A biologist's guide to assessing ocean currents: a review

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ABSTRACT: We review how ocean currents are measured (in both Eulerian and Lagrangian frameworks), how they are inferred from satellite observations, and how they are simulated in ocean general circulation models (OGCMs). We then consider the value of these 'direct' (*in situ*) and 'indirect' (inferred, simulated) approaches to biologists investigating current-induced drift of strong-swimming vertebrates as well as dispersion of small organisms in the open ocean. We subsequently describe 2 case studies. In the first, OGCM-simulated currents were compared with satellite-derived currents; analyses suggest that the 2 methods yield similar results, but that each has its own limitations and associated uncertainty. In the second analysis, numerical methods were tested using Lagrangian drifter buoys. Results indicated that currents simulated in OGCMs do not capture all details of buoy trajectories, but do successfully resolve most general aspects of current flows. We thus recommend that the errors and uncertainties in ocean current measurements, as well as limitations in spatial and temporal resolution of the surface current data, need to be considered in tracking studies that incorporate oceanographic data. Whenever possible, cross-validation of the different methods (e.g. indirect estimates versus buoy trajectories) should be undertaken before a decision is reached about which technique is best for a specific application.

KEY WORDS: Geostrophic · Ekman drift · Dispersal · Orientation · Turtle · Marine mammal · Plankton · Argos · Satellite-tracking

INTRODUCTION

Currents are a fundamental feature in the oceans and have a number of profound impacts on animal and plant movements (Chapman et al. 2011). Consequently information about currents is often useful to biologists. For example, currents will disperse small animals that cannot swim strongly and thereby influence their distribution and abundance (e.g. Munk et al. 2010, Putman et al. 2010a, Hamann et al. 2011) as well as genetic structuring and connectivity of populations (e.g. Dawson et al. 2005, Godley et al. 2010,

White et al. 2010, Casabianca et al. 2012). For decades, marine biologists have therefore needed some knowledge of physical oceanography. Historically, this knowledge was often simply a rudimentary understanding of the main ocean currents (Scheltema 1966, Kleckner & McCleave 1985). For example, almost 30 yr ago, it was inferred that the anticyclonic (clockwise) flow of the North Atlantic gyre would carry hatching turtles from nesting beaches in Florida across the Atlantic to distant sites such as the Azores (Carr 1987). More recently, the easy access to direct measurements of currents has led biologists

to examine some of the subtleties of current flows (Beaulieu et al. 2009, Landry et al. 2009, Lobel 2011). In some cases, biologists are also interested in knowing the currents at specific locations and at specific times where direct measurements are not always available. For instance, estimating the ocean currents along the paths of satellite-tracked marine species, such as sea turtles, sea birds or marine mammals, may allow inferences of how environmental factors contribute to the animal's movement and behaviour (e.g. Sakamoto et al. 1997, Nichols et al. 2000, Hatase et al. 2002, Luschi et al. 2003a, Gaspar et al. 2006, Cotté et al. 2007, Seminoff et al. 2008, Bailleul et al. 2010).

Three general approaches have been adopted to estimate the effects of currents along the paths of satellite-tracked marine animals. Lagrangian drifter buoys (see Appendix 1) provide 'direct' *in situ* information on surface currents (Campagna et al. 2006, Horton et al. 2011), although there are caveats related to buoy performance. Two additional techniques are well established: (1) satellite observations are used to infer surface current fields at regular intervals (Gaspar et al. 2006, Cotté et al. 2007, Seminoff et al. 2008, Bailleul et al. 2010, Campbell et al. 2010); and (2) particles are tracked in numerical ocean circulation models to mimic Lagrangian drifter buoys (Bonhommeau et al. 2009, Sleeman et al. 2010, Kobayashi & Cheng 2011). While surface currents may be estimated from satellite observations at a spatial resolution of about 25 to 100 km (Rio & Hernandez 2004, Pascual et al. 2006, Rio et al. 2011), the current fields simulated in ocean general circulation model (OGCM) hindcasts (e.g. Chassignet et al. 2007, Lambrechts et al. 2008, Grist et al. 2010, Storkey et al. 2010) may be of finer spatial resolution, higher temporal resolution, and are not compromised by several physical approximations and assumptions, particularly in regions of swift flow. On the other hand, models do not correctly represent all physical processes, and so simulated currents also have limitations that must be considered.

Given the variety of techniques now available for assessing ocean currents, some of which have only recently been used by biologists, it is timely to review the strengths and weaknesses of these different approaches. This paper is organised as follows. We first briefly summarise the physics of ocean currents, paying particular attention to the large-scale circulation. In the subsequent section, we review 3 approaches to surface current estimation. We begin by examining the utility of *in situ* measurements of currents and some of the key resources available to

biologists. We then consider various approaches for inferring current fields when *in situ* measurements are not available. We use satellite-tracked leatherback turtles *Dermochelys coriacea* as a case study, and, when possible, we compare the methodologies to each other. Additionally, we highlight some of the potential limitations for inferring animal behaviour from these measures of ocean current data. In this way we identify some general rules to follow when interpreting the paths of satellite tracked marine animals and provide guidance for biologists interested in using ocean current information.

THE PHYSICS OF OCEAN CURRENTS

A number of well known physical processes generate ocean currents. Under a prevailing wind, the balance of surface wind stress and the Coriolis force (see Appendix 1) due to the spin of the Earth result in near-surface 'Ekman' currents (see Appendix 1), with net flow in a surface Ekman layer (the upper few 10s of m) oriented to the right of the wind direction in Northern Hemisphere and to the left of the wind direction in the Southern Hemisphere (Stewart 2008). The resulting 'Ekman transport' further results in variations in the height of the sea surface, which in turn generates horizontal gradients in water pressure. Where the associated pressure gradient force is balanced to first order by just the Coriolis force (where inertial and frictional effects are negligible), the balanced current is termed 'geostrophic' (see Appendix 1) (Stewart 2008).

Geostrophic currents dominate the large-scale ocean circulation. A geostrophic current is a flow moving along contours of equal pressure, often equivalent to sea surface height. The orientation of the flow in relation to the horizontal gradient of pressure, or sea surface height, depends on the hemisphere: viewed from above, geostrophic flow in a subtropical gyre (with central high pressure) is clockwise in the Northern Hemisphere and counterclockwise in the Southern Hemisphere. The strength of a geostrophic current is proportional to the associated pressure (or sea surface height) gradient. The utility of the link between sea surface height and geostrophic currents is emphasised below, where we explain how surface currents are inferred from satellite altimetry.

Weak 'interior' currents across broad expanses of the subtropical ocean basins are essentially in full geostrophic balance. In contrast, narrow, swift currents are found on the western side of the subtropical

basins, due to the direction in which the Earth rotates (see Stewart 2008 for a detailed explanation). These 'western boundary currents' include the Gulf Stream (North Atlantic), the Kuroshio (North Pacific) and the Agulhas Current (South Indian), and are only in approximate geostrophic balance. As flow speed increases, geostrophy breaks down to an appreciable extent, the boundary currents become unstable, and meandering develops. Downstream of the meandering a rich 'eddy' field is observed, and the flow may be regarded as rather chaotic, although the weaker flow in individual eddies, drifting away from the boundary current, may return close to geostrophic balance. While some notable currents are also observed on the eastern side of the basins, these are principally linked to surface heat loss and shelf edge topography, and are not intrinsically driven by the wind.

ESTIMATING OCEAN CURRENTS

Measuring surface ocean currents and surface drift

In situ measurements of current flows have traditionally been made in 2 different ways. Eulerian measurements (see Appendix 1) involve recording the currents at one location over time, often with a current meter deployed from a ship or mooring. By contrast, Lagrangian measurements involve releasing an object, often a tracked buoy, to record how a particular 'parcel' of water moves. Current data from these 2 types of measurement are now widely available on the Internet. For example, the PIRATA and TAO moorings in the Atlantic and Pacific provide current meter data at a range of depths from oceanic sites (Table 1). Similarly, Lagrangian data are available for near-surface tracked buoys as well as ARGO floats that travel with deep ocean currents and periodically return to the surface to relay their location (Table 1).

Perhaps the most accessible information on ocean currents for biologists to use is the Atlantic Oceanographic and Meteorological Laboratory (AOML) Lagrangian drifter buoy data set, which extends from 1979 to the present (Table 1). The data consist of numerous trajectories of surface floats attached via a thin tether to a sub-surface drogue (see Appendix 1) centred at 15 m. As the drogue dominates the area of the instrument, the trajectory is determined primarily from the near-surface currents rather than the surface wind (Fig. 1). The buoys are tracked by using the Argos system and then 6 h interpolated locations are provided via a web interface. These Lagrangian drifter trajectories provide a 'direct' *in situ* measurement of near-surface flows. However, it is important to recognise that even Lagrangian drifters do not provide an exact description of the ocean circulation. Drifters are susceptible to slip with respect to the water at 15 m depth, due to the drag on both the tether and the drogue from shear currents, direct wind forcing on the float and impact of surface waves. For instance, at 10 m s^{-1} wind speeds and related wave conditions, the drifter's slip can reach 0.7 m s^{-1} (Niiler & Paduan 1995, Niiler et al. 1995). In addition, the presence of some undrogued drifters in the AOML data set can also result in errors in the measured current velocity (Grodsky et al. 2011). Yet examining groups of drogued drifter trajectories remains a reliable method to reveal the mean flow in a specific area while individual trajectories reveal the complexity underlying these general patterns.

Building on the work of Carr (1987), for example, Lagrangian drifter trajectories have been used to show the variability of the current flows in the North Atlantic gyre. These findings suggest that some hatchling sea turtles passively drifting near the ocean surface could be carried from the coast of Florida on northerly trajectories to the coasts of the UK, Ireland and France. By contrast, others may become entrained in the central part of the North Atlantic gyre (the Sargasso Sea) for long periods, and still others may be carried around the North Atlantic gyre passing the Azores before returning towards the Caribbean (Fig. 1).

More recently, Lagrangian drifters have also been used to test hypotheses of population genetic structuring. For example, for green turtles *Chelonia mydas* in the North Atlantic, haplotypes evident in nesting turtles in Suriname, Ascension Island and Guinea Bissau have also been recorded in juveniles of this species foraging in Cape Verde Islands (Monzón Argüello et al. 2010). Lagrangian drifter trajectories have revealed that passive drift of hatchling turtles is possible between these widely (>1000 km) separated breeding and foraging sites. Hence, the sites that turtles inhabit as juveniles may simply be a consequence of the prevailing surface currents encountered during early life stages rather than some innate tendency to actively swim to particular sites. Lagrangian drifter trajectories can therefore provide information on general current patterns (see also Scott et al. 2012). However, it is difficult to use such drifters to obtain quantitative information about the frequency of different drifting scenarios, for instance.

Table 1. Summary of oceanic physical data-sets and tools to manipulate NetCDF data and for particle tracking

| Name	Description	Data access and extraction services	Data format	Website
AVISO	Access to sea surface heights (SSH), dynamic topography (MDT, MADT), sea level anomalies (SLA, MSLA), wind and wave data	AVISO data extraction tool, FTP access, Live access server	NetCDF GDR	www.aviso.oceanobs.com/
CTOH Legos	Access to global surface currents from 1999–2009: Geostrophic current anomalies from altimetry, Ekman currents at 15 m depth from Quickscat scatterometry and mean geostrophic circulation from a climatological mean sea surface product	Online form, FTP access	NetCDF	http://ctoh.legos.obs-mip.fr/products/global-surface-currents
CERSAT	Access to daily wind stresses derived from Quickscat scatterometer measurements	Online form, FTP access, Data browser		www.ifremer.fr/cersat
HYCOM	Numerical ocean general circulation model with hybrid vertical coordinate (combining vertical levels and isopycnal layers). Access to near real time global HYCOM + NCODA-based ocean prediction system output. Daily global model output available spanning November 2003 to present at a resolution of 0.08°	Live access server, FTP access, THREDDS access using OPeNDAP	NetCDF	www.hycom.org/
ICHTHYOP	Software tool for offline trajectory calculations with ROMS, MARS and NEMO datasets. Also permits the modelling of certain biological parameters important in characterising the movement of ichthyoplankton	On request (follow website instructions)	JAVA	www.brest.ird.fr/ressources/ichthyop/index.php
NEMO	Numerical ocean general circulation model with constant depth levels as vertical coordinates. Access to 1958–2007 global hindcasts at resolutions of 0.25° and 0.08°	By collaboration with NEMO team	NetCDF	www.noc.soton.ac.uk/nemo/
ARIANE	Software tool for offline trajectory calculations with NEMO datasets	On request (follow website instructions)	Fortran 90 and ancillary files	http://stockage.univ-brest.fr/~grima/Ariane/
Global Lagrangian Drifter Data	Data from satellite-tracked drifting buoys ('drifters') which collect measurements of upper ocean currents and sea surface temperatures (SST) around the world as part of the Global Drifter Program. Observation dates: 1979/02/15 to 2010/12/31	Online form, FTP access	Ascii	www.aoml.noaa.gov/envids/gld/
USGODAE Argo Page	The USGODAE server is one of the 2 Argos Global Data Assembly Centers. Access to entire set of delayed-mode data from the Argo temperature-salinity profiling floats	Live access server, USGODAE Argo GDAC data browser FTP access	NetCDF	www.usgodae.org/argo/argo.html
TAO: Tropical Atmosphere Ocean project	Access to real-time data from 70 moored ocean buoys in the Tropical Pacific Ocean, telemetering oceanographic and meteorological data to shore in real-time via the Argos satellite system	Live access server, Online form, FTP site	Ascii NetCDF	www.pmel.noaa.gov/tao/index.shtml
PIRATA: Prediction and Research Moored Array in the Tropical Atlantic	Access to real-time and delayed mode data from moored ocean buoys in the Atlantic Ocean, telemetering oceanographic and meteorological data to shore in real time via the Argos satellite system	Live access server, Online form, FTP site	Ascii NetCDF	www.brest.ird.fr/pirata/pirata.php
OPeNDAP	Freeware to access and manipulate NetCDF data			www.opendap.org/
Ncdump	Freeware to access and manipulate NetCDF data			www.unidata.ucar.edu/software/netcdf/docs/ncdump-man-1.html
Unidata	List of software packages for manipulating or displaying NetCDFdata			www.unidata.ucar.edu/software/netcdf/software.html
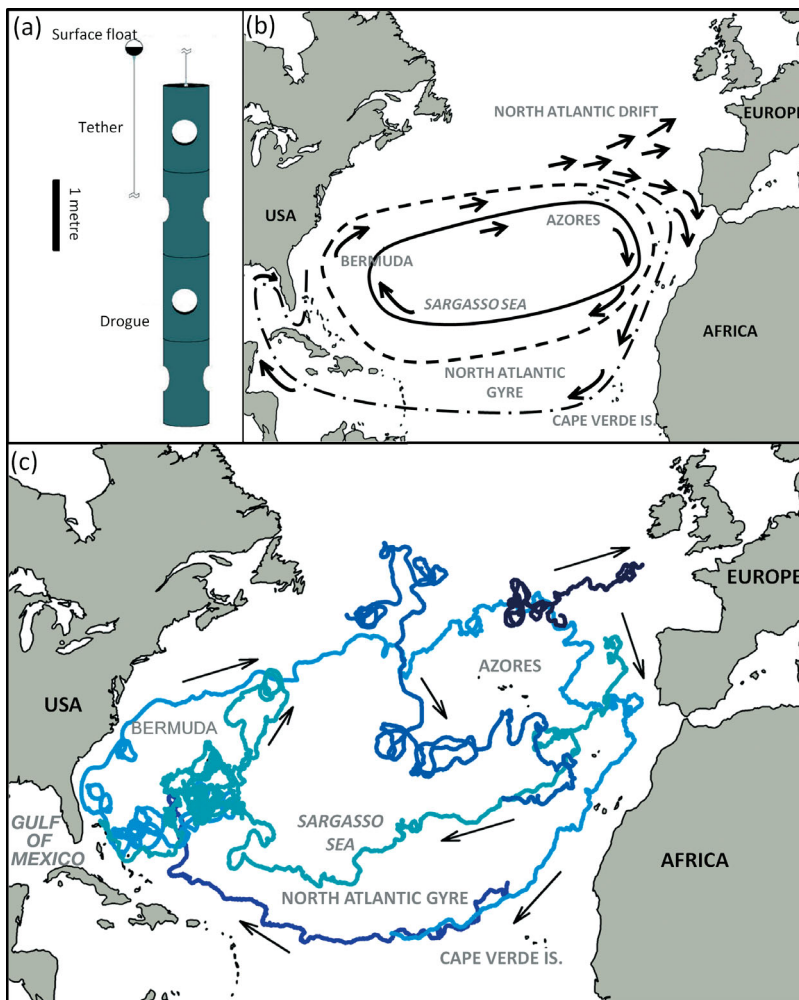
Fig. 1. (a) Schematic diagram of the typical AOML Lagrangian drifter used to determine surface currents (modified from www.aoml.noaa.gov/phod/dac/gdp_drifter.php). The surface float ranges in diameter from 30.5 to 40 cm and contains an Argos transmitter. The drogue is centred at a depth of 15 m. The drogue is cylindrical and each drogue section contains 2 opposing holes, which are rotated 90 degrees from one section to the next. The outer surface of the drogue is made of nylon cloth. The design is thought to be optimum for measuring near-surface currents. Drifters typically function for around 400 d. The AOML Lagrangian drifter data-set contain 1250 individual trajectories. See www.aoml.noaa.gov/envids/gld/. (b) A representation of the general currents in the North Atlantic, modified from Carr (1987). (c) Examples of Lagrangian drift trajectories from the North Atlantic showing the general characteristics of the anticyclonic (clockwise) flow in the North Atlantic as well as the variability in current flows. These trajectories reveal some of the likely variation in the trajectory of animals that are carried passively by the current

The tracks of large marine animals that can swim strongly, such as adult sea turtles or marine mammals, have also been compared to Lagrangian drifter trajectories (e.g. Luschi et al. 2003b, Craig et al. 2004, Campagna et al. 2006, Bentivegna et al. 2007, Horton et al. 2011). The use of drifters in this context can give insights into the general water circulation in an area

and how ocean migrants travel long distances with swimming being facilitated or impeded by prevailing currents (Fig. 2). However, due to the dynamic nature of ocean currents, inferences about the movement process of individual animals requires that the drifters (1) occur in close proximity to the location of the tracked animal and (2) that the drifter and animal are transmitting positional data at the same time. For example, comparing movements of southern elephant seals *Mirounga leonina* in the South West Atlantic with those of surface drifters, coinciding in time and space, revealed a strong coupling between the swimming dynamics of seals and the speed and direction of surface currents (Campagna et al. 2006). However Lagrangian drifter buoys often do not cover a sufficient area of ocean to provide estimates of current conditions at the precise location of the marine animal being tracked. Moreover, slight differences in position and timing can greatly affect the path of a buoy. Thus, the path of a single buoy might or might not follow a 'typical' trajectory, and it is also impossible to ascertain whether the velocity field a buoy encounters is representative of that experienced by an animal some distance away. In addition, there may also be inter-annual variability in ocean currents (e.g. Hays et al. 1993), which reiterates the importance of comparing animal tracks and current information from the same time. Therefore, when using Lagrangian drifter buoys to assess ocean currents in a specific area, a conservative approach might be to focus initially on understanding the local circulation patterns by assessing several buoy trajectories before drawing conclusions from any one of them. This approach was used in a study of adult leatherback turtles satellite tracked off the coast of South Africa (Luschi et al. 2003b). Turtles spent weeks or months moving in circles within mesoscale eddies (see Appendix 1) (Fig. 2). This pattern of movement was also observed in Lagrangian drifters tracked over the same period, though leatherbacks displayed more
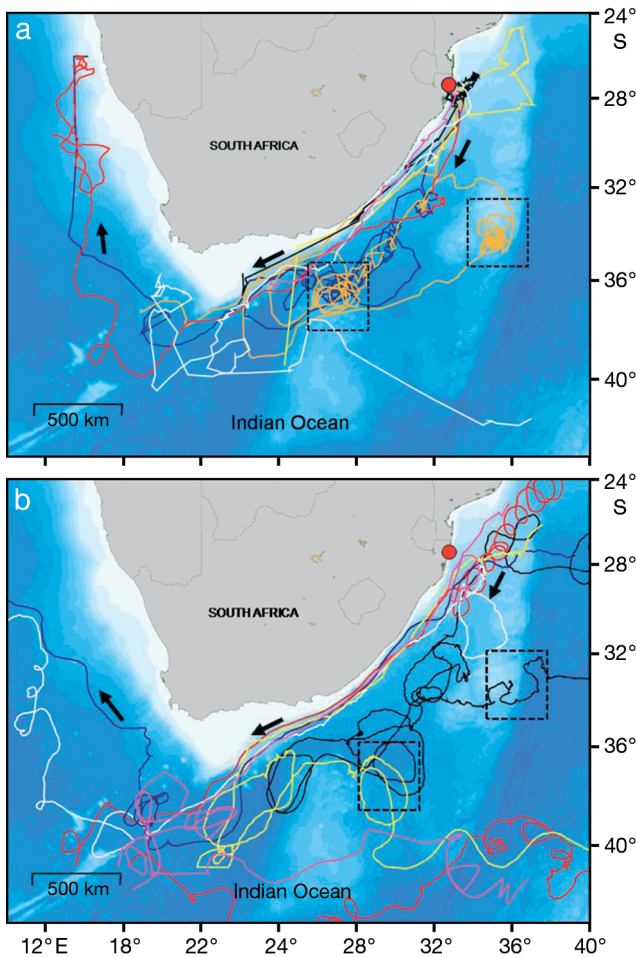
Fig. 2. (a) Routes followed by satellite-tracked leatherback turtles and (b) Lagrangian drift trajectories. Both animal and drifter tracks show prolonged periods of circling in meso-scale eddies (highlighted by dashed black squares; note that eddies are not exactly at the same place on both maps), suggesting the turtles may simply drift passively at these times. The red dot on both maps indicates the deployment location of tags onto turtles. Modified from Luschi et al. (2003b)

tightly constrained circuitous paths (Fig. 2). Data from Lagrangian drifter buoys was insufficient to determine whether the extended time turtles spent within these eddies was the result of passive entrainment or whether turtles actively maintained their position within these areas. A more detailed analysis of the turtle tracks was therefore conducted using sea surface height anomaly (SSHA) maps generated from satellite altimetry measurements. Results suggested that the movement of the turtles was dominated by strong currents within the Agulhas system (Luschi et al. 2003b, Lambardi et al. 2008).

Several other studies have also relied on SSHA maps to get information on the position and dynamics of mesoscale eddies located along the path of a

satellite-tracked animal (Polovina et al. 2004, Hays et al. 2006, Sasamal & Panigraphy 2006, Hatase et al. 2007, Revelles et al. 2007, Doyle et al. 2008, Mansfield et al. 2009, Fossette et al. 2010a, Howell et al. 2010, Mencacci et al. 2010). These studies suggest that in order to make inferences about the behaviour of a marine animal, in addition to Lagrangian drifter trajectories, some numerical methods are often needed to estimate the current velocities along its track.

Inferring surface ocean currents with satellite observations

In the absence of direct, *in situ* measurements, and for more complete spatial/temporal coverage, ocean currents may be estimated from satellite observations, based on an informed knowledge of the leading physical balances. Ekman transports and geostrophic currents have been estimated from satellite observations: Ekman transports are computed from winds, inferred in turn from the surface roughness measured by scatterometers; geostrophic currents are estimated from sea surface height fields that are measured by satellite altimeters (Table 1). The effects of geostrophic currents (velocity and direction) on animal movements have been investigated in several marine species (e.g. Polovina et al. 2000, Horrocks et al. 2001, Ream et al. 2005, Seminoff et al. 2008, Godley et al. 2010). However, the state-of-the art approach is now to estimate the effects of total surface currents on animal movements by combining both the mean and anomaly of the surface geostrophic flow and an inferred surface Ekman current (e.g. Gaspar et al. 2006, Shillinger et al. 2008, Fossette et al. 2010b, Robel et al. 2011).

A mean geostrophic current field can be derived from the Mean Dynamic Topography (MDT) (Rio & Hernandez 2004, Rio et al. 2011), while the local anomaly of the surface geostrophic current can be deduced from gridded fields of sea-level anomalies (SLA). Estimation of the surface Ekman current, or drift, involves more assumptions. First, it must be assumed that the winds are changing slowly enough for a quasi-balance between frictional (wind stress) and the Coriolis force, in the Ekman layer. Rapid changes in the winds will give rise to 'inertial oscillations', but this variability can be neglected for currents varying on timescales in excess of around a day. Then, considering the surface Ekman layer for a given constant vertical eddy viscosity (see Stewart 2008), surface Ekman currents may be simply com-

puted from the wind stress. A more sophisticated approach may involve eddy viscosity that can vary in time and space, and the use of an Ekman model (e.g. Rio & Hernandez 2003). In either way, the Ekman component of the current can be deduced using gridded fields of daily wind stresses.

Satellite-derived current products, such as those provided by LEGOS-CTOH (Sudre & Morrow 2008) or OSCAR (Johnson et al. 2007), have been routinely validated with various *in situ* data sets such as the global surface drifter dataset. Consistent agreement has been found between these satellite-derived currents and drifter currents (Pascual et al. 2006, Sudre & Morrow 2008, Dohan et al. 2010). However, it is important to keep in mind that fine-scale features, typically those with a spatio-temporal scale smaller than the resolution of the satellite measurements, may not be well resolved by this technique, which in turn may introduce some uncertainty in the overall current estimates.

Simulating ocean currents and particle drift

Numerical OGCMs are developed with the same equations from which the Ekman and geostrophic currents are estimated. These models mathematically describe current flows by forcing the ocean surface with wind data and buoyancy fluxes (heat and freshwater exchange). OGCMs can be used from a Eulerian perspective or, if combined with particle-tracking software, from a Lagrangian perspective. Particle-tracking calculations are widely used by physical oceanographers for purposes unrelated to biology. Physical oceanographers may be interested in the large-scale circulation, specifically the formation, pathways, and 'destruction' or 'consumption' of water masses — parcels of water with particular properties, most commonly temperature and salinity (e.g. Speich et al. 2002, Koch-Larrouy et al. 2010, Lique et al. 2010). In shelf seas or coastal sites, the interest may be the dispersion of radioactive plumes (e.g. Periáñez & Pascual-Granged 2008) or other pollutants (e.g. oil, Díaz et al. 2008). Other applied uses of these models include helping police forces with hindcast model runs to predict where corpses washed ashore are likely to have entered the water (Ebbesmeyer & Scigliano 2009). Particle tracking has been practised for several decades and the models have greatly improved over time because (1) increased computational power has improved model resolution; (2) the numerical schemes used to solve the model equations have become more sophisti-

cated; and (3) the data used for forcing the models at the surface have become more accurate. In coastal areas, high resolution models may additionally resolve tidal flows that are often the most important component of the current in these areas (e.g. Holt et al. 2005, Cheng & Wang 2009, Hamann et al. 2011). In the open ocean, tidal flows are very weak and can generally be ignored. Regional Ocean Model Systems (ROMS) models have also been used to describe present ocean circulation patterns but also allow projections of future circulation patterns in specific areas used by marine vertebrates (Olsen et al. 2009, Costa et al. 2010).

Particle tracking has also been widely used by biologists to infer the movements of animals as diverse as hatchling turtles (Hays et al. 2010, Putman et al. 2010b, Hamann et al. 2011) and various types of plankton (Speirs et al. 2006, Zhu et al. 2009, Mariani et al. 2010). In some cases, 'behaviour' has been placed within these models. For example, some coastal marine plankton may adjust their depth in the water column depending on the state of the tide, in order to influence their horizontal movement, and this behaviour can be parameterised within particle-tracking models (North et al. 2008, Gilbert et al. 2010, Butler et al. 2011). As a corollary, the same type of approach is used to infer the movement of insects drifting in the atmosphere, with behaviour again added to passive drift scenarios (Reynolds et al. 2009).

In the use of models, perhaps the main limitation is that processes smaller than the horizontal resolution of the models are not explicitly represented. For example, early comparisons of then state-of-the-art ocean particle-tracking models in the 1990s with Lagrangian drifters were undertaken with models that did not resolve mesoscale variability (Hays & Marsh 1997). As the large-scale currents are typically broader and slower at low resolution, such models also tended to underestimate drift times by a factor of ~2. Likewise, many contemporary ocean circulation models take a daily, weekly or even monthly average of current velocities, which are unlikely to be representative of what the animal experiences continuously. Regardless of limitations, the modelling approach has greatly improved over recent decades and has become a powerful tool for assessing the ocean currents encountered by marine animals.

Finally, animal-borne sensors are increasingly providing *in situ* data that is combined with direct or indirect measurements to improve current estimation and resolution, particularly in inhospitable locations (e.g. Boehme et al. 2008, Charrassin et al. 2008, Grist

et al. 2011). As the symbiosis of physical and biological data collection increases, so do the opportunities for studies of animal behaviour in the marine environment. Ultimately, the quality of ocean current estimates along the path of a tracked animal will influence our ability to infer the animal's behaviour.

CASE STUDIES

Comparing modelled and satellite-derived currents

The net movement of animals swimming through the ocean can be strongly influenced by the velocity of the fluid through which they are travelling. The speed and direction of their movement is the sum of their own velocity and that of the fluid. For instance, estimates of ocean currents along the animal's path are required to infer what component of these movements is due to active swimming by the animal itself and what component is caused by passive transport in the current (Chapman et al. 2011). Here, we compared current estimates along model trajectories calculated using particle-tracking software with surface currents estimated from combined altimetry and scatterometry satellite observations (following the method of Gaspar et al. 2006) for the path of a satellite-tracked leatherback turtle. To do this, we started with 4 tracks of leatherback turtles travelling through the North Atlantic Ocean (Fossette et al. 2010b). For each track, interpolated locations were calculated every 8 h (see Fossette et al. 2010b). For each 8 h re-sampled location, we calculated the apparent turtle velocity (i.e. the velocity over the ground) and subtracted from it an estimate of the surface current velocity.

The surface current velocity was estimated through the 2 different approaches. Satellite-derived surface current velocity was estimated as the sum of the mean and anomaly of the surface geostrophic current plus the surface Ekman current, deduced from altimetry and wind-stress data, respectively. The Ekman component of the current was computed from daily wind stress data obtained from CERSAT (Table 1) on a regular 0.5° × 0.5° grid using the Rio & Hernandez (2003) model. The anomaly of the surface geostrophic current was computed from weekly gridded fields of sea-level anomalies obtained from AVISO (Table 1) on a 1/3° × 1/3° Mercator grid. The mean of the surface geostrophic current was provided by Rio & Hernandez (2004) on a regular 1° × 1° grid. Then, at each 8 h re-sampled location, the 3 components of the surface current underwent a time

and space linear interpolation from the gridded velocity fields. The accuracy of this method to estimate the overall surface currents has been assessed by Pascual et al. (2006) and Sudre & Morrow (2008).

Modelled surface current velocities were calculated by using the particle-tracking program ICHTHYOP v.2 (Lett et al. 2008) applied to surface currents from the Global Hybrid Coordinate Ocean Model (HYCOM) (Bleck 2002). Global HYCOM output in this configuration has a spatial resolution of 0.08° (~7 km at mid-latitudes) and a daily time step. HYCOM uses data assimilation to produce 'hindcast' model output that better reflects *in situ* and satellite measurements. Global HYCOM thus resolves mesoscale processes such as meandering currents, fronts, filaments and oceanic eddies (Bleck 2002, Chassignet et al. 2007), which are important in realistically characterising oceanic features that affect the movements of individual animals. For advection of particles through HYCOM velocity fields, ICHTHYOP implements a Runge Kutta 4th-order time-stepping method, whereby particle position is updated hourly (Lett et al. 2008). Modelled surface current velocities are calculated by releasing 100 particles in the HYCOM model. These are randomly distributed within a 0.08 × 0.08° box (i.e. the resolution of Global HYCOM) centred on each turtle location. For each release, particles are allowed to drift for 8 h and the mean current vector is then determined by measuring the distance and direction between the start location (0 h) and end location (8 h) of all 100 particles and calculating the arithmetic mean.

We then calculated the turtle swimming velocity as the vector difference between the apparent and the current velocities and reconstructed the turtle's current-corrected tracks using current estimates from both methods. The 2 methods gave similar current-corrected tracks (Fig. 3a). The satellite and HYCOM methods for estimating the direction of currents along the length of these tracks did not significantly differ from each other for Turtle i (1-sample *t*-test on the distribution of oriented angular differences, mean angular difference = 8.2°, 95% CI = −5.8 to 22.3°, p = 0.248) and for Turtle ii (1-sample *t*-test, mean angular difference = 4.3°, 95% CI = −5.0 to 13.7°, p = 0.365). Significant differences were observed between methods in the case of Turtle iii (1-sample *t*-test, mean angular difference = 22.9°, 95% CI = 12.3 to 33.6°, p < 0.05) and Turtle iv (1-sample *t*-test, mean angular difference = 17.0°, 95% CI = 8.9 to 25.2°, p < 0.05). Currents estimated using the particle-tracking technique in
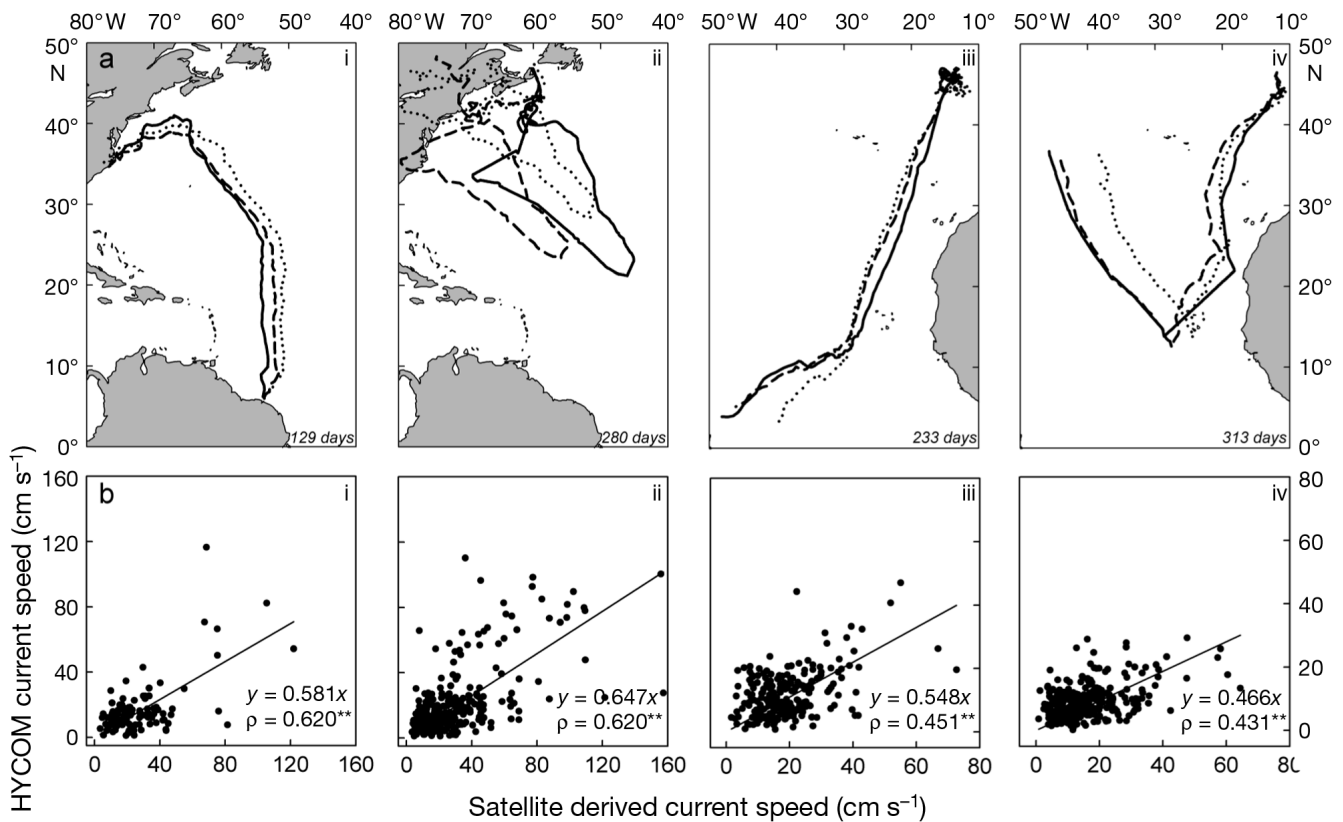
Fig. 3. (a) Observed Argos track (solid line) and current-corrected tracks obtained by using surface currents estimated by the numerical model HYCOM (dotted line) or by satellite observations (dashed line) for 4 leatherback turtles (i, ii, iii, iv) during their post-nesting migration in 2005 to 2006 in the North Atlantic Ocean. (b) Relationships between the speed of the currents estimated by the numerical model HYCOM and the currents derived from satellite observations at each location along the observed turtle tracks. Regression lines, corresponding equations and correlation coefficients are shown in each graph. **p < 0.01

HYCOM were systematically slower than satellite-derived estimated currents (about 40% slower, i.e. slope of the relationship ranging from 0.466 to 0.647, Fig. 3b). A possible explanation is that, for Lagrangian particle-tracking techniques, velocity was estimated using the straight-line distance from the start point of particles to their end point in 8 h. Mesoscale processes in HYCOM might tend to reduce the distance travelled by particles (and apparent velocity) compared to the Eulerian satellite-derived current estimates.

In any case, while our analyses suggest that these 2 methods are roughly equivalent, what this comparison does not provide is an indication of how well these methods of current estimates account for the actual current velocities the turtles were exposed to. Such information is clearly of paramount importance in assessing the validity of the conclusions about behaviour derived from current estimates.

Testing numerical methods using Lagrangian drifter buoys

Lagrangian drifter buoys are a valuable tool for validating and parameterising modelled and satellite-derived currents (e.g. Rio & Hernandez 2003, Barron et al. 2007, Dohan et al. 2010). Accordingly, even though the Lagrangian drifter buoy data set has primarily been used by biologists to describe general patterns of ocean circulation, it can also be used to assess how accurately other methods for estimating currents can predict the movement of an object in the ocean. For instance, Lagrangian drifter buoys used as 'null models' could provide an indication of the precision with which biologists can discriminate the passive versus active components of the movement of a satellite-tracked animal.

Robel et al. (2011) reconstructed the current-corrected path of a surface drifter using satellite-derived estimated currents (see previous subsection for

details about the method). Despite the drifter being by definition passive, a current-corrected trajectory was obtained, highlighting some uncertainty in the current estimates. A method was then developed by those authors (op. cit.) to allow this uncertainty to be taken into account when investigating the impact of ocean currents on an animal's behaviour. In brief, this method consisted of launching numerical particles in a reconstructed current velocity field along the path of a satellite-tracked animal at regular time intervals. This created an envelope of possible passive trajectories for the actual animal path showing the uncertainties in the velocity field. By juxtaposing the actual track with the cloud of synthetic trajectories, the extent to which the animal displays active or passive movements could then be determined.

As another example, we applied the HYCOM/ICHTHYOP method to several Lagrangian drifter buoy trajectories across the North Atlantic. We selected 6 buoys from the North Atlantic that showed a range of trajectories (Fig. 4a). Each trajectory consisted of locations every 6 h. We used HYCOM hindcast output to provide current estimates for the same times and locations as the buoy data. For the time of each buoy location, we ran HYCOM with 100 particles released randomly within a 0.08 × 0.08° box centred on the buoy location. For each release, particles were allowed to drift for up to 14 d and the particle position was recorded every 6 h. The mean current vector of the first 6 h of each particle release was then determined (hereafter referred to as 'particle vector'). As the displacement of the buoy is entirely driven by ocean currents, we determined the currents experienced by the buoy as the vector between successive buoy locations (hereafter referred as 'buoy vector').

We then compared the currents estimated by HYCOM with those experienced by the drifting buoys by calculating the difference between the buoy vectors
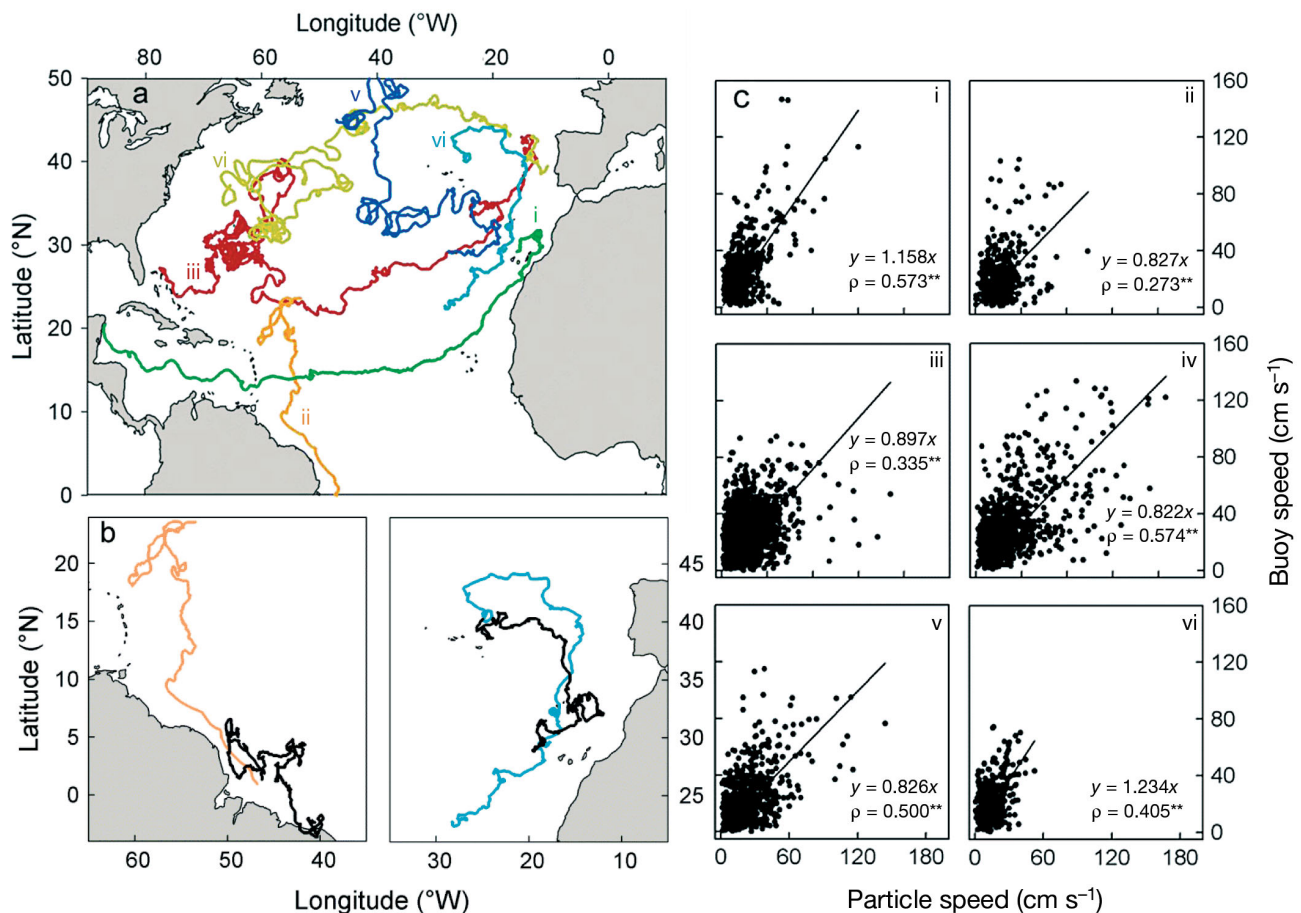

Fig. 4. (a) Trajectories of 6 satellite-tracked drifter buoys in the North Atlantic Ocean (i, ii, iii, iv, v, vi). (b) Observed trajectories (orange and blue lines) and current-corrected tracks (black lines) of drifters (ii) and (vi) (left and right panel respectively). (c) Relationships between the speed of the buoys (i, ii, iii, iv, v, vi) calculated every 6 h and the speed of numerical particles released in the ocean circulation model HYCOM at each drifter location and run for 6 h. Regression lines, corresponding equations and correlation coefficients are shown in each graph. **$p < 0.01$

and the particle vectors along the drifter trajectory. If both methods were equivalent, the difference between the buoy vectors and the particle vectors would be nil and the current-corrected trajectory of the buoy would be static. However, in all 6 cases, the buoys' current-corrected trajectories were not static, suggesting that the currents estimated by both methods were not equivalent (Fig. 4b). Accordingly, the correlation between the speed of the currents experienced by the buoys and the speed of the numerical particles was relatively weak (range = 0.273 to 0.574) but significant (Fig. 4c). In addition, the slope of the relationship was different from 1 in all cases, ranging from 0.8 to 1.2 (Fig. 4c). Four buoys went slower than the numerical particles while the 2 other buoys went faster, suggesting an absence of systematic bias in the model output. Accordingly, the mean angular difference between the particle vectors and the buoy vectors (mean = 14.5°, 95 % CI = −0.99 to 29.9°) was not significantly different from 0 (1-sample t-test, t_5 = 2.406, n = 6 buoys, p = 0.061). When looking at the impact of ocean currents on animal's movements, such non-biased uncertainties in modelled currents should not affect the overall outcome of the analysis even though they may introduce a larger variation in the data set.

In validation studies of numerical models, the separation distance between both kinds of drifters, i.e. simulated and observed Lagrangian drifters, is typically reported (e.g. Edwards et al. 2006, Barron et al. 2007). Here we found an average distance of 6.7 km between each particle and the next location of the drifter buoy after 6 h. This distance increased to 20.1 km after 1 d and to 77.9 km after 5 d (Fig. 5a,b). These distances are in the same range as values found in previous large scale validation studies of numerical models (Barron et al. 2007). Finally, we assessed the mean 'predictive ability' of HYCOM for

Fig. 5. (a) Drifter track (grey line) with numerical particle trajectories superimposed. For the time of each buoy location the HYCOM model was run with 100 particles released randomly within a 0.08 × 0.08° box centred on the buoy location. Each clump of particles is the particle position after 1 d (for a total of 5 d). Coloured boxes denote the 'start location' on the buoy track. Black boxes indicate the 0.08 × 0.08° box around the buoy location after 1 d. The 5 boxes following the start location are in accordance with the 5 d plotted for particle trajectories. (b) Mean separation distance between each numerical particle and the location of the drifter buoy at each successive time-step (6 h, 12 h, 18 h, 1 d, 2 d, etc.). Dashed lines: 95 % confidence interval. (c) Mean predictive ability for all 6 buoys, defined as the proportion of the track in which at least 1 numerical particle enters a 0.08 × 0.08° box around the buoy location at the appropriate time-step. Dashed lines: 95 % confidence interval
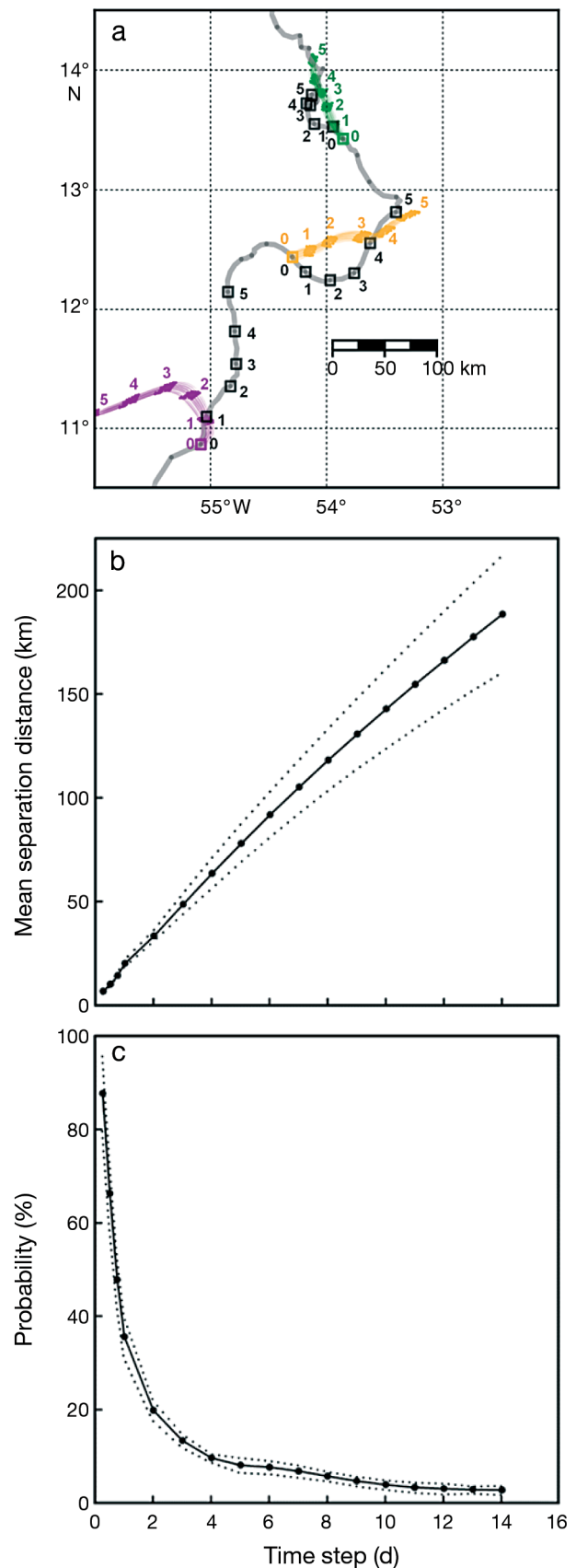
all 6 buoys. For that, we counted the probability
along the track that at least 1 numerical particle
enters a 0.08 × 0.08° box around the buoy location at
the appropriate time-step: 6 h, 12 h, 18 h, 1 d, 2 d, etc.
(Fig. 5c). At 6 h, this value was 0.88. It decreased to
0.35 at 1 d, and was 0.08 at 5 d (Fig. 5c).

These results show that, as for satellite-derived esti-
mated currents, there is some uncertainty in OGCM
estimated currents as well. This uncertainty needs to
be taken into account by biologists when investigating
the impact of ocean currents on animal movements
and behaviour. Our analysis notably suggests that,
overall, a cloud of particles released in HYCOM will
provide a good estimate of the main features of the
current flow (direction and speed) and, at least ini-
tially, accurately represent the path of a buoy. How-
ever, individual particle tracks should be treated with
caution. Therefore, when using outputs from OGCMs
to investigate the impact of currents on the movement
of a satellite-tracked animal, we suggest a methodol-
ogy similar to that of Robel et al. (2011). Numerical
particles should be released along the actual path of
the animal at regular, relatively short time intervals,
i.e. between 6 h and 2 d, as that might give a better es-
timate of the current speed and direction. The size of
the release box can be adjusted according to the qual-
ity of the animal location data, i.e. Argos quality or
GPS quality. Every segment of the actual path of the
satellite-tracked animal should then be juxtaposed
with each resulting cloud of numerical trajectories to
distinguish between active and passive movements.

RECOMMENDATIONS

Our study shows that the different methods avail-
able to measure or estimate ocean currents are not
equivalent, notably in terms of spatio-temporal cov-
erage and accuracy. Drifters provide direct measure-
ments of surface current velocities with a very high
temporal and spatial resolution, but are limited in
spatial coverage. By contrast, numerical methods
offer a more consistent and regular spatial and tem-
poral coverage. However, the spatio-temporal reso-
lution of numerical methods may sometimes be too
low to capture fine-scale mesoscale oceanographic
features. Therefore, each method's limitations should
be carefully considered before a decision is reached
about the most appropriate technique for a particular
application. As each of these methods have already
been evaluated and validated, errors and uncertain-
ties in ocean current measurements, as well as limita-
tions in spatial and temporal resolution of the data

sets, should always be taken into account or at least
discussed in any tracking study.

Best uses of Lagrangian drifter buoys

For studies on the movement of marine animals, La-
grangian drifter buoys are best suited for elucidating
the general current patterns individuals might en-
counter in a specific area (e.g. Landry et al. 2009, Hor-
ton et al. 2011), testing the connectivity between spa-
tially separated oceanic sites (e.g. Fossette et al.
2010a, Monzón Argüello et al. 2010) and comparing in
a qualitative way passive versus active movement
patterns (e.g. Lambardi et al. 2008). In order to use La-
grangian drifter data in a quantitative way, the drifter
must occur in close proximity to the tracked animal
and transmit positional data at a similar time (Cam-
pagna et al. 2006). Moreover, this data set provides a
rich resource for assessing how accurately other
quantitative techniques for estimating currents can
predict the movement of an object in the ocean (see
the previous section on testing numerical methods for
examples of 'accuracy assessment' techniques).

We also note the reservation that AOML drifters
are drogued to 15 m, while small pelagic animals
may drift with the 'surface' current; thus, it is impor-
tant to keep in mind that substantial current shear
between the surface and 15 m will inevitably lead to
divergence between actual surface currents and
drifter trajectories. Finally, although these drifter
buoys only capture velocity fields of the near surface
(upper ~15 m), it would still be wise to use them for
'accuracy assessment' techniques when examining
the movement of pelagic animals at depth.

Best uses of satellite-derived
and modelled current data

Satellite-derived estimates of ocean currents and
ocean circulation models have been validated in a
number of studies and shown to reproduce ocean cur-
rents with a high-degree of reliability (e.g. Chassignet
et al. 2007, Sudre & Morrow 2008). However, when
comparing satellite-derived estimates of currents to
Lagrangian drifters, smoothing is often applied to the
tracks of drifters to remove short-period signals not
detected by altimetric measurements or sampled
weekly winds (e.g. Sudre & Morrow 2008). Likewise,
studies comparing simulated particle tracks in ocean
circulation models to Lagrangian drifters routinely
perform additional computations to exclude the influ-

ence of wind and surface waves that cause drifter 'slip' (e.g. Edwards et al. 2006). Thus, the reported performance of these tools may tend to overestimate the reliability of such techniques when applied to the tracks of marine animals.

Another important caveat for biologists to keep in mind is that validation studies typically use 1000s of measurements (e.g. 3101 Lagrangian drifters in Sudre & Morrow 2008), whereas biologists are usually only examining 10s of individuals. Thus, while satellite-derived or modelled currents might have a high correlation factor with currents inferred from 1000s of buoy trajectories, any particular handful of trajectories might be quite poorly correlated (e.g. Sudre & Morrow 2008: their Fig. 7 shows a high degree of scatter in the correlation between satellite-derived estimates of currents along the paths of Lagrangian drifters). Thus, it is of paramount importance for biologists, when using estimated currents to infer behaviour of a tracked animal from ocean current data along its path, to perform the same analyses on a comparable number of drifters in close proximity to the study area. In this way the uncertainty and errors in the numerical method used can be parameterised or, at a minimum, acknowledged (Robel et al. 2011).

When used appropriately, these current estimates offer broad flexibility and utility. As illustrated here, these methods can be used to estimate currents along the length of an animal's track and thus infer what component of the path is caused by active movement versus passive drift (e.g. Gaspar et al. 2006, Sleeman et al. 2010). This is critical to discriminate foraging and travelling behaviour (Gaspar et al. 2006, Fossette et al. 2010b, Robel et al. 2011), evaluate orientation and navigation abilities (Girard et al. 2006, 2009, Luschi et al. 2007, Mills Flemming et al. 2010), or understand the influence of the ocean circulation on the spatio-temporal distribution of oceanic migrants (Shillinger et al. 2008, Campbell et al. 2010, Cotté et al. 2011).

Another application is the use of particle-tracking models to infer the general patterns of dispersion for passively drifting organisms (Bonhommeau et al. 2009, Mariani et al. 2010, Hamann et al. 2011). Our results show that groups of trajectories from numerical models do indeed provide a general description of the paths that passively drifting animals will follow. But drift times inferred from the numerical particle trajectories may be different from drift times inferred from drifter buoys (Fig. 4). So this highlights again the importance for biologists to apply their particular particle-tracking models to buoy trajectories so that they understand the strengths and weaknesses of the modelled results. A final important point is that numerical models simulate the 3-dimensional current field. For animals diving to/from different depths, models may thus provide useful additional information on vertical shear in horizontal currents.

CONCLUSIONS

We have a number of recommendations for biologists wanting detailed information on ocean currents. The first is to encourage biologists to make use of the global Lagrangian drifter dataset, which provides readily available 'control data'. However, it is important to recognise that, before drawing conclusions from a specific buoy trajectory, considering several buoy trajectories in the studied area is an essential first step to understand the local circulation patterns. In cases where there is a need for information on the currents at specific locations and times where buoy data is unavailable, satellite observations and/or numerical OGCMs should be used to estimate currents, but data from these methods should be treated with appropriate caution. For analyses that rely on precise measurements of environmental data (such as those designed to examine orientation or navigation behaviour, energetic output, etc.), possible false signals or noise should be parameterised against drifting buoys, for instance. When used appropriately, these approaches can provide useful insights, but they can equally lead to erroneous conclusions. Our findings suggest that people might, for instance, run the risk of reading too much into the 'current-corrected tracks' or could even run into trouble assuming that a deviation from the current is attributable to the animal's own movement (see also Robel et al. 2011). Nevertheless, it is important to keep in mind that these current estimates are the only available ones, and that often, it may be more informative to get an estimate of currents rather than to ignore them entirely.

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Appendix 1. Glossary

Coriolis: The Coriolis force is caused by the rotation of the Earth. In simple terms, when air or water flows from areas of high pressure to low pressure, the rotation of the earth makes the wind or current follow a curved path. Wind and currents tend to turn to the right of their direction of motion in the Northern Hemisphere, and to the left in the Southern Hemisphere. The Coriolis force is zero at the Equator. The Coriolis force is responsible, for example, for the rotation of cyclones.

Ekman flow: Ekman flow is a wind-driven current. Surface waters can be set in motion by the wind blowing across the ocean. Due to the Coriolis effect, this shallow layer of surface water is deflected to the right of the wind direction in the Northern Hemisphere and to the left in the Southern Hemisphere. This surface layer would drag the layer beneath it which in turn would drag the next layer and so on. As each moving layer is deflected slightly to the right (in the Northern Hemisphere) of the overlying layers' movement, the direction of water movement changes with increasing depth, resulting in a so-called 'Ekman spiral'. The total average flow, integrated over depth is called Ekman transport and is oriented 90° to the right (left) of the wind in the Northern (Southern) Hemisphere. The lower limit of the wind's influence on ocean movement is at a depth of about 100 to 150 m. This transport of water due to coupling between wind and surface waters further results in variations in the height of the sea surface which in turn generate horizontal gradients in water pressure. These pressure gradients, in turn, induce geostrophic flow.

Eulerian: measurement of the speed and direction of a current at a fixed point over time, often with a current meter deployed from a ship or mooring.

Geostrophic flow: A geostrophic current is an oceanic flow in which the pressure gradient force (i.e. the force pushing the water from a region of high pressure towards a low pressure region) is balanced by the Coriolis force in the horizontal momentum balance, resulting in the flow moving along the lines of equal pressure (isobars). Viewed from above, geostrophic flow in a subtropical gyre (with central high pressure) is clockwise in the Northern Hemisphere and counter-clockwise in the Southern Hemisphere All the major ocean currents such as the Gulf Stream, the Kuroshio Current and the Agulhas Current are approximately in geostrophic balance and are generally regarded as geostrophic currents (although the geostrophic balance appreciably breaks down with current speed increasing to high values, as non-linear terms become important in the momentum balance).

Lagrangian: measurements of the speed and direction of a current by means of a device, often a tracked buoy, which follows the movement of a particular 'parcel' of water.

Mesoscale: The term mesoscale is used to describe ocean dynamical features having horizontal scales ranging from a few to several hundred kilometres, such as ocean eddies or fronts separating water of different properties (temperature and salinity). In the ocean, mesoscale features are associated with ocean dynamics that are largely controlled by geostrophy

Sub-surface drogue: A drifter consists of a surface buoy and a sub-surface drogue or sea anchor usually attached by a long, thin tether to the buoy (see Fig. 1a). The drogue can be centred at different depths (e.g. 15 m for AOML Lagrangian buoys) beneath the sea surface and measures mixed layer currents in the upper ocean. The buoy can measure sea surface temperature, wind speed or salinity and relay these data via satellites.