones 2018). Existing studies have dealt with staging behaviour and most of them have estimated positions distributions by applying KDE on a scatter of light-derived positions (Bächler et al. 2010; Stenhouse et al. 2012). Travelling periods are usually discriminated from resting periods by fixing empirical thresholds on distance to the colony (Leal et al. 2017) or on change in longitude (Guilford et al. 2009). In this study, we estimated maps of error range, and year-round position distribution of FdN's masked boobies, suggesting that masked boobies are resident at FdN. One could argue that it would be impossible to detect wide range movements in case seabirds would have changed of breeding location or simply skipped the breeding season. Indeed, because birds with archival tags needed to be recaptured, we only recovered tags that have been deployed on birds that bred at the same place for two consecutive years. However, previous observations (Kepler 1969), as well as our own with recovery rate around 90%, suggest that such behaviour would be rather rare, especially since the remaining fraction cannot be disentangled from natural mortality previously estimated at 8.6% (Woodward 1972).

Our study reveals joint-periodicity between longitude and saltwater immersion time-series. These periodicities might hypothetically have resulted from bias in the measure of light-level intensity when masked boobies sit on water and that they have not travelled eastward to FdN. This is however unlikely since shading due to immersion could explain a positive twilight deviation, but not the negative twilight deviation observed in Fig. 2e. Indeed negative twilight errors are theoretically impossible with GLS data in environments with no artificial lights. Finally, GPS tracking of masked boobies in the same colony during the breeding season conducted every April between 2017 and 2019 revealed that masked boobies from FdN foraged almost exclusively at the east of the archipelago, and that they occasionally spent one night at sea, eastward of their breeding locations (8 out of 130 recorded trips, S. Bertrand, unpubl. data). Such nights at sea should be observable in GLS data, and in April a few males showed indeed a joint periodicity of period 48 h, which could correspond to trips lasting about 24 h (Fig. 4). Based on our analysis, we are thus confident that masked boobies travelled way and back to the colony during the non-breeding season and at the beginning of breeding season, and that the eastward deviation consisted in real movements of about 150 km eastward to FdN.

### Masked boobies' year-round residency

The year-round residence of masked boobies might be related to the presence of twice more productive areas at the
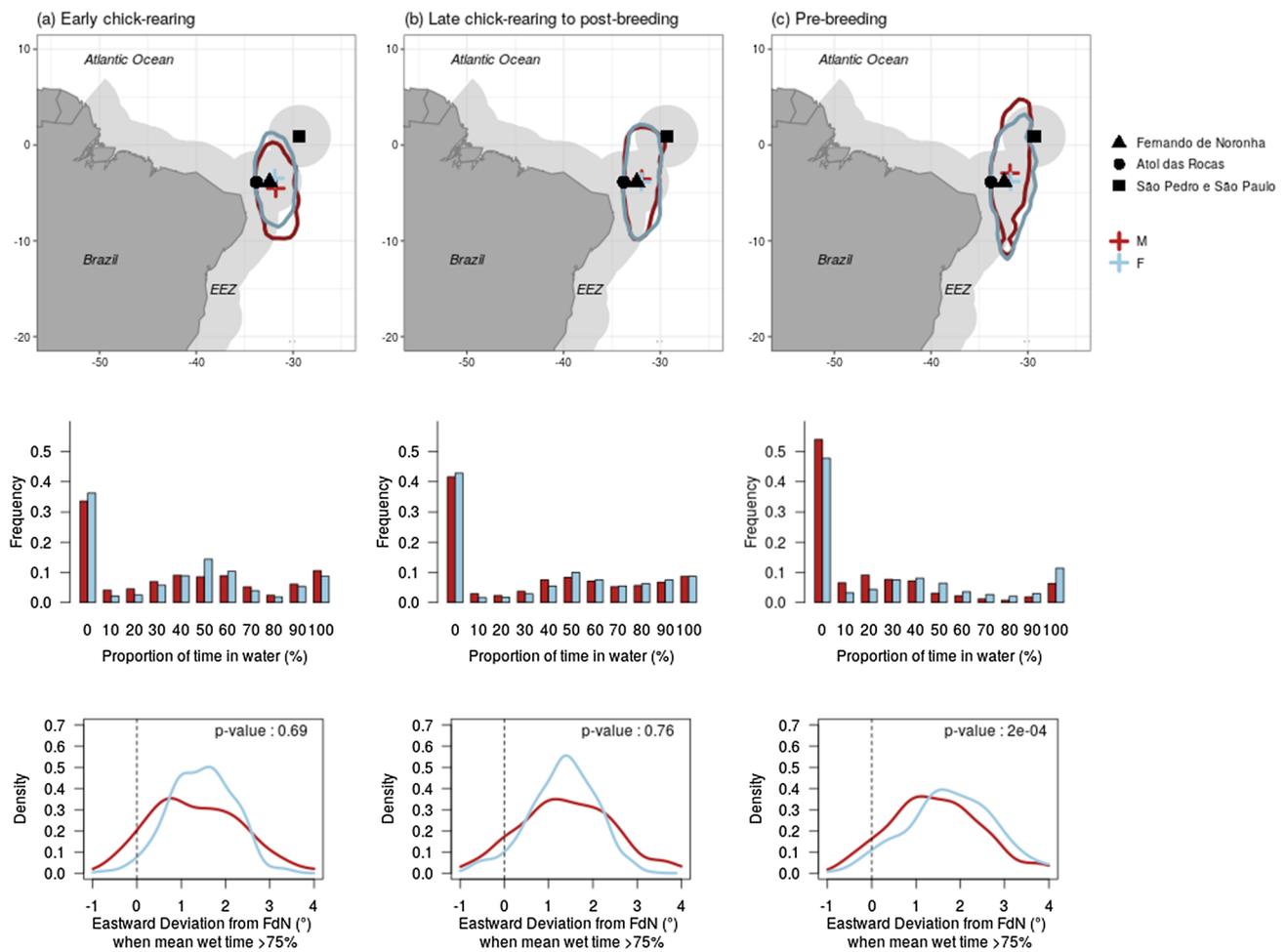
**Fig. 5** Sex-specific positions distributions for specific time-windows, where columns correspond to time-windows described in Fig. 4. **a** Early chick-rearing, **b** late chick-rearing to post-breeding and **c** pre-breeding periods. Maps illustrate the position distribution by sex (F: females-light blue, M: males-red) for the associated periods. Contours represents position distribution of 90%, and crosses the mean positions. Black points refer to main islands around FdN. Histograms (center panels) show at which frequency birds spent proportion of time rather in wet or dry environment during the associated period. Density plots (lower panels) illustrate the eastward deviations of positions with activity higher to 75% for the associated periods. *p*-values specify the significance of difference in mean between the two distributions derived from Welch Two Sample *t*-test

north-east of FdN due to the island effect of São Pedro e São Paulo offshore archipelago (SPSP). This area triggers a local enrichment in the surrounding waters through an upwelling island effect (Campelo et al. 2019), and also supports a resident population of brown boobies *Sula leucogaster* (Nunes et al. 2018). The average structure of this local upwelling is notably described by an average SST decreasing gradually between FdN and SPSP with an average difference of about 0.5 °C (Campelo et al. 2019). This small effect is indeed observed with GLS-derived temperature data as deviation in mean temperature were in average 0.5 °C higher during calibration than when masked boobies spent time in water eastward to FdN (Fig.2b, f). The bias in temperature deviation during calibration is however likely to be due to skin warming according to previous *in situ* observation in the

same area (Clayson and Weitlich 2007). The intermittent way back to the colony is also consistent with the territorial behaviour of masked boobies, known to come back to the colony intermittently during post-breeding period (Nelson 2005).

Most studies on seabirds at FdN relied on colony-based sightings (Antas 1991; Mancini et al. 2016; Sazima and de Almeida 2008) and stable isotope analyses for trophic ecology (Mancini et al. 2013, 2014). Studies underlined the need for going further in the study of the ecology of seabirds at FdN, especially on their movement and the definition of their habitat, so as to improve conservation strategies (Mancini et al. 2016). This work provides a first answer on masked boobies year-round behaviour. In particular, we show that masked boobies stay within the Brazilian EEZ throughout

the year, which brings valuable information for developing relevant conservation strategies such as designing Marine Protected Areas.

## Stage-related and sex-specific activity patterns

If some uncertainties remain on the exact home range of masked boobies due to GLS inaccuracy, our study brings new insights into temporal, year-round, variation of their space use. In particular, we show that the duration of trips outside FdN is strongly related to breeding constraints. Laying, incubating and hatching periods were associated with no joint periodicity, suggesting that the range and duration of foraging trips during these periods are below the error threshold of the signal provided by light and activity. These breeding stages are characterized by substantial thermal and energetic constraints linked to reproduction, since adults need to incubate or to brood and feed their chick. They mostly share time between defending the nest site or their chick and foraging at sea. Therefore, they are not expected to spend time resting at the sea surface for long periods during breeding (e.g., within the timeframe of two locations per day derived from GLS). Even if they forage far from their colony, they have to come back frequently and are likely to be observed at FdN. When chicks are older and can survive without the protection of their parents (i.e., rearing to fledging), the release of the thermal constraints was evidenced by joint-periodicity with gradually increasing periods.

Interestingly, when there was no constraint related to reproduction (i.e., no strict obligation to return to the nest), males and females showed slight differences in cross-wavelet power, particularly the few months prior breeding. During this specific period (January–March), the cross-wavelet analysis revealed higher power coefficients for females, which can be explained by longer trips and longer time spent on water. This confirms the fact that for this species, attendance at site prior to mate is larger for males than for females. Males are territorial and work at conquering and defending a nest place at that period (Nelson 2005). By travelling further eastward and resting on water for longer period, females may reach and stay in more productive area (Campelo et al. 2019), at a period where they need to accumulate energy for the ovogenesis. Sexual differences in space use and activity patterns in the pre-breeding period (which is not observed during the breeding period) provides a new light on reversed sexual dimorphism of masked boobies. One of the functions proposed for RSD is niche segregation, especially to avoid intersexual competition and optimize the use of resources (Serrano-Meneses and Székely 2006). Where many studies have failed to demonstrate differences in foraging behaviours of masked boobies in order to explain masked boobies' RSD, our study provides relevant sex-specific activity patterns during the pre-breeding period i.e. pre-laying (Poli et al. 2017; Sommerfeld et al. 2013; Young et al. 2010).

## Wavelet analysis of geolocation data

When dealing with GLS data deployed on resident or other non-migratory animals, the question might not be "where is the animal?" but rather "did the animal move?". External data might be helpful to examine movement based on a relevant correlation, particularly close to the equator where error in latitude are the highest (Hill 1994). This is the case in our study, where we aimed at determining masked boobies' movements by elucidating the relationships between saltwater immersion and longitude. Our analytical framework could easily be used to investigate the space-uses of other resident seabirds, but also to tell if high deviations in position are due to shading caused by clouds (Lisovski et al. 2018). It could also be extended on analysis of change in latitude, or in distance to the colony coupled with any other relevant external data (e.g., weather data, behavioural data), because it is a convenient and powerful tool for studying the sequentiality of noisy time-series.

Despite the inaccuracy of GLS geolocation, our study shows that these devices are appropriate for revealing year-round whereabouts of a resident tropical seabird over long periods, such as during the non-breeding season. Based on external data with higher precision and reliability than light-based geolocation, we elucidated activity patterns that correlate with periodic change in position. We brought new insights on masked booby year-round movements related to breeding constraints, and we revealed pre-breeding sex-specific movements that had not been observed to date. Finally, we demonstrated that wavelet analysis is a relevant way to extract more out of GLS data further broadly, to provide strong demonstration of animal movement or residency, and to avoid the possible over-interpretation of GLS data.

**Data/Code availability** Data and code are available on our github page: https://github.com/AmedeeRoy/WaveLightGLS.

## Declarations

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical approval** This work was conducted with the approval of the Brazilian Ministry of Environment—Instituto Chico Mendes de Conservação da Biodiversidade (Authorization No 52583-5).

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