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Ecology of Weddell seals during winter: Influence of environmental parameters on their foraging behaviour

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ABSTRACT

Studying the foraging strategies of top predators can provide information on both how animals interact with their environment and the distribution of their prey. We studied the winter foraging behaviour of Weddell seals in Adélie Land, East Antarctica, and the influence of abiotic parameters (bathymetry, hydrology, sea ice, light intensity) on their foraging behaviour. A total of six seals were fitted with Conductivity Temperature Depth Satellite Relayed Data Loggers (CTD-SRDL) at Dumont D'Urville (~67°S, 140°E) during the austral winters in 2007 and 2008. The tags transmitted positions and dive information over 169 ± 31 day, providing a total of 20,400 dive profiles and 2350 CTD profiles. Significant environmental influences on seal diving behaviour and habitat use were detected. Seals dived deeper, longer and increased their foraging effort during the day than at night with intermediate values for twilight. During the winter season the maximum dive depth decreased in association with an increase in dive duration, but foraging effort was unchanged. Seals spent more time at the bottom of their dives in shallow waters associated with relatively smooth bathymetry and dominated by Antarctic Surface Water. Considering the whole winter, Weddell seals tended to favour enriched, warmer and less dense water masses following their seasonal appearance on the shelf (Antarctic Surface Water and Modified Circumpolar Deep Water). Our results are consistent with seals feeding primarily on *Pleuragramma antarcticum* during winter, tracking their vertical diel migrations and foraging in areas associated with bathymetric and hydrographic features likely to concentrate prey patches.

1. Introduction

The Antarctic margin is highly productive in particular areas, such as the coastal margins of the Antarctic continent, and coastal polynyas (Burns et al., 2004). This primary production is generally linked to the shallow seasonal mixed layer that forms as sea ice melts each spring (Ducklow et al., 2007) and is associated with a high biomass of top predators, such as seabirds and marine mammals (Ainley et al., 1998; Burns et al., 2004; (Chapman et al., 2004). However, the nature of the trophic links between physical characteristics of the environment and biological production, zooplankton and resource distribution, and how these impact predator foraging performance remains poorly known. During the Antarctic winter, predators face darkness, reduced productivity, increased ice cover, modified hydrographical regimes and associated changes in prey abundance and availability (Bailleul et al., 2007; Burns et al., 2004).

Located at the top of the food web, seabirds and marine mammals can integrate the temporal and spatial variations of the lower trophic levels (Hindell et al., 2003). Their movement patterns and diving behaviour reflect to some extent the distribution and availability of their prey (Biuw et al., 2007; Bost et al., 2008; Durand et al., 2009). Recent developments in telemetry technology allow us to simultaneously record data on horizontal and vertical movements of predators, and high quality data on the in situ physical environment in which they inhabit (Rutz and Hays, 2009; Williams et al., 2011). This is particularly useful to

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investigate how top predators use the physical marine environment and how these parameters can influence their foraging strategies (Biuw et al., 2007, 2010; Charrassin and Bost, 2001; Fedak, 2004).

Weddell seals (*Leptonychotes weddellii*) are the most southerly breeding seal and the only predator, along with the Emperor penguin (*Aptenodytes forsteri*), to inhabit sea-ice during the whole year (Burns and Kooyman, 2001). Weddell seals forage under the sea-ice, and also use it as a substrate to breed (with female giving birth on the ice) and moult (Castellini et al., 1992; Cornet and Jouventin, 1980). The Weddell seal is the second deepest phocid diver of the Southern Ocean after the southern elephant seal attaining more than 600 m in the Ross sea (Castellini et al., 1992). The Weddell seals are opportunistic predators feeding mainly on fish, but also on cephalopods and crustaceans, in proportions that vary according to age, location and season (Lake et al., 2003). Weddell seal foraging behaviour has been extensively studied in summer and studies conducted in the Wedell Sea (Plötz et al., 2001) and the Ross Sea (Watanabe et al., 2003) suggest that there was an influence of summer oceanographic conditions and physiography on the Weddell seals diving behaviour. Winter movements and diving behaviour have been studied at several Antarctic locations, including the Ross sea (Burns and Kooyman, 2001; Castellini et al., 1992; Testa, 1994), and in Pridz Bay (Lake et al., 2005,2006). However, winter studies are still few and the interaction between Weddell seals foraging strategies and their environment remains poorly known.

Here, we present the first study on Weddell seal foraging ecology in Adélie Land, characterizing their winter diving behaviour and movement patterns. The coastal area off Adélie Land is associated with complex bathymetry and hydrology, with inshore depressions and canyons, and is influenced by several water masses (Marsland et al., 2004; Williams and Bindoff, 2003). We aimed to determine if the winter movements and diving behaviour of Weddell seals were influenced by key physical parameters of their marine habitat, including bathymetry, seafloor rugosity, sea ice concentration and water masses. Bathymetry features can influence the hydrological regimes of an area, which could enhance ecosystem productivity (Prézelin et al., 2000; Tynan, 1999) and can also serve as prey refuges (Zhou and Dorland, 2004). Thus, we expected Dumont D'Urville seals to select more productive and shallow waters associated with higher prey availability and accessibility; and also to forage in areas associated with lighter sea ice concentrations in order to facilitate their surface access. We also investigated the influence of decreasing light intensity as winter advanced on their diving behaviour and use of the water column as they were likely to adapt their diving behaviour to the diel and seasonal migrations of their prey.

2. Methods

2.1. Animal handling and tagging

Eight adult female Weddell seals were captured in February after their annual moult at Dumont D'Urville (66°40′S, 140°00E) during two successive summers, in 2007 (n=3, 337 ± 16 kg, 238 ± 5 cm) and 2008 (n=5, no mass data, 235 ± 8 cm). Each seal was fitted with a CTD-SRDL (Sea Mammal Research Unit [SMRU], University of St. Andrews, Scotland). The seals were approached on the ice by foot and temporarily restrained with a head bag and an intravenous injection of Zoletil (1:1 mixture of tiletamine and zolazepam), at a dosage of 0.5 mg kg^{-1}, was administered (Andrews-Goff et al., 2010; Wheatley et al., 2006). Initial dosages prior to capture were estimated for all seals. The CTD-SDRL was attached to the head with the antenna facing forward using a two component industrial epoxy (Araldite AW 2101). The seal was observed during recovery from anaesthesia and allowed to enter the water when no longer sedated. For the purpose of this paper, six seals out of eight (n=3 in 2007 and n=3 in 2008) had sufficient data covering the austral winter season to be included in the analyses.

2.2. Data collected from the tags

The CTD-SRDLs measure standard oceanographic data and transmit a simplified profile of the data along with the seal position through the Argos satellite system (for more details on the CTD-SRDLs, see Boeheme et al., 2009). Hydrographic data were recorded every second during the ascent phase of the dives. Temperature and conductivity were measured with resolutions of 0.006 °C and 0.004 mS cm^{-1} S, respectively. Salinity was calculated on board before transmission from conductivity measurements. The tags were calibrated before deployment and hydrographical data were corrected for pressure effect as described in Roquet et al. (2011). After correction, pressure (P), temperature (T) and salinity (S) accuracies were 2 dbar, 0.01–0.02 °C, and 0.03, respectively (Charrassin et al., 2008; Roquet et al., 2011). The two deepest CTD profiles were kept for each six hours period and transmission of those profiles was attempted when the seal was at the surface. Transmission constraints (narrow bandwidth of the Argos satellite system and limited seal surface time) resulted in a reduction of the T and S profiles to 20 data points selected as described in Roquet et al. (2011) and in an average of two complete CTD profiles transmitted per seal per day (Table 2). The SDRLs were programmed to record dive depth and time every 4s during diving, from which dive start and end time, dive duration and post-dive surface interval were determined. Uplinks were attempted every 40 s when the seal was surfacing. For each dive, tags transmitted only the four main inflexion time-depth points where the dive shape changed most rapidly.

2.3. Argos Kalman filtering

Argos location accuracy depends on the duration and number of transmissions between satellites and SDRLs. For each Argos location, a location class (3, 2, 1, 0, A, B and Z from the more accurate to the less accurate class) is assigned giving information on the number of satellite transmissions and the location accuracy (Patterson et al., 2010; Service Argos 2010). Approximately 40% of the locations of our study were associated with an estimated error (from less than 250 m to more than 1500 m, classes from 3 to 0), 50% had no accuracy estimation (classes A and B) and 10% were invalid (class Z). Argos locations were filtered using a combination of heuristic speed filtering and a Kalman filter that accounted for location error of the different Argos location classes as described in Patterson et al. (2010). Kalman smoothed locations were provided at the time of each original Argos location, along with a bivariate Gaussian error ellipse describing the uncertainty around each location (Patterson et al., 2010). All further analyses were then conducted on the corrected, Kalman filtered positions.

2.4. Bathymetry and sea-ice data

We used two bathymetry datasets according to their spatial resolution. Fine-scale bathymetry (Beaman et al., 2010; 500 m per cell grid) was used for analytical purposes (http://data.aad.gov.au/). The GEBCO_08 database (30 s per cell grid (≈ 1 km)) was used for graphical purposes only (http://www.gebco.net/). Using the Beaman et al. (2010) bathymetry, an index of seafloor rugosity