



Frigatebird behaviour at the ocean–atmosphere interface: integrating animal behaviour with multi-satellite data

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Marine top predators such as seabirds are useful indicators of the integrated response of the marine ecosystem to environmental variability at different scales. Large-scale physical gradients constrain seabird habitat. Birds however respond behaviourally to physical heterogeneity at much smaller scales. Here, we use, for the first time, three-dimensional GPS tracking of a seabird, the great frigatebird (*Fregata minor*), in the Mozambique Channel. These data, which provide at the same time high-resolution vertical and horizontal positions, allow us to relate the behaviour of frigatebirds to the physical environment at the (sub-)mesoscale (10–100 km, days–weeks). Behavioural patterns are classified based on the birds’ vertical displacement (e.g. fast/slow ascents and descents), and are overlaid on maps of physical properties of the ocean–atmosphere interface, obtained by a nonlinear analysis of multi-satellite data. We find that frigatebirds modify their behaviours concurrently to transport and thermal fronts. Our results suggest that the birds’ co-occurrence with these structures is a consequence of their search not only for food (preferentially searched over thermal fronts) but also for upward vertical wind. This is also supported by their relationship with mesoscale patterns of wind divergence. Our multi-disciplinary method can be applied to forthcoming high-resolution animal tracking data, and aims to provide a mechanistic understanding of animals’ habitat choice and of marine ecosystem responses to environmental change.

Keywords: marine top predators; frigatebirds; (sub-)mesoscale; habitat choice; Lagrangian structures; remote sensing

1. INTRODUCTION

In the open ocean, the physical landscape is characterized by strong contrasts on the scales of tens to hundreds of kilometres in extension and of days to weeks in time. This variability is often referred to as the ‘ocean weather’ and covers the mesoscale and part of the submesoscale regime, which is hereafter referred to as the (sub-)mesoscale. The combination of lateral stirring and vertical motion induces a cascade of

large-scale ocean heterogeneity towards smaller scales [1–4], shaping the distribution of chemical and physical tracers. It results in particular in marked mesoscale and submesoscale frontal regions where biogeochemical fields show strong spatial gradients affecting, in turn, ecosystem distribution and functioning. Fronts are therefore key locations for the coupling between the environment and the different components of biotic communities.

Increasing evidence has been recently produced that the distribution of species at different trophic levels is influenced by (sub-)mesoscale fronts. Most of this evidence is related to phytoplankton. Satellite, *in situ* and

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Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsif.2012.0509> or via <http://rsif.royalsocietypublishing.org>.

model data show that fronts induced by lateral stirring and (sub-)mesoscale vertical motion exert a strong control on the patchiness of primary production [5,6]. Phytoplanktonic communities also appear to be partitioned in fluid-dynamical niches induced by lateral stirring [7,8]. Turbulence can moreover locally enhance the density of suspended particles at transport fronts [9]. Although the observational evidence is more sparse, zooplankton and fish have also been associated with (sub-)mesoscale fronts such as eddy peripheries [10–12].

Although lower trophic levels are largely affected by stirring of the water mass they belong to, large marine predators are capable of displacements on the regional to the basin scale [13], and may therefore ‘filter out’ (sub-)mesoscale spatial heterogeneity and only respond to large-scale gradients. Even if lower trophic levels are localized in particular regions of the sea, the sharpness of these locations could in principle blur out as the trophic level increases, and animal mobility with it. Nevertheless, a large number of marine top predator species have been shown to be associated with (sub-)mesoscale fronts [14,15], including cetaceans [16], squid [17], turtles [18], seabirds [19–22] and sharks [23]. Tracking programmes have revealed that, in spite of displacement velocities capable of overcoming ocean currents, animals’ trajectories often select, in the apparently homogeneous landscape of the open ocean, (sub-)mesoscale transport structures. This is true not only for species that can directly sample the water characteristics, swimming or floating at the sea surface, but also for those, such as frigatebirds, that never touch the water and should then be predominantly affected by atmospheric structures for their movements.

Why and how top predators choose (sub-)mesoscale structures is still unclear, and explanations for this phenomenon have mostly concentrated on a cascading effect of the food chain heterogeneous repartition [16,22,24]. However, other than being regions of enhanced productivity in the ocean, such structures are also dynamically active zones that can constrain predator mobility. In particular, oceanic heterogeneities can give rise to strong atmospheric contrasts and be potentially exploited by flying top predators, either for displacement or for detection of foraging sites. Here, we address this issue for frigatebirds of the Mozambique Channel by coupling analysis of the physical environment with that of animal behaviour. Behavioural patterns are derived from the three-dimensional bird trajectory and analysed in relation to their dynamic, physical environment shaped by horizontal transport—in particular to (sub-)mesoscale frontal structures derived by remote-sensing data analysis. Our results indicate that birds respond to the presence/absence of physical fronts with behavioural patterns associated not only with foraging (fast descents) but also with horizontal and vertical displacement (commuting between transport and sea surface temperature (SST) fronts, and soaring over temperature gradients). We suggest that the combination of high-resolution (GPS) tracking and remote-sensing data analysis is a promising approach in observing the behavioural response of top predators to the physical features of their open ocean habitat.

Frigatebirds are marine top predators living in a tropical environment characterized by an oligotrophic marine ecosystem and by dominant, low-intensity winds. Feeding events occur to a large extent in association with subsurface predators [25]. Frigatebirds display a peculiar flying and foraging behaviour: they are the only oceanic predator that never touches the sea surface, maintaining flight for days, even sleeping and catching prey aloft [21,26]. Previous studies have addressed the movements of frigatebirds foraging from the Europa Island [21,22,27], tracking either the azimuthal position of birds or their altitude. In this study, birds were tracked by GPS telemetry providing simultaneously, for the first time, latitude, longitude and altitude localization. The analysis of their three-dimensional movement enables us to access the behavioural patterns in their environmental context, defined by high-resolution physical parameters that are retrieved through Lagrangian re-analyses of multi-satellite data.

2. RESULTS

In September–October 2008, 16 individual great frigatebirds (*Fregata minor*) were equipped with 25–30 g GPS recorders (Technosmart, Rome, Italy) on Europa Island, Mozambique Channel (22 S/40 E). Birds were equipped during the early chick rearing period, for one to three successive foraging trips (details of the colony and the attachment procedure are given in Weimerskirch *et al.* [21]). A total of 21 complete trajectories were obtained, nine of which were long-distance flights that lasted between 16 and 59 h, spanning a region several hundreds of kilometres wide around the island, so that birds had the occasion to repeatedly sample the (sub-)mesoscale structures of that region. Figure 1 displays a typical trajectory for a frigatebird, represented for clarity in two projections: altitude versus time (figure 1a) and an azimuthal view (figure 1b). A three-dimensional plot of the same trajectory is displayed in the electronic supplementary material, figure S1.

Thanks to the three-dimensional identification of frigatebird positions, we could assign a behaviour to each datum point. The rules for assigning behavioural patterns have been defined by comparing our GPS data with previous behavioural analyses (mainly based on vertical movements) from direct observations [28] and altimeter data [21,26,27], which we summarize as follows. Although the average flight altitude of frigatebirds is at about 200 m, frigatebirds do not usually maintain a constant height but instead fly, both day and night, in a succession of climbs and descents each spanning several tens and hundreds of metres. Climbing (up to more than 500 m and, episodically, more than 2000 m) is mainly achieved by exploiting ascending winds (when soaring frigatebirds never flap their wings for an extended period of time). These soaring bouts may take from tens of minutes to hours. Altitude is lost in two different ways: fast descents (several hundred metres in a few minutes), which are associated with the identification of possible feeding opportunities; and slow descents (gliding), which are typically associated with commuting. Frigatebirds may also remain at low altitude (below 15 m) when tracking

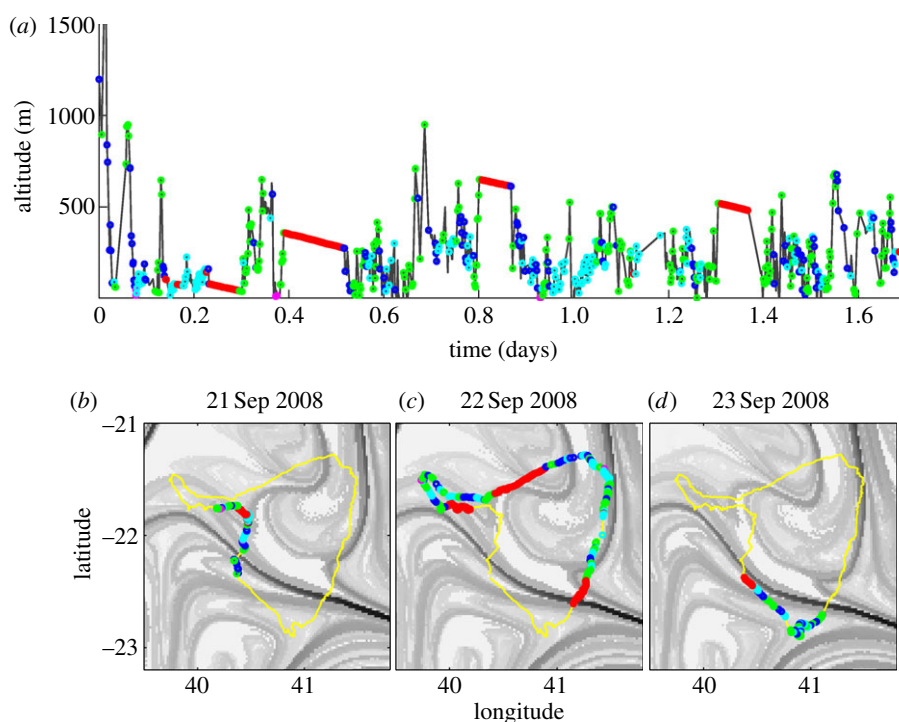


Figure 1. A representative trajectory for a frigatebird (bird tag no. 542309082) during a 40 h trip (21–23 September 2008) from Europa Island, with identified behaviours in colour (low-altitude flight, magenta; fast descent, blue; slow descent, red; slow ascent, green; fast ascent, cyan) over the bird's trajectory: (a) altitude as a function of time elapsed from the beginning of the flight along the bird's trajectory; (b–d) azimuthal projection (yellow line) superimposed on the finite-size Lyapunov exponent map, used to identify transport fronts, for the 3 days spanned by the bird's flight (grey scale from 0 to 0.3 day^{-1}). The trajectory for this individual bird in three dimensions is presented in the electronic supplementary material, figure S1, and its azimuthal projection, superimposed on the finite-size Lyapunov exponent fronts and SSTs at daily resolution, is displayed in the electronic supplementary material, figure S2.

objects of interest such as prey, although this behaviour is more occasional than up-and-down flight. Guided by this information and as detailed in the electronic supplementary material, we have defined an algorithm that automatically identifies the following behaviours: fast ascent (FA, soaring), slow ascent (SA), slow descent (SD), fast descent (FD) and low-altitude flight (LF). Bouts that could not be related to a clear biological meaning—for instance, transition phases between clear-cut behaviours—have been labelled as 'other'. The association of these behaviours with the azimuthal position of the bird (figure 1) allows us to map behavioural patterns over the physical landscape shaped by surface currents and to interpret the behaviours in terms of the bird's foraging strategy. The same behaviour is typically maintained over regions that span spatial ranges of the order of tens of kilometres, hence pointing to the (sub-)mesoscale as the key regime of interaction between physical structures and animal behaviour.

The (sub-)mesoscale physical environment that birds scan along their flights changes on a time scale slower than behavioural switches (days/weeks versus minutes/hours). We can hence characterize it by means of physical diagnostics at a daily resolution that we reconstruct by multi-satellite data reanalysis as explained in §4. We identify different, although not necessarily disjoint, (sub-)mesoscale structures: transport fronts, thermal fronts and regions of ascending wind (see §4 for details).

Note that transport fronts and SST fronts are closely related, as they both depend on stirring [29]. In

particular, transport fronts are characterized by convergent dynamics transverse to them and divergent dynamics along them, which tend to align the front of any advected tracer (and hence SSTs) with the transport front. This is particularly evident in our case, as we reconstruct SST fronts by stirring low-resolution, microwave SST maps with oceanic currents derived from altimetry. In this regard, the SST fronts we are able to detect in this study correspond to a subset of transport fronts.

Our aim is to examine whether birds modify their behaviour in relation to the heterogeneity of the environment, and in particular if their behavioural patterns change when flying over specific (sub-)mesoscale regions of the open ocean. Previous work indeed showed that they are more often found over Lagrangian structures induced by horizontal transport [22]. We make a binary classification of every bird's position, depending on whether a position falls inside or outside one of the four regions identified by physical parameters: transport fronts, thermal fronts, regions of ascending vertical wind (as identified either by wind divergence or by crosswind SST gradient). As an example of our integration of multi-satellite data and bird behaviour, see the electronic supplementary material, figure S2a, which displays transport fronts identified by the criterion that the finite-size Lyapunov exponent exceeds 0.1 day^{-1} .

For each repartition of the space in regions 'on' and 'outside' (sub-)mesoscale structures, we compute the

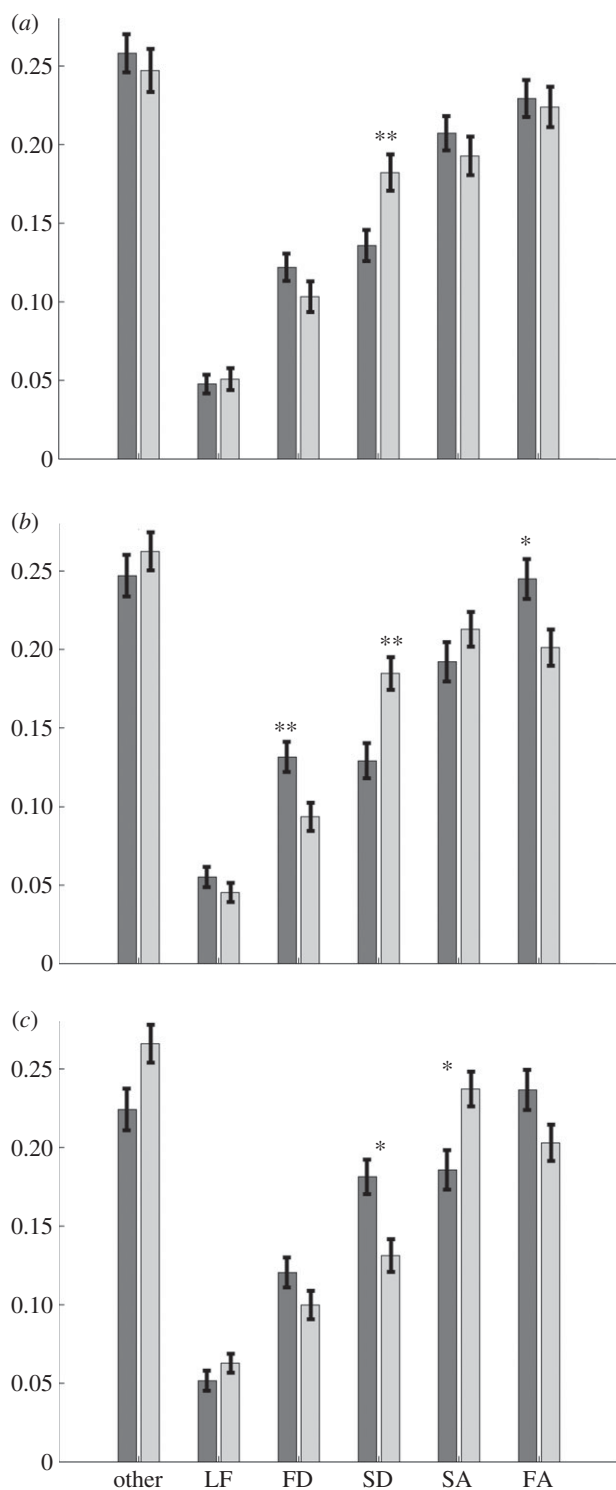


Figure 2. Behavioural patterns observed on (filled bars) and outside (unfilled bars) the (sub-)mesoscale regions identified on the basis of the environmental diagnostics (in parenthesis, the fraction of flight time spent over that region): (a) transport fronts (56%); (b) thermal fronts (46%); (c) regions of ascending vertical wind identified by negative wind divergence (54%). Filled bars, positive; unfilled bars, negative. Fractions are normalized for each value of the binary classification, e.g. all behaviour fractions inside a transport frontal region sum up to 1. Error bars are computed as explained in the text and electronic supplementary material, and measure one standard deviation of the distribution obtained by bootstrapping, centred in the frequency of occurrence of a given behaviour with respect to the total flight time.

frequencies for each of the six previously described behaviours (figure 2), that is, the fraction of time that birds spend doing that behaviour, given one of such environmental conditions (e.g. the time spent slowly descending outside thermal fronts, relative to the total flight time). Birds show different average behaviour repartition along their trajectory, depending on the physical condition, but this could just be due to sampling uncertainties. In order to test whether the observed differences in the frequencies are significant or they are due to the finiteness in the number of independent observations, we carried out an unpaired two-sample *t*-test based on bootstrapping, by which we reshuffled the independent behavioural observations randomly along the trajectories (see the electronic supplementary material). The null hypothesis is that the observed difference in frequencies has a zero mean and fluctuations due to the finiteness in the number of observations. The error bars in figure 2 indicate one standard deviation of the bootstrapping distribution. Cases where the null hypothesis can be rejected with 90% and 95% confidence are highlighted with one and two asterisks, respectively.

There is no clear-cut association between frigatebird behaviour and physical structures when looking at single trajectories. However, when we compare the fraction of time spent in each behaviour inside and outside the (sub-)mesoscale regions (see §4 and figure 2), significant associations stand out between physical diagnostics and behaviour types. These associations suggest functions for certain behaviours, based on hypotheses on how birds sense and respond to such physical heterogeneity. Moreover, these associations can help us to single out the key physical structures that constrain predator behaviour among the many complex processes occurring at the ocean–atmosphere interface.

We first consider the two diagnostics related to ocean properties that identify transport and thermal fronts. The only behaviour that is significantly different on and outside transport fronts is SD, which occurs more often outside those Lagrangian structures (figure 2a). This is consistent with the interpretation of such descents, where birds glide with minimal energy expenditure, as commuting between regions of higher interest (the fronts).

The behavioural patterns over thermal fronts reveal a more clear-cut scenario with respect to transport fronts (figure 2b). First of all, there is a much larger difference between the fraction of the trajectory spent on fronts (46%) and the fraction of surface, in a square of 7.5° longitude \times 6° latitude around Europa Island, occupied by these fronts ($24 \pm 2\%$). These fractions were instead 56 per cent versus 52 (± 2) per cent in the case of transport fronts, indicating that the thermal gradient is an environmental diagnostic more strictly related to the bird behaviour than to transport fronts. With respect to the case of transport fronts, the difference in SDs is more pronounced: birds glide prominently outside thermal fronts. Moreover, two other behaviours appear to be significantly more common over thermal fronts: FDs ($p < 0.05$) and FAs ($p < 0.1$). LF and SAs, instead, do not show any such significant difference.

LFs may be primarily associated with foraging, because being near the surface is undoubtedly a prerequisite for feeding. However, the foraging strategy of frigatebirds is to scan vast areas of the ocean from a high altitude and to descend rapidly to the sea surface when feeding opportunities are detected [26]. Rather than low flight, rapid altitude loss can hence be a more appropriate indicator that potential feeding opportunities were spotted, even if birds eventually stop descending because their target disappears. The more frequent occurrence of FDs, associated with active search for prey, over thermal fronts reflects the bottom-up effect on the ecosystem of the enrichment of the lower trophic levels in or at the thermal fronts [16,22,24].

FAs also occur most often at thermal fronts. Because our classification is based on average vertical velocities, such events correspond in general to long-term soaring whereby birds can attain altitudes above 2000 m. This behaviour can be just the other side of the coin with respect to the previous case: while FDs would be associated with prey identification, climbing is motivated by the need for prospection of the sea surface. However, feeding and displacing are intrinsically related to different aspects of the physical environment. Although we expect prey location to be independent of the atmospheric circulation, ascents must be linked to the air–sea dynamics. The particular morphology of frigatebirds—low body mass and large wing surface—makes them specialized at using vertical upward air movements, such as thermals over land or vertical wind movements over the sea.

In order to clarify the role of wind at the ocean surface in determining the behaviour of the birds, we explore how the behavioural patterns relate to two vertical wind diagnostics derived by remote-sensing data. In the absence of a direct measure of vertical wind speed and direction, we use such diagnostics to infer wind orientation at the birds' location. The two ways this information can be retrieved based on different remote-sensing data reflect different mechanisms able to generate winds with a vertical component (i.e. ascending or descending wind): the convergence or divergence of air masses, and the presence of thermal gradients at the sea surface (§4).

Frigatebirds appear to respond to vertical wind conditions as identified by horizontal wind divergence, the two behaviours strongly associated with a definite wind direction being SDs and SAs (figure 2*c*). SDs, which we interpret as commuting, are most often associated with descending wind (positive wind divergence), suggesting that a long-distance displacement could be halted when birds detect ascending wind. This is also supported by the fact that SAs, where birds weave in positive and negative vertical displacements, occur most often in ascending wind conditions, where birds can exploit even faint upwards currents to minimize their energetic expenditure.

In a more elaborated analysis of satellite products, the study of physical fronts can be refined by computing the crosswind SST gradient (see §4 and electronic supplementary material, figure S3). This second diagnostic, based on a mechanistic relation between

thermal fronts and vertical winds, however, does not provide further insights about the use of wind by frigatebirds.

3. DISCUSSION

It has been suggested that the enhanced flight efficiency of frigatebirds, which have the lowest wing-loading of all birds, has evolved to allow them wide-ranging searching directed towards locating scarce and patchy food resources at low foraging costs [21,26,28]. Consistent with the presence of a scattered prey, previous studies found that, at the population level, frigatebirds do not seem to have a preferred, fixed geographical region for foraging, but disperse over long distances (approx. 100 km) when looking for feeding opportunities [21,26]. More recently, it has been shown that frigatebird locations correspond well to mesoscale eddy fields and, in particular, to transport fronts generated by mesoscale turbulence [22]. By using multi-satellite-based, nonlinear diagnostics here, we have reconstructed the ocean–atmosphere physical environment associated with these fronts and compared it with behavioural patterns derived from three-dimensional, high-resolution tracking. By analysing the differences in frigatebird behaviour associated with such environmental parameters, we have revealed some key reasons and mechanisms for frigatebirds in selecting (sub-)mesoscale frontal regions within their foraging range.

A first result of this analysis is that frigatebirds glide between transport fronts. Nevertheless, and quite surprisingly, they do not seem to forage or soar significantly more often on transport fronts than outside them. Transport fronts induced by the mesoscale eddy field however structure other physical fields, and, in particular, SSTs (SST fronts typically appear next to transport fronts). Therefore, we identified SST fronts and found that frigatebirds prefer these structures both in terms of feeding opportunities and for soarings. We then mapped vertical winds at the scale of bird behaviour. We found that gliding is significantly associated with regions of positive wind divergence (with prevalent descending winds) and that SAs are associated with regions of negative wind divergence, which the birds may exploit for uplifting. Nevertheless, our attempt to associate vertical winds directly with SST fronts by computing the crosswind SST gradient did not provide any significant relation.

On the basis of these results, several aspects of frigatebird ecology and in particular their interaction with the physical environment can be further discussed. The presence of behaviours associated not only with feeding, but also with climbing opportunities makes SST fronts key features for maintaining a positive energy budget, and hence may have driven the evolution of the extreme morphology, physiology and behaviour of frigatebirds. Generally, top predators are supposed to favour SST frontal regions solely because they are richer in prey. However, the specialized foraging strategy of frigatebirds, which requires the concomitant presence of small fish or squid and of subsurface predators, does not allow us to support a purely bottom-up structuring of the food

web spatial distribution. One could indeed think that the presence of other predators, specifically subsurface predators, rather than directly of their prey, drives frigatebird positioning, questioning the preference of other marine species for thermal fronts. Moreover, the stronger connection to eddy edges, where (sub-)meso-scale activity is especially high, of frigatebirds when compared with that in tuna [30] is coherent with our hypothesis on the use of fronts for purposes other than foraging.

Frigatebirds may exploit vertical winds not only for sustaining their flight, but also for locating fronts even when these structures are not visible. More generally, a predator's ability to optimally exploit patchily distributed resources relies on its behavioural choices in response to environmental cues [31–33]. Following favourable winds may constitute a good searching strategy for locating prey-enriched filaments (fluid dynamical niches [8]) in two-dimensional space. Even though more refined diagnostics for the identification of vertical winds at the (sub-)mesoscale (and in particular thermals related to daytime) are needed, our analysis suggests that winds play a prominent role in habitat-sensing and choice by frigatebirds. This mechanistic relationship between wind and behaviour indeed can lay the basis for climate change-induced modification of frigatebird ecology, analogous to that recently evidenced in albatross populations [34].

Marine top predators play a fundamental role in maintaining and assessing the health of open ocean ecosystems [35]. Large-scale, climatological measures of biogeochemical and physical parameters indicate which environmental features constrain the home range of top predators. However, a mechanistic understanding of predator habitat selection requires an analysis of their behaviour at the spatio-temporal scales of the environmental heterogeneity they detect. The multi-disciplinary methodological approach we propose here—namely high-resolution, three-dimensional animal tracking coupled with Lagrangian reconstruction of synoptic environmental maps from multi-satellite data—could be applied to other marine predators in order to shed light on the constraints and adaptations that couple the geophysical dynamics to animal behaviour. Current efforts for better understanding the ocean–atmosphere dynamics at the (sub-)mesoscale [36] and increased resolution in climate-resolving circulation models may help us to address this challenge and provide more quantitative diagnostics able to better assess the quality of a species range in the wake of climate change.

4. METHODS

4.1. *Frigatebird tracking data analysis*

The position (latitude, longitude and altitude) of 16 frigatebirds was recorded approximately every 2 min, and nine long trajectories, for a total 316 h of flight time, have been selected for analysis. Measures with unrealistic values of the vertical position, likely to be due to incorrect functioning of the beacons or of the geolocalization, have been filtered from the dataset, as detailed in the electronic supplementary material. Most of the

mismatching events occurred jointly, so that we removed whole sections of trajectories in order to minimize artefacts in the behavioural analysis.

We distinguish five principal behavioural classes, motivated by the classifications proposed in the literature [23,26–28], on the basis of the patterns of vertical displacement (see the electronic supplementary material for details): LF—low-altitude flight (magenta), below 20 m of altitude; FD—fast descent (blue), sustained negative vertical velocity less than -0.3 m s^{-1} ; SD—slow descent (red), negative average vertical velocity greater than -0.05 m s^{-1} ; SA—slow ascent (green), average vertical velocity between 0.01 and 0.22 m s^{-1} ; FA—fast ascent (cyan), average vertical velocity greater than 0.22 m s^{-1} . The sixth class ‘other’ includes all cases when none of these behaviours is identified. The behaviours are overlaid onto one bird's track in figure 1*a*, illustrating the outcome of the automatic classification algorithm.

These classes were identified from moving averages in windows of 9 min for descents and of 21 min for ascents, centred at the point of interest, in order for the classification to reflect the expert's assignment to one of the known behaviours. Except for the case SA, which includes fluttering flight with alternating ascents and descents, regions with high-frequency shifts have thus been excluded from the classification. This choice reflects the reasoning that behavioural patterns occurring on a time scale too short compared with the time birds usually spend on identifiable (sub-)mesoscale structures are not to be included in the present analysis. Although other criteria could be applied, the classification proposed here catches most bouts of frigatebird behaviour that are identifiable by visual inspection, and thus correspond to direct observation-based classifications [26]. Data and algorithms can be obtained on request, respectively, to H. Weimerskirch (henriw@cebc.cnrs.fr) and S. De Monte (demonte@biologie.ens.fr).

4.2. *Remote-sensing measures of the physical landscape*

We combined satellite-derived measures of altimetry (AVISO), SST (AMSR-E) and wind (QuikScat) in order to obtain diagnostics of the physical landscape at the (sub-)mesoscale.

Because frigatebirds are found in association with Lagrangian coherent structures of the surface velocity field [22]—i.e. transport fronts induced by lateral stirring—we first identify fronts by a Lagrangian reanalysis of altimetry-derived surface currents [37]. The Lyapunov exponent was used to identify from surface velocity field regions of confluence among water masses of different origin (see [7] for details). Following previous analyses [7,22], we define ‘transport fronts’ as the region where the finite-size Lyapunov exponent exceeds a threshold of 0.1 per day, as illustrated in the electronic supplementary material, figure S2*a*.

As a second diagnostic, and following the study of Desprès *et al.* [29], we obtain a high-resolution SST field by advecting for 3 days with altimetry-derived surface currents a low-resolution SST map (in our case, AMSR-E 3 day composite at 0.25°). Consequently, we define ‘thermal fronts’ as the regions

where the SST gradient exceeds 2°C/100 km. In many cases, thermal frontal regions are also transport frontal regions where water masses of different origin—and of different surface temperature—are juxtaposed by advection.

In order to quantify the impact of the atmospheric dynamics on frigatebird behaviour, we diagnosed vertical wind direction and intensity. A first measure of vertical wind that is considered is the divergence of the QuikScat wind field (available at a nominal 0.25° resolution), where a positive divergence corresponds to descending wind and a negative divergence to ascending wind. There are no direct observations of vertical wind. However, a theoretical framework has been proposed that combines SST anomalies with horizontal wind in a single index, the crosswind SST gradient [38,39]. This diagnostic is based on the mechanistic reasoning that vertical winds should compensate for temperature-driven changes in surface wind speed. The crosswind SST gradient is correlated to QuikScat divergence, however, only on a large scale and in a climatological sense (see the discussion of error bars in fig. 4 of Chelton *et al.* [39]). We thus use this as a second wind diagnostic, in order to associate a vertical wind velocity to the (sub-)mesoscale thermal fronts we detect. Also in this case, ascending wind regions are the locations where crosswind SST gradients are negative. The code for the Lagrangian analysis can be requested from F. d'Ovidio (francesco.dovidio@ocean-ipsl.upmc.fr). Figures S1 and S2 in the electronic supplementary material display the aforementioned four environmental diagnostics in the space and time interval covered during one bird's trajectory.

We thank the Forces Armées de la Zone Sud de l'Océan Indien (FAZSOI) for transport to, and logistical support on, Europa Island, and the TAAF Administration for allowing us to work on Europa Island. We thank the fieldworker involved in the study on Europa, and, in particular, Hélène Maeho for her continuous and efficient involvement. This study is part of the program FREGATE, funded by AAP 'Iles Eparses' of the CNRS INEE Department. C.C. was funded by a CNES postdoctoral fellowship. The results relative to the SST advection are a contribution to the programme ANR 09-Blan-0365-03 REDHOTS. Altimetry data were produced by CLS with support from CNES. AMSR-E data were produced by Remote Sensing Systems and sponsored by the NASA Earth Science MEaSUREs DISCOVER Project and the AMSR-E Science Team. QuikScat data were produced by Remote Sensing Systems and sponsored by the NASA Ocean Vector Winds Science Team. The authors thank Mary-Anne Lea for useful discussions. We thank two anonymous reviewers for their comments and criticisms, which have greatly helped us in improving the manuscript.

REFERENCES

- Lévy, M., Klein, P. & Tréguier, A.-M. 2001 Impacts of sub-mesoscale physics on phytoplankton production and subduction. *J. Mar. Res.* **59**, 535–565. (doi:10.1357/002224001762842181)
- Mahadevan, A. & Campbell, J. W. 2002 Biogeochemical patchiness at the sea surface. *Geophys. Res. Lett.* **29**, 192632. (doi:10.1029/2001GL014116)
- Benitez-Nelson, C. R. & McGillicuddy, D. J. 2008 Mesoscale physical–biological–biogeochemical linkages in the open ocean: an introduction to the results of the E-Flux and EDDIES programs. *Deep-Sea Res. II* **55**, 1133–1138. (doi:10.1016/j.dsr2.2008.03.001)
- Klein, P. & Lapeyre, G. 2009 The oceanic vertical pump induced by mesoscale eddies. *Annu. Rev. Mar. Sci.* **1**, 351–375. (doi:10.1146/annurev.marine.010908.163704)
- Strass, V. H., Naveira Garabato, A. C., Pollard, R. T., Fischer, H. I., Hense, I., Allen, J. T., Read, J. F., Leach, H. & Smetacek, V. 2002 Mesoscale frontal dynamics: shaping the environment of primary production in the Antarctic Circumpolar Current. *Deep-Sea Res. II* **49**, 3735–3769. (doi:10.1016/S0967-0645(02)00109-1)
- Lévy, M., Iovino, D., Resplandy, L., Klein, P., Madec, G., Tréguier, A.-M., Masson, S. & Takahashi, K. 2012 Large-scale impacts of submesoscale dynamics on phytoplankton: local and remote effects. *Ocean Model.* **43–44**, 77–79. (doi:10.1016/j.ocemod.2011.12.003)
- Lehahn, Y., d'Ovidio, F., Lévy, M. & Heifetz, E. 2007 Stirring of the northeast Atlantic spring bloom: a Lagrangian analysis based on multisatellite data. *J. Geophys. Res.* **112**, C08005. (doi:10.1029/2006JC003927)
- d'Ovidio, F., De Monte, S., Alvain, S., Dandonneau, Y. & Levy, M. 2010 Fluid dynamical niches of phytoplankton types. *Proc. Natl Acad. Sci. USA* **107**, 18 366–18 370. (doi:10.1073/pnas.1004620107)
- Perlekar, P., Benzi, R., Nelson, D. R. & Toschi, F. 2010 Population dynamics at high Reynolds number. *Phys. Rev. Lett.* **105**, 144501. (doi:10.1103/PhysRevLett.105.144501)
- Labat, J. P., Gasparini, S., Mousseau, L., Prieur, L., Boutoute, M. & Mayzaud, P. 2009 Mesoscale distribution of zooplankton biomass in the northeast Atlantic Ocean determined with an optical plankton counter: relationships with environmental structures. *Deep-Sea Res. I* **56**, 1742–1756. (doi:10.1016/j.dsr.2009.05.013)
- Sabarrós, P. S., Ménard, F., Lévêze, J. J., Tew-Kai, E. & Ternon, J. F. 2009 Mesoscale eddies influence distribution and aggregation patterns of micronekton in the Mozambique Channel. *Mar. Ecol. Prog. Ser.* **395**, 101–107. (doi:10.3354/meps08087)
- Santora, J. A., Sydeman, W. J., Schroeder, I. D., Wells, B. K. & Field, J. C. 2011 Mesoscale structure and oceanographic determinants of krill hotspots in the California current: implications for trophic transfer and conservation. *Progr. Oceanogr.* **91**, 397–409. (doi:10.1016/j.pocean.2011.04.002)
- Block, B. A. *et al.* 2011 Tracking apex marine predator movements in a dynamic ocean. *Nature* **475**, 86–90. (doi:10.1038/nature10082)
- Bost, C. A., Cotté, C., Bailleul, F., Cherel, Y., Charrassin, J. B., Guinet, C., Ainley, D. G. & Weimerskirch, H. 2009 The importance of oceanographic fronts to marine birds and mammals of the southern oceans. *J. Mar. Syst.* **78**, 363–376. (doi:10.1016/j.jmarsys.2008.11.022)
- Ainley, D. G., Dugger, K. D., Ford, R. G., Pierce, S. D., Reese, D. C., Brodeur, R. D., Tynan, C. T. & Barth, J. A. 2009 Association of predators and prey at frontal features in the California Current: competition, facilitation, and co-occurrence. *Mar. Ecol. Prog. Ser.* **389**, 271–294. (doi:10.3354/meps08153)
- Cotté, C., d'Ovidio, F., Chaigneau, A., Lévy, M., Taupier-Letage, I., Mate, B. & Guinet, C. 2011 Scale-dependent interactions of Mediterranean whales with marine dynamics. *Limnol. Oceanogr.* **56**, 219–232. (doi:10.4319/lo.2011.56.1.0219)
- Waluda, C. M., Rodhouse, P. G., Trathan, P. N. & Pierce, G. J. 2001 Remotely sensed mesoscale oceanography and

- the distribution of *Illex argentinus* in the South Atlantic. *Fish Oceanogr.* **10**, 207–216. (doi:10.1046/j.1365-2419.2001.00165.x)
- 18 Polovina, J., Uchida, I., Balazs, G., Howell, E. A., Parker, D. & Dutton, P. 2006 The kuroshio extension bifurcation region: a pelagic hotspot for juvenile loggerhead sea turtles. *Deep-Sea Res. II* **53**, 326–339. (doi:10.1016/j.dsr2.2006.01.006)
- 19 Nel, D. C., Lutjeharms, J. R. E., Pakhomov, E. A., Anson, I. J., Ryan, P. G. & Klages, N. T. W. 2001 Exploitation of mesoscale oceanographic features by grey-headed albatross *Thalassarche chrysostoma* in the southern Indian Ocean. *Mar. Ecol. Prog. Ser.* **217**, 15–26. (doi:10.3354/meps217015)
- 20 Cotté, C., Park, Y. H., Guinet, C. & Bost, C.-A. 2007 Movements of foraging king penguins through marine mesoscale eddies. *Proc. R. Soc. B* **274**, 2385–2391. (doi:10.1098/rspb.2007.0775)
- 21 Weimerskirch, H., Le Corre, M., Jaquemet, S., Potier, M. & Marsac, F. 2004 Foraging strategy of a top predator in tropical waters: great frigatebirds in the Mozambique Channel. *Mar. Ecol. Prog. Ser.* **275**, 297–308. (doi:10.3354/meps275297)
- 22 Tew Kai, E., Rossi, V., Sudre, J., Weimerskirch, H., Lopez, C., Hernandez-Garcia, E., Marsac, F. & Garçon, V. 2009 Top marine predators track Lagrangian coherent structures. *Proc. Natl Acad. Sci. USA* **106**, 8245–8250. (doi:10.1073/pnas.0811034106)
- 23 Sims, D. W. & Quayle, V. A. 1998 Selective foraging behaviour of basking sharks on zooplankton in a small-scale front. *Nature* **393**, 460–464. (doi:10.1038/30959)
- 24 Hunt Jr, G. L., Mehlum, F., Russell, R. W., Irons, D., Decker, M. B. & Becker, P. H. 1999 Physical processes, prey abundance, and the foraging ecology of seabirds. In *Proc. 22nd Int. Ornithol. Congr., Durban, South Africa, 20–22 August 1998* (eds N. J. Adams & R. H. Slotow), pp. 2040–2056. Johannesburg, South Africa: BirdLife South Africa.
- 25 Ashmole, P. 1971 Seabird ecology and the marine environment. In *Avian biology* (eds D. S. Famer & J. R. King), pp. 223–286. New York, NY: Academic Press.
- 26 Weimerskirch, H., Chastel, O., Barbraud, C. & Tostain, O. 2003 Frigatebirds ride high on thermals. *Nature* **421**, 333–334. (doi:10.1038/421333a)
- 27 Weimerskirch, H., Le Corre, M., Tew Kai, E. & Marsac, F. 2010 Foraging movements of great frigatebirds from Aldabra Island: relationship with environmental variables and interactions with fisheries. *Progr. Oceanogr.* **86**, 204–213. (doi:10.1016/j.pocean.2010.04.003)
- 28 Pennycuik, C. J. 1983 Thermal soaring compared in three dissimilar tropical bird species, *Fregata magnificens*, *Pelecanus occidentalis* and *Coragyps atratus*. *J. Exp. Biol.* **102**, 307–325.
- 29 Desprès, A., Reverdin, G. & d'Ovidio, F. 2011 Summer-time modification of surface fronts in the North Atlantic subpolar gyre. *J. Geophys. Res.* **116**, C10003. (doi:10.1029/2011JC006950)
- 30 Tew Kai, E. & Marsac, F. 2010 Influence of mesoscale eddies on spatial structuring of top predators' communities in the Mozambique Channel. *Progr. Oceanogr.* **86**, 214–223. (doi:10.1016/j.pocean.2010.04.010)
- 31 Nevitt, G. A., Veit, R. R. & Kareiva, P. M. 1995 Dimethyl sulphide as a foraging cue for Antarctic Procellariiform seabirds. *Nature* **376**, 680–682. (doi:10.1038/376680a0)
- 32 Vergassola, M., Villermaux, E. & Shraiman, B. I. 2007 'Infotaxis' as a strategy for searching without gradients. *Nature* **445**, 406–409. (doi:10.1038/nature05464)
- 33 Reynolds, A. M. & Rhodes, C. J. 2009 The Lévy flight paradigm: random search patterns and mechanisms. *Ecol. J.* **90**, 877–887. (doi:10.1890/08-0153.1)
- 34 Weimerskirch, H., Louzao, M., de Grissac, S. & Delord, K. 2012 Changes in wind pattern alter albatross distribution and life history traits. *Science* **335**, 211–214. (doi:10.1126/science.1210270)
- 35 Boyd, I. 2006 *Top predators in marine ecosystems: their role in monitoring and management*. Cambridge, UK: Cambridge University Press.
- 36 Chelton, D. B. & Shang-ping, X. 2010 Coupled ocean–atmosphere interaction at oceanic mesoscales. *Oceanography* **23**, 52–69. (doi:10.5670/oceanog.2010.05)
- 37 d'Ovidio, F., Fernandez, V., Hernandez-García, E. & Lopez, C. 2004 Mixing structures in the Mediterranean Sea from finite-size Lyapunov exponents. *Geophys. Res. Lett.* **31**, L17203. (doi:10.1029/2004GL020328)
- 38 O'Neill, L. W., Chelton, D. B. & Ebensen, S. K. 2003 Observations of SST-induced perturbations of the wind stress field over the Southern Ocean on seasonal time-scales. *J. Climate* **16**, 2340–2354. (doi:10.1175/2780.1)
- 39 Chelton, D. B., Schlax, M. G., Freilich, M. H. & Milliff, R. F. 2004 Satellite measurements reveal persistent small-scale features in ocean winds. *Science* **303**, 978–983. (doi:10.1126/science.1091901)