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Foraging spots of streaked shearwaters in relation to ocean surface currents as identified using their drift movements

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ABSTRACT

Ocean currents are in continuous motion and strongly influence oceanic ecosystems. In situ observation of currents is of primary importance for understanding how marine animals respond to ocean surface currents at various scales and for realizing effective ecosystem-based management and realistic oceanographic modelling. We developed a new method for obtaining in situ current measurements by using seabirds as Lagrangian current sensors akin to drifting buoys. We deployed high-resolution global positioning system (GPS) loggers on streaked shearwaters (*Calonectris leucomelas*) foraging in the Oyashio-Tsugaru Warm Current confluence in Japan, which is one of the most productive oceans in the world. The seabirds repeatedly performed foraging trips, including searching for prey and resting on the sea surface, over several hundred kilometres. The seabirds spent half of their time resting on the water surface and tended to be passive drifters. We inferred that the drift movements of *C. leucomelas* provided a direct and detailed description of the ocean surface currents, because currents deduced from their drift movements were in good agreement with ocean surface currents derived from in situ and satellite data. In addition, we extracted details of shearwaters' intense searching flights associated with feeding (i.e. foraging spots) from GPS tracks. *C. leucomelas* did not forage at the core of anticyclonic eddies; rather, they used the boundary areas between eddies and the edge of eddies where primary productivity and prey density are thought to be high. Our study demonstrated that animal-borne GPS data can provide a detailed and cost-efficient tool for observing ocean surface currents and can reveal the ways in which marine animals respond to these currents at a fine scale.

1. Introduction

Ocean currents are in continuous motion and strongly influence oceanic ecosystems. The dynamics of ocean currents affect primary productivity and its heterogeneity (McGillicuddy et al., 1998, 2007; Martin, 2003; Mitchell et al., 2008), and the distribution of zooplankton and fish (Seki et al., 2002; Bakun, 2006; Hernández-León et al., 2007; Zainuddin et al., 2008; Sabarros et al., 2009). Thus, ocean circulation influences the distribution of top predators such as seabirds (Ribic et al., 1997; Tew Kai et al., 2009; Tew Kai and Marsac, 2010), pinnipeds (Ream et al., 2005; Campagna et al., 2006; Biuw et al., 2007; Robinson et al., 2012), and cetaceans (Davis et al., 2002; Woodworth et al., 2012), which are known to associate with mesoscale (of the order of 10^2 km) currents. As such, ocean currents strongly influence the locations of biologically important areas (e.g. areas of high productivity and biodiversity) in the marine environment (Olson et al., 1994). Understanding the relationships between animal behaviour and ocean currents can contribute vital information for the conservation of marine biodiversity and efficient management of ecosystem-based fisheries.

Developments in animal tracking technology (i.e. development of position-determining systems) have helped stimulate research on the ways in which marine animals respond to ocean surface currents (Tremblay et al., 2009) such as geostrophic currents (i.e. the flow in which the Coriolis and pressure-gradient terms are balanced) and ageostrophic flow driven by direct wind stress (i.e. Ekman drift) and driven by waves (i.e. Stokes drift). Two methods for estimating current along the travel paths of tracked marine animals are currently available: in situ current observations and satellite altimetry (Fossette et al., 2012). In situ current meters, such as Lagrangian drifters, current moorings, and ship-board acoustic Doppler current profilers (ADCPs that emit acoustic pulses that are backscattered by small particles in the water), record ageostrophic components in addition to geostrophic currents. However, in situ methods can have spatial and temporal limitations (Campagna et al., 2007) because data are only available if the drifters or moorings occur in close proximity, in both space and time, to the individual animals being tracked (Fossette et al., 2012).

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Satellite-derived altimetry performs better than in situ current meters in observing surface geostrophic currents at relatively large spatial scales. However, the satellite-based approach has several disadvantages. First, the spatial and temporal resolution is not adequate for the scales relevant to marine animals (i.e. metres to kilometres and hours to days), since altimeters only measure sea-surface heights directly below satellites and only measure a given location a few times per day. Sub-mesoscale features on the order of 1–100 km cannot be readily detected by conventional altimeters (Fu and Ferrari, 2008), but the distributions of marine animals are affected by eddies with radii of several kilometres (Haney, 1988; Hyrenbach et al., 2006). Environmental factors such as prey suitability or patch characteristics should be measured from the animals' point of view, and thus at spatial and temporal scales that are relevant to them (Benoit-Bird et al., 2013). Second, although coastal areas include some of the most important habitats for marine organisms, altimetry data for coastal regions have previously been considered unreliable (Cipollini et al., 2010). Third, the surface geostrophic current can be measured by satellite altimeter, but the actual current is composed of both geostrophic currents and ageostrophic components. Therefore, Lagrangian surface current sensors (e.g. drifter buoys) that can measure the actual currents play an important role in understanding marine ecosystems at the surface as they contribute to the study of dispersal or concentration of organisms, and continued development of new methods and instruments for direct current observations is thus required (Niiler, 2009). Fourth, biologically important areas ('hotspots') cannot be identified using only previously existing types of current meters.

Recently, animal-borne instruments have been used to sample in situ oceanographic data in important and productive areas (Boehme et al., 2010). Marine top predators are particularly promising as new subjects for providing in situ ocean current data that can improve estimation and resolution (Fossette et al., 2012). Studies of deep-diving marine mammal use conductivity-temperature-depth data loggers to identify temperature signatures, thereby revealing large-scale fronts (Charrassin et al., 2008; Grist et al., 2011). Although this method does not provide direct information on currents, inferences about ocean flows can be made from oceanic water masses with different physical properties. Therefore, instrumentation of deep-diving marine mammals is useful for observing global ocean currents and physical structures at depth, but not for observing surface ocean currents at fine spatial and temporal scales.

Seabirds, which are wide-ranging and fast-moving organisms, have been used to collect information on environmental variables such as temperature and light by attaching environmental sensors with position-determining systems to the birds (Wilson et al., 2002; Sokolov et al., 2006). When using seabirds as biomonitors, the animals' individual positions are recorded to indicate their spatial distributions. However, it may also be noted that animals' individual positions and tracks also contain behavioural information (Tremblay et al., 2009). In particular, global positioning systems (GPS) enable the most accurate information on seabirds' positions to be captured (Burger and Shaffer, 2008), to the extent that the drifting of seabirds on ocean flows can be visualized (Shamoun-Baranes et al., 2011; Zavalaga et al., 2012). Although drift movements have been regarded as unfavourable for use in reconstructing 2D/3D trajectories of animal movements using dead-reckoning methods (Wilson et al., 1991; Shiomi et al., 2008), the drift behaviour itself should reflect ambient ocean currents. Thus, a seabird-borne GPS is not only a position-determining system, but also a new method for observing ocean surface currents at the scale relevant to the animal.

In this study, we used streaked shearwaters (*Calonectris leucomelas*) as Lagrangian current sensors akin to drifting buoys. Streaked shearwaters are shallow divers whose maximum diving depths rarely exceed 5 m (Matsumoto et al., 2012). During the chick-rearing period, shearwaters feed on small pelagic fish such as Japanese anchovy (*Engraulis japonicus*) in offshore areas up to 800 km from their island breeding colonies (Matsumoto et al., 2012; Shiomi et al., 2012; Ito et al., 2013). In our study site, the nutrient-rich Oyashio (the western subarctic gyre of the North Pacific) flows from the north and is mixed with the Tsugaru Warm Current (TWC) (Fig. 1) creating dynamic flow such that a large number of eddies and rings appear (Vastano and Bernstein, 1984; Itoh and Yasuda, 2010). Therefore, *C. leucomelas* inhabiting this area would be suitable for testing the potential to identify surface ocean flow using seabirds. Concomitant with the recording of drift behaviour, we extracted the intense searching flights associated with feeding (i.e. foraging spots) from the GPS tracks. *C. leucomelas* 'foraging spots are likely to reflect oceanographic processes that influence marine productivity and the concentration of its prey. We related the foraging spots of shearwaters to ocean currents identified by the birds' drifting behaviour.

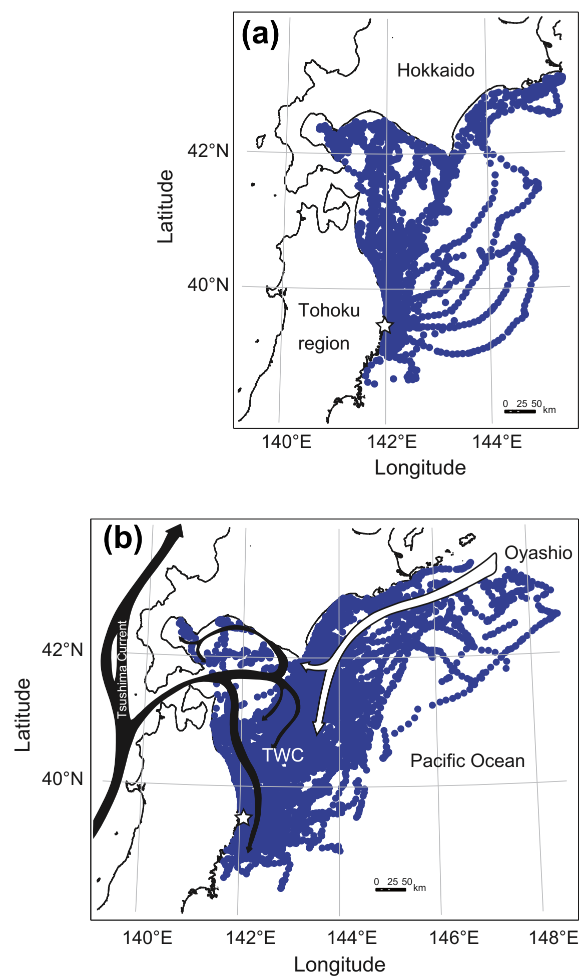

Fig. 1. GPS tracking data from streaked shearwaters in (a) 2010 and (b) 2011 (blue). The map includes 106 foraging tracks from Funakoshi-Ohshima Island (star). The typical current patterns are indicated by the arrows in (b): the open white arrow indicates the Oyashio current, and the black arrows indicate the Tsushima Current and the Tsugaru Warm Current (TWC) (modified from Kawai (1972)). The streaked shearwaters used areas in the Oyashio-TWC confluence during their foraging trips. GPS data were down-sampled at every 20 points for display. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)