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Influence of sea-ice conditions on the diving activity of a marine predator: The Adélie penguin (*Pygoscelis adeliae*)

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To finish, to the birds, that made this project possible. Learning things about you is always fascinating.

Synthèse étendue

L'océan Austral fait l'objet de changements environnementaux majeurs affectant notamment la couverture de glace de mer. La formation de la glace de mer conduit au piégeage d'une quantité non négligeable de nutriments, affectant ainsi les cycles biogéochimiques (Sedwick and DiTullio, 1997; Wang et al., 2014) mais elle constitue un habitat favorable pour les microalgues, proies majoritaires du krill (Knox, 2006). Le krill étant un maillon essentiel de la chaîne alimentaire dans l'océan Austral, consommé par la plupart des meso-prédateurs, la glace de mer a donc des conséquences majeures sur le fonctionnement d'un tel écosystème, depuis les producteurs primaires jusqu'aux hauts niveaux trophiques. Pour étudier de tels écosystèmes, les oiseaux marins apparaissent comme de bons éco-indicateurs (Furness and Camphuysen, 1997; Boyd and Murray, 2001; Frederiksen et al., 2007) puisqu'ils sont relativement accessibles, qu'ils intègrent et amplifient les effets survenant aux niveaux trophiques inférieurs (Hindell et al., 2003) et qu'ils sont connus pour être particulièrement sensibles aux pressions anthropiques et aux variations environnementales (Croxall et al., 2002; Smith et al., 1999; Bost et al., 2009). De par son abondance et sa distribution circumpolaire, le manchot Adélie constitue un modèle biologique pertinent pour cette étude, suspecté d'être particulièrement touché par les changements affectant la glace de mer (Woehler and Johnstone, 1991; Ainley, 2002). Cette variable environnementale influence notamment la survie et la reproduction des oiseaux (Croxall et al., 2002; Barbraud and Weimerskirch, 2003; Gaston et al., 2005), en conditionnant la disponibilité et l'accès à la ressource et en étant à l'interface entre les colonies et les zones d'alimentation (Knox, 2006). Comprendre la relation entre la glace de mer et le succès reproducteur des manchots Adélie nécessite d'étudier l'activité de plongée des adultes puisque leur efficacité alimentaire conditionne la survie et la croissance des poussins, facteurs à l'origine du bon déroulement du cycle de reproduction (Wilson, 1995). Le stade de garde des poussins est notamment intéressant puisqu'il s'agit d'une période où les parents alternent voyages en mer et soins apportés aux poussins, et ce jusqu'à leur indépendance thermique (Ainley, 2002). A cette période, l'effort alimentaire est donc déterminé par les propres besoins énergétiques des parents et par ceux des poussins (Charrassin et al., 1998).

L'objectif de cette étude consiste à mieux comprendre comment les variations de couverture de glace de mer affectent les stratégies alimentaires des manchots Adélie. Nous nous sommes donc intéressés à l'activité de plongée d'une centaine d'individus au stade de garde de la colonie de Dumont D'Urville (Terre Adélie, Antarctique) échantillonnés sur 9 années contrastées en termes de glace de mer entre 1995 et 2014. Nous nous sommes notamment intéressés à l'existence d'une gamme optimale de couverture de glace en termes d'efficacité alimentaire et de succès reproducteur, l'objectif ultime de cette étude étant de savoir si le manchot Adélie constitue réellement un éco-indicateur pertinent concernant les changements de glace de mer, dans un contexte de changement climatique.

Pour tenter de répondre à ces questions, des données de concentration de glace de mer ont été collectées auprès de l' « Australian and Antarctic Division » (AAD) et ont permis de calculer pour chaque jour de la saison la concentration moyenne (en %) et l'étendue de glace de mer (en km²), la distance entre la colonie et l'eau libre et celle entre la colonie et les polynies (zones libres de glace au milieu de la banquise conférant un accès à la ressource). Ces données ont pu être confrontées aux données de plongée de 121 manchots Adélie échantillonnés sur 9 années, issues du Programme 1091 soutenu par l'Institut polaire français Paul-Emile Victor et WWF). Différents paramètres de plongée ont été explorés dans cette étude tels que la profondeur maximale, le temps passé au fond, le temps de récupération ou encore le temps de descente et de remontée. L'organisation des plongées dans le temps (analyse des séquences de plongées, rythme journalier et complexité comportementale) a également pu être étudiée. En outre, nous avons intégré des données de succès reproducteur, nous permettant d'identifier les années les plus favorables, afin de mieux comprendre les mécanismes impliqués dans cette relation entre la glace de mer et l'activité de plongée.

Pour modéliser la relation entre le succès reproducteur et la glace de mer, nous avons utilisé un Modèle Additif Généralisé (GAM), permettant un ajustement souple aux données. Le GAM a révélé la présence d'un seuil de glace de mer (autour de 20%) en dessous et au-dessus duquel le succès reproducteur s'effondre, suggérant notamment l'existence d'une gamme optimale de glace pour ce trait d'histoire de vie. Deux arguments majeurs peuvent potentiellement expliquer cette tendance. D'une part, il s'avère que le krill, proie majoritaire des manchots Adélie, est peu abondant lorsque la couverture de glace est faible puisqu'il se nourrit sur des communautés vivant sous la glace (Knox, 2006; Nicol, 2006). L'efficacité alimentaire des parents est par conséquent affectée, faisant chuter le succès reproducteur. A l'inverse, lorsque la couverture de glace est très importante, les adultes doivent parcourir de longues distances pour atteindre les zones d'alimentation. L'effort à terre étant plus coûteux que l'effort en mer chez cette espèce, cela impacte la condition corporelle des parents qui doivent alors prioriser leurs propres besoins, impliquant un espacement des épisodes de nourrissage des poussins ou dans le pire des cas la désertion des nids (Davis, 1982).

Compte-tenu du lien étroit entre succès reproducteur et efficacité alimentaire (i.e. la croissance des poussins est directement dépendante du succès alimentaire des parents), nous supposons également l'existence d'un optimum de glace concernant les paramètres de plongée. La relation entre ces derniers et la glace de mer a été étudiée grâce à des Modèles Linéaires Mixtes (LMM) dans le cas d'une loi gaussienne et à des Modèles Linéaires Mixtes Généralisés (GLMM) sinon, avec un effet aléatoire placé sur l'identifiant des individus. Les résultats ont montré que les années intermédiaires en termes de conditions de glace de mer avaient des profils de plongée bien différents des autres années, marqués par des individus qui exploitent moins la phase de fond au profit des phases de descente et de remontée. En outre, ils effectuent des plongées plus profondes, nécessitant un temps de récupération plus important. Ainsi, une certaine flexibilité comportementale a pu être mise en évidence selon les

différentes conditions de glace. Lors des années extrêmes, les individus exploitent davantage la phase au fond sans pour autant que la plongée soit efficace (Viviant et al., 2016). Ces variations interannuelles peuvent éventuellement s'expliquer par des différences de qualité et/ou de quantité de proies rencontrées selon les années. Il semblerait alors que lors des années intermédiaires, les oiseaux se nourrissent sur des bancs plus gros, plus denses ou plus énergétiques (variations du ratio krill/poisson).

En parallèle, l'étude de l'organisation des plongées dans le temps a montré que lors des années intermédiaires, les individus ont un rythme d'activité plus faible, marqué par un nombre de plongées par jour et un nombre de séquences de plongées par jour (regroupement de plongées très rapprochées dans le temps) moins importants. En outre, les résultats de l'analyse jour/nuit des fréquences de plongée suggèrent un rythme de plongée plus régulier lors des années intermédiaires (plongées réparties de façon homogène tout au long de la journée); suggérant probablement un rythme d'activité moins contraint, en lien avec des conditions environnementales plus favorables. L'analyse des fractales, quant à elle, a permis de mettre en évidence une augmentation de la complexité du comportement de plongée selon un gradient décroissant de concentration de glace de mer, suggérant que lors des années de forte couverture de glace, les oiseaux sont davantage contraints dans leur comportement (révélant notamment l'importance des polynies dans ces conditions).

La confrontation des données de plongée, de succès reproducteur et de glace de mer dans une analyse à long-terme a permis de mettre en évidence des différences de stratégies alimentaires à différentes échelles (saison de reproduction, voyage alimentaire, journée, plongée). Les résultats ayant montré qu'il semble y avoir une gamme optimale de glace de mer en termes d'efficacité alimentaire et de succès reproducteur chez le manchot Adélie, cette étude fournit des arguments supplémentaires pour conforter l'idée qu'il s'agit certainement d'une bonne espèce eco-indicatrice concernant les conditions de glace. En outre, les arguments avancés n'auraient pu être possibles sans la multiplicité des approches utilisées dans cette étude. Une étude à plus long terme permettrait de mieux caractériser cette gamme optimale. En outre, il serait intéressant d'avoir plus d'informations sur les individus, notamment concernant leur efficacité alimentaire (données de condition corporelle, de régime alimentaire, de localisation avec GPS) afin de mieux comprendre les mécanismes impliqués dans cette plasticité comportementale.

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Glossary

Bout: sequence of multiple dives over a certain period of time.

Central-place forager: animal that must return to its central place (e.g. nest) regularly during the breeding season

Colony: large congregation of breeding birds.

Eco-indicator: indicator which refers to ecological processes and which is used to communicate information about ecosystems and anthropogenic impacts on ecosystems.

Fledging: characteristic of a chick that has grown enough to acquire its adult plumage.

Foraging: act of searching for food

Polynya: area of unfrozen sea within the ice pack.

School: aggregation of individuals with polarized orientation, all moving in the same way at the same time.

List of abbreviations

BCI: Bout Criterion Interval

CCAMLR: Commission for the Conservation of Antarctic Marine Living Resources

DFA: Detrended Fluctuation Analysis

GAM: Generalized Additive Model

LMM: Linear Mixed Model

PCA: Principal Component Analysis

SIC: Sea-Ice Concentration

SIE: Sea-Ice Extent

TCPUE: Attempts of Catch per Unit Effort

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1. Introduction

Marine ecosystems are experiencing different types of disturbances such as climate change, overfishing or invasion of exotic species, yet they remain understudied (Richardson and Poloczanska, 2008). If we are willing to protect marine ecosystems, it is fundamental to determine how and to what extent organisms are able to cope with environmental changes. This is especially true in polar regions, where the effects of climate change are the strongest (Clarke and Harris, 2003; Gaston et al., 2005). For instance, the Southern Ocean experiences regional changes in air and water temperatures that cause a cascade of changes in oceanic currents, water column thermal stratification and sea-ice cover, which consequently affect food availability and trophic network structure (Trathan and Agnew, 2010; Constable et al., 2014). Sea-ice dynamics are particularly important as they can affect the stability of the Antarctic ecosystem by turning from solid to liquid easily, making it more fragile. Sea ice forms at the surface once the temperature drops to the freezing point, which is about -1.9°C for a salinity of 35 (Weeks and Ackley, 1982; Ainley, 2002). During austral summer (from October to March), the -1.9°C isotherm retreats toward the pole with rising temperatures, reducing the sea-ice extent. At its maximal extent (in September), the Antarctic pack ice covers 40% of the Southern ocean (between 17.5 and 19 million square kilometres), which corresponds to 6% of the world's oceans (Ainley, 2002; Meier et al., 2013).

Sea ice has strong impacts on biogeochemical cycles and marine ecosystems (Sedwick and DiTullio, 1997; Wang et al., 2014). Sea ice removes nutrients from seawater during its formation (Wang et al., 2014) so that changes in sea-ice cover alter the nutrient cycling, inducing seasonal variations of nutrients availability (Wang et al., 2014). The Southern Ocean is considered as a High Nutrients, Low Chlorophyll area (HNLC) meaning that the concentration of nutrients is sufficient but that the primary production observed is lower than expected. Productivity is actually limited by low iron availability (Martin et al., 1990; Wang et al., 2014) and sea-ice melting represents a non-negligible iron resource (Aguilar-Islas et al., 2008). In addition, as sea ice reduces the amount of light available, limiting phytoplankton growth rate (Buckley and Trodahl, 1987; Knox, 2006), phytoplankton blooms are always observed where there is recent melting of sea ice (Smith and Nelson, 1985; Wang et al., 2014). Yet, sea ice provides a highly favourable habitat for microalgae and bacteria that are well adapted to a dynamic salinity regime and have the potential to photosynthesize even in low light conditions (Knox, 2006). As krill is known to feed on sea-ice microalgae (Brierley et al., 2002), marine predators take advantage of this association between sea ice and krill to feed on concentrated prey within a small volume (Knox, 2006). In other words, sea ice has major consequences on the Southern Ocean ecosystem structure and functioning, from grazers up to the highest trophic levels. At a time when climate is prone to abrupt changes, this ecosystem deserves a close monitoring.

However, monitoring an entire ecosystem is logistically challenging, especially in the Antarctic region. To address this difficulty, ecologists often use meso and top-predators, like seabirds and marine mammals, as eco-indicators of their ecosystem (Furness and

Camphuysen, 1997; Boyd and Murray, 2001; Frederiksen et al., 2007). Predators at high levels of the trophic network are indeed expected to integrate and amplify the effects occurring at lower trophic levels (Hindell et al., 2003). Predators have to face two major constraints: to find prey before starving and to make sure that the energetic cost of pursuit, catch and ingestion is not too high so that it, at minimum, balances the cost of acquiring the food (Sinervo, 1997). As prey distribution is often patchy, predators search for prey over extensive areas and travel long distances (Weimerskirch et al., 2005).

Seabirds are abundant wide-ranging predators (Cairns, 1987) and major consumers of marine food resources. In 2004, the annual food consumption of all the world's seabirds amounted 70 million tons, which was similar to the global fisheries landings, reaching 80 million tons the same year (Brooke, 2004). They are also widely used as environmental indicators because they are sensitive to human pressure and environmental variability (Croxall et al., 2002; Smith et al., 1999; Bost et al., 2009). Changes in sea-ice cover and distribution are major determinants of seabirds' survival and reproduction in the Southern Ocean (Croxall et al., 2002; Barbraud and Weimerskirch, 2003; Gaston et al., 2005). Sea ice is actually at the interface between nesting grounds and foraging areas (Knox, 2006), making this parameter a primary factor affecting populations (Fraser et al., 1992; Kato et al., 2002). As such, understanding the relationship between sea ice and breeding success cannot be achieved without assessing the feeding activity of parents foraging at sea (Wilson, 1995). The breeding success is indeed linked to the chick's growth, which is directly depending on the successful foraging activity of parents. This highlights the necessity to investigate the relationship between sea ice and diving behaviour. In addition, seabirds are central place foragers (Orians and Pearson, 1979) meaning that individuals return regularly to land to breed; making them easily accessible to researchers (Piatt et al., 2007). Finally, the miniaturization of electronic devices has allowed researchers to develop animal-embarked data recording loggers to track the fine-scale activity of seabirds at sea, an approach known as bio-logging (Ropert-Coudert and Wilson, 2005; Ropert-Coudert et al., 2012).

Among seabirds, penguins represent up to 90% of the total avian biomass in the Southern Ocean (Woehler, 1995; Knox, 2006; Halsey et al., 2007) and the Adélie penguin (*Pygoscelis adeliae*) is one of only two species of penguins found in Adélie land (with the Emperor penguin, *Aptenodytes forsteri*) (Woehler, 1995). They play a fundamental role in the southern part of the Southern Ocean's trophic network, with breeding adults estimated to consume 24% of the fish and 90% of the crustaceans of the area (Woehler, 1995). The biomass of Adélie penguins' prey is strongly dependent on primary production and sea-ice conditions (Jenouvrier et al., 2006). As such, and because of its abundance reaching 3.79 million of breeding pairs (Lynch and Larue, 2014) and its circumpolar distribution, the Adélie penguin appears as a relevant eco-indicator of the Southern Ocean ecosystem. This is particularly the case for marine Antarctic habitats that are sensitive to changes affecting the sea ice (Woehler and Johnstone, 1991; Ainley, 2002).

The Adélie penguin is a colonial and mainly monogamous species (Schwartz et al., 1999), which can live up to 20 years. The age of first breeding averages 5 years for females and 6.2 years for males (Ainley, 2002). The species breeds during the austral summer

(October - March), gathering in colonies located on shores around the Antarctic continent. Despite its lifespan and its abundance, the IUCN status of this species has been upgraded to Near Threatened (NT) in 2012 because its population is expected to undergo a rapid decline in the forthcoming years in relation with global change (BirdLife International, 2012). The annual cycle of Adélie penguins includes a pre-migratory phase of feeding and fattening, a spring migration towards the different colonies, nesting, and moult (Ainley, 2002) (Fig. 1).

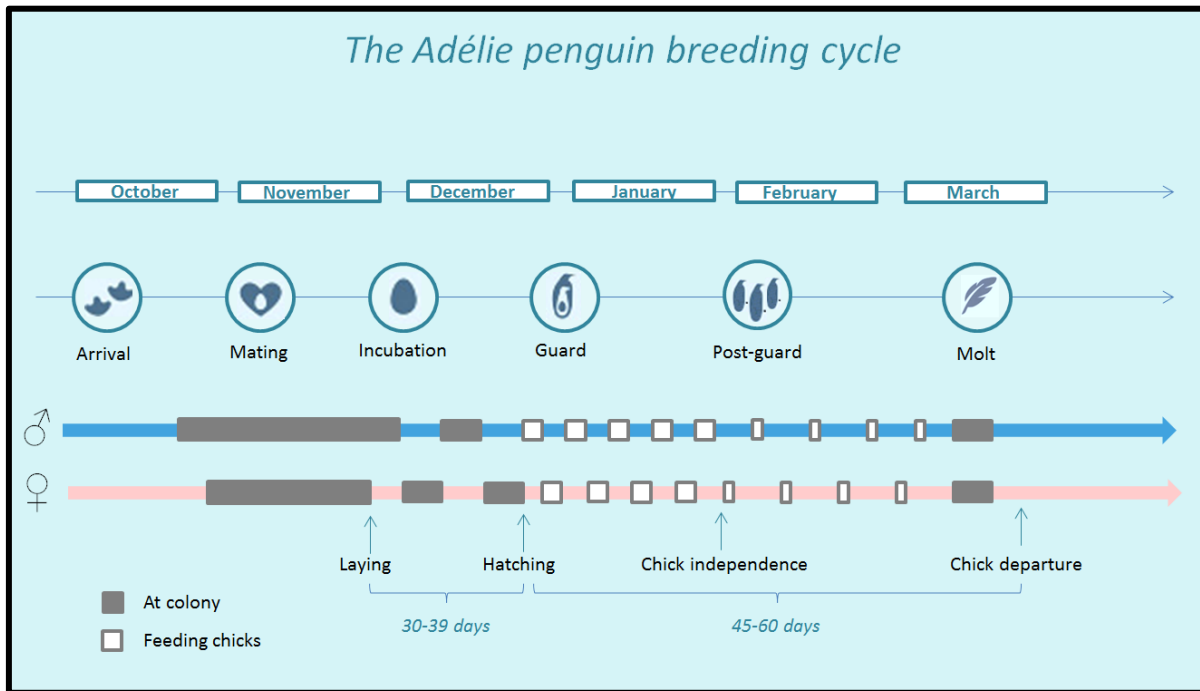


Figure 1: Illustration of the Adélie penguin’s breeding cycle.

Birds arrive at their breeding sites around mid-October to form pairs (end of October – beginning of November) and build nests (Southwell et al., 2010) (Fig. 1). After laying one or two eggs, the incubation period, which ranges from 30 to 39 days for this species, follows with a single adult at a time incubating (Southwell et al., 2010; Ainley, 2002). Indeed, as soon as the second egg is laid, the female leaves the nest for the sea in order to replenish its body reserves and then return from foraging to relieve the male from its duties which in turn leaves the colony to forage (Ainley, 2002) (Fig. 1). During the whole incubation period, the eggs are alternately guarded by a single parent while the other one is at sea (Southwell et al., 2010; Ainley, 2002). Over the next stage, the « guard stage », both parents keep alternating foraging at sea with chick attendance at the nest until the chicks reach thermal independence (Ainley, 2002) (Fig. 1). Guard stage lasts 22 days on average and parents change roles every 1-3 days (Ainley, 2002). In central place foragers, such as Adélie penguins, the foraging effort at this stage is determined by the energetic requirement to forage, the energy required to restore body condition and the energy demand of the chicks (see an example for king penguins *Aptenodytes patagonicus* in Charrassin et al., 1998). As the chicks grow and their food requirements increase, both parents undertake foraging trips simultaneously. Because chicks still need protection from predators, they form groups known as crèches (Ainley, 2002) (Fig. 1). The chicks moult, fledge and leave the colony when they are around 60 days old. After

moulting, adult Adélie penguins embark on a winter migration, which takes them away from the breeding site for 8 months (Knox, 2006). With the coming of spring, birds start to migrate towards land where they will engage in a new breeding attempt.

The Adélie penguin feeds essentially on krill, a tiny shrimp living in schools (Hardy and Gunther, 1935; Stretch et al., 1988). Their main prey are the Antarctic krill (*Euphausia superba*), which is the dominant species of krill in the Southern ocean, and the ice krill (*E. crystallophias*), but they also occasionally feed on Antarctic silverfish (*Pleuragramma antarcticum*) and jellyfish (Cherel, 2008; Libertelli et al., 2003; Croxall and Lishman, 1987; Volkman et al., 1980; Thiebot et al. 2016). Stomach content studies in Dumont D'Urville have shown that the Antarctic krill seems to occur in much lower number than the ice krill but contributed slightly more by biomass (41% vs 38%) (Ridoux and Offredo, 1989). However, this may vary annually and seasonally. Adélie penguins spend more than 90% of their time at sea (Ainley, 2002). They are visual predators, feeding as deep as the penetration of light into the water allows, but spending most of their time diving to depths considerably less than they are capable of, where there is sufficient light to be able to see their prey (Wilson, 1993). They are highly capable swimmers, with a mean swim speed measured around 2.03m/s and can reach up to 4m/s (~15.8km/h) (Ropert-Coudert et al., 2002).

The quality of a given habitat can be associated with the matching between the predators' requirements and the prey availability in terms of period, biomass and accessibility (Durant et al., 2007). In the Southern Ocean, the quality of the habitat seems to be highly correlated with the annual primary production, which is known to depend on sea-ice conditions (Quetin and Ross, 2001). In this context, studying the foraging activity, and in the case of diving predators, the diving behaviour appears to be crucial because it reflects both the availability of prey and sea-ice conditions. In addition, the use of the 3D habitat provides a better understanding of the impact of climate variability on ecosystems (Hooker and Baird, 2001; Hickmott, 2005).

Several studies have already investigated the relationship between Adélie penguins' foraging behaviour and sea ice. They all converged towards the idea that sea ice plays a fundamental role in foraging strategies and success. Habitat use in relation with sea-ice distribution was especially examined but it was exclusively spatial analyses. For example, in Widmann et al. (2015), authors have shown that in the Dumont D'Urville Sea, foraging areas could differ according to changes in sea-ice extent, highlighting the strong dependence of birds on the access to polynyas (areas of unfrozen sea within the ice pack) during guard stage. In parallel, Cottin et al. (2012) also investigated foraging strategies of Adélie penguins in relation with sea ice. Findings revealed a positive relationship between body condition and the maximum distance reached during the foraging trip, both linked to sea ice. Then, comparing two different situations enabled scientists to discover the potential impacts of differences in sea-ice conditions. In Watanuki et al. (1997), differences in at-sea behaviour (dive depth, dive duration and walking/swimming ratio) were observed between two colonies: Lützom-Holm Bay, where sea ice remained during summer and Magnetic Island, where sea ice disappeared in January. These behavioral variations probably reflect differences in the availability of feeding sites in relation to the contrasted sea-ice distributions. However, comparisons between

sites can be biased by other potential factors that can be responsible for the differences observed between two locations. Comparisons have also been done between two periods for the same colony. Indeed, binary results were obtained from [Rodary et al. \(2000\)](#) concerning Adélie penguins' diving behaviour in relation to sea ice at Dumont D'Urville. Authors have shown that differences in diving metrics previously occurring in different locations could also be observed for a single colony over two consecutive years. In addition, [Beaulieu et al. \(2010\)](#) monitored responses of Adélie penguins in terms of diving metrics, diet, foraging range and breeding success during two seasons of contrasting timing of sea-ice retreat. Findings revealed that birds seem to be able to adjust their behaviour while at-sea for survival and reproduction purposes. On the other side, in [Bost et al. \(2015\)](#), authors underlined that the analysis of a long-term dataset could be a powerful approach in order to identify the mechanisms involved in the relationship between environmental variables and king penguin's population dynamics. Long term studies performed on a single colony could clearly enable us to have gradations of the impact of sea ice on populations.

With the objective of understanding how sea ice influences the ecology of Adélie penguins in a context of global warming, the main research question is: How changes in sea-ice parameters affect the diving activity and the breeding success of this marine predator? At first, we were interested in investigating the effect of changes in sea-ice conditions on breeding success. Then, we examined the influence of sea ice on the diving behavior of Adélie penguins at different scales, meaning that we studied both the diving parameters and the temporal organisation of dives. To this end, we compared the breeding success and the diving behavior of chick-rearing Adélie penguins from a single colony in Adélie Land over nine austral summers with contrasted sea-ice conditions. In relation with the ecological theory, the underlying assumption that we were especially interested in was: Is there an optimal range of sea-ice cover in terms of foraging efficiency and breeding success? The ultimate aim of the present study was to investigate if Adélie penguins are relevant eco-indicators of sea ice.

2. Material and Methods

2.1. Study site and period

The study was conducted on Adélie penguins breeding near the Dumont D'Urville scientific station (66°40'S, 140°01'E), Adélie Land, Antarctica (Fig. 2) over nine austral summers (October-March) between 1995 and 2014 (Program 1091 of IPEV and WWF).

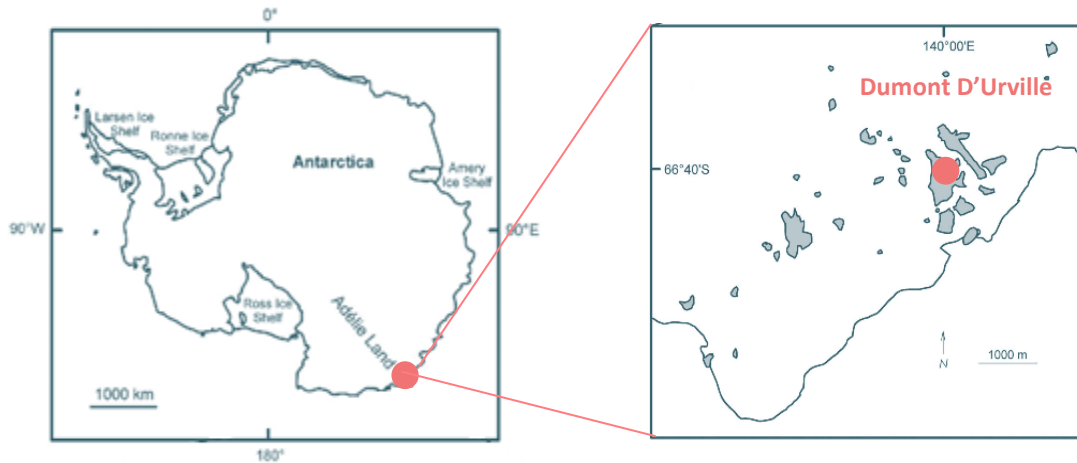


Figure 2: Location of the Dumont D'Urville scientific station, Adélie Land, Antarctica.

Three different types of data were used in this study: (i) sea-ice data, (ii) breeding success data and (iii) diving data.

2.2. Sea-ice parameters at different scales

We used satellites' passive microwaved measurements of daily sea-ice concentration (SIC) downloaded from the Australian and Antarctic Division website (<https://github.com/AustralianAntarcticDivision/raadtools>) to characterize the sea-ice conditions encountered by the studied individuals. Two different temporal scales were considered in this study: (i) the period concerned by diving data (daily scale) and (ii) the period corresponding to both incubation and guard-stage (global scale). As the foraging trips of Adélie penguins at the Dumont D'Urville colony extend from 63.7°S to 66.6°S and from 134.7°E to 142.3°E for the whole breeding season, corresponding to an area of 119 389 km² (Widmann et al., 2015; Cottin et al., 2012), we considered a slightly larger area to extract the sea-ice data at the global scale (from 62°S to 68°S, and from 134°E to 144°E). For the days concerned by diving data, a shorter area was chosen because during guard stage, the foraging extent is smaller than during incubation (Widmann et al., 2015). We defined the guard phase foraging zone as 139-141°E and 67-65.5°S. Sea-ice data were processed using the R package 'raster' (Hijmans et al., 2016) with a resolution of 25 km (Appendix I).

Basically, daily maps were created with a single value of sea-ice concentration in each cell of the raster. Sea-ice concentration describes how much percentage of a 25 km by 25 km box is covered by ice (compared to a reference established on a 1981-2010 baseline), 0% being open water and 100% full ice coverage (NSDIC, 2016). Four sea-ice parameters were calculated from these maps: the mean sea-ice concentration (SIC), the sea-ice extent (SIE), the distance between the colony and the open-water and finally the distance between the colony and the polynyas. The sea-ice extent corresponds to the total area covered by sea ice in square kilometres. For each cell, we defined a binary term according to the typical threshold of 15% chosen by NASA which determines if a cell has ice or not: pixels with more than 15% of sea-ice concentration are considered as "ice-covered" (value of 1) and pixels with less than 15% of sea-ice concentration are considered as "open water" (value of 0) (Meier et al., 2015).

Sea-ice extent was calculated by summing the area of all grid cells that contained sea ice (i.e. cells with a value of 1). In addition, the distance between the colony and the open water was also calculated using the threshold of 15%. Polynyas were defined as a cell or a group of cells with less than 15% of sea-ice concentration surrounded by cells of more than 15% of sea-ice concentration. The presence of polynyas was taken into account because birds are known to rely on the opening of polynyas during chick-rearing in order to improve prey accessibility and breeding success (Kato et al., 2002; Widmann et al., 2015).

2.3. Breeding success data analysis

Breeding success data for Adélie penguins in Dumont D'Urville were provided by the Programme IPEV 109 and are available for 20 years from 1995 to 2014 (Barbraud et al., 2015). Breeding success is defined here as the ratio of the number of chicks counted in the area in February (end of the breeding season) to the number of incubating pairs in December. We investigated the relationship between Adélie penguins' breeding success and sea-ice concentration using a non-parametric smoothing regression technique. A generalized additive model (GAM) was fitted to the time series of breeding success. GAMs are the preferred approach for modelling the nonlinear relationships between predators and environmental parameters (Redfern et al., 2006). A GAM corresponds to a flexible extension of a Generalized Linear Model that can combine parametric forms along with nonparametric smoothers. Therefore, this model is more sensitive to nonlinear patterns (Wood, 2006).

In this study, the GAM was specified with a Gaussian family to investigate temporal variations in breeding success. We used the 'mgcv' package from R (version 3.2.3) to fit the GAM to our data (Wood, 2006) (Appendix II). In 'mgcv', the smooth functions are represented as spline functions (polynomial functions often used to represent smoothed and nonlinear relationships). In the present study, a cubic regression spline was used, which means that the predictor X (sea-ice parameter) is divided into a certain number of intervals and in each segment, a cubic polynomial is fitted ($Y = \alpha + \beta X + \mu X^2 + \gamma X^3$). The fitted values per interval are then joined together to create the smoothing curve. The cubic regression spline ensures that the curve will look smooth at the knots (points between intervals) using first order and second order derivatives. The problem with modelling GAMs with spline functions is to make sure that the model does not overfit but approximates the patterns in the data. Indeed, the objective is to have a smooth connection at the knots. The optimal amount of smoothing was estimated using knots recommendations from Zuur et al. (2009). Authors suggest using 3 knots if there are less than 30 observations and 5 knots if there are more than a hundred observations. In this study, the dataset was quite small (around 20 values) and the SIC values were not evenly spaced (with a lot of values between 17% and 22%). As a consequence, the model, which used 10 knots by default, placed multiple knots in this segment, tending to overfit in this region and giving a wiggly curve, which was ecologically meaningless. This is the reason why a smaller number of knots has been chosen, following Zuur et al. (2009).

2.4. Diving data collection and processing

In order to reduce the variability due to the differences in foraging strategies at the different breeding stages, we decided to focus our study to a single breeding stage. We selected the guard stage (end of December - beginning of January) because as sea ice is known to constraint birds in terms of trip duration and foraging range, the behaviour reflects local conditions. A total of 121 birds were considered in this study (Table 1).

Table 1: Number of birds studied over the nine austral summers.

Year	Males	Females	Unknown	Total
1995	8	-	-	8
1998	-	-	13	13
2001	-	-	21	21
2007	5	5	-	10
2009	5	-	-	5
2010	6	-	-	6
2011	13	-	-	13
2012	17	18	-	35
2014	5	5	-	10
Total	59	28	34	121

2.4.1. *Field procedure*

Diving behaviour of adult Adélie penguins was recorded by miniature data loggers attached to the birds. Birds were captured while leaving for a foraging trip and equipped with Time-Depth Recorders (TDRs). These devices record time-series of depth readings taken regularly at pre-determined intervals (1s or 5s) (Table 2) (Luque, 2007). Loggers were attached to the lower back of penguins using waterproof tape (Wilson and Wilson, 1989) except LUL type, which was attached to a leg band. After one foraging trip that lasted a few days, birds were recaptured upon their return to the colony, and the loggers were retrieved. In addition to recording depth as a function of time, TDRs also recorded water temperature data. Loggers were cylindrical or box-shaped and had different characteristics (Table 2).

Table 2: Table of loggers' characteristics.

Year	<i>Loggers' characteristics</i>				
	Logger type	Provider	Size	Sampling interval	Depth accuracy (m)
1995	mk5	Wildlife computer, USA	57*13mm	5 s	2
1998	UWE-PDT	Little Leonardo, Japan	102*20 mm	1 s	0.5
2001	M190-D2GT	Little Leonardo, Japan	53*15 mm	1 s	0.1
2007	mk9	Wildlife computer, USA	68*17 mm	5 s	0.5
2009	M190-DT	Little Leonardo, Japan	53*15 mm	1 s	0.1
2010	M190-DT	Little Leonardo, Japan	53*15 mm	1 s	0.1
2011	M190-DT	Little Leonardo, Japan	53*15 mm	1 s	0.1
2012	M190-DT	Little Leonardo, Japan	53*15 mm	1 s	0.1
2014	LUL	IPHC, France	20*10mm	1 s	0.3

2.4.2. Extracting diving data

Upon recovery, depth data were downloaded onto a computer and analysed using IGOR Pro (WaveMetrics, 2015, Version 6.3, Oregon, USA) with the WaterSurface function of the Ethographer (Sakamoto et al., 2009). IGOR Pro is an integrated program to visualize, analyse, transform and represent experimental data (WaveMetrics 2015). Pressure transducers in TDRs may drift over time because of temperature changes, inducing deviations in recorded depth. Zero offset correction (ZOC) of the measured depth is thus required in order to remove artefacts (Luque and Fried, 2011). Identification of the points corresponding to depth of 0 m (water surface) is easy in seabirds as they must return to the surface regularly to breathe, providing a reference point for calibration (Luque and Fried, 2011).

The idea is to calculate the histogram for the raw depth data. As the data concern animals which stay at the water surface for a certain time, the mode corresponds approximately to a depth of 0 m. Then, the procedure fits a Gaussian distribution to the histogram of raw depth data and extracts the depth data in the range of $\text{mean} \pm 3\text{SD}$, which represents water surface. The next step consists in performing a regression analysis for the extracted data in order to examine the relationship between depth and temperature, by giving the degree of temperature drift of pressure sensor (because these data points are supposed to indicate water surface). Raw data are then corrected using the regression line. To finish, the procedure updates the histogram by using the corrected depth data and fits a Gaussian distribution to the histogram again (Sakamoto, 2012). This process permits to have the dive profile of each bird (Fig. 3).

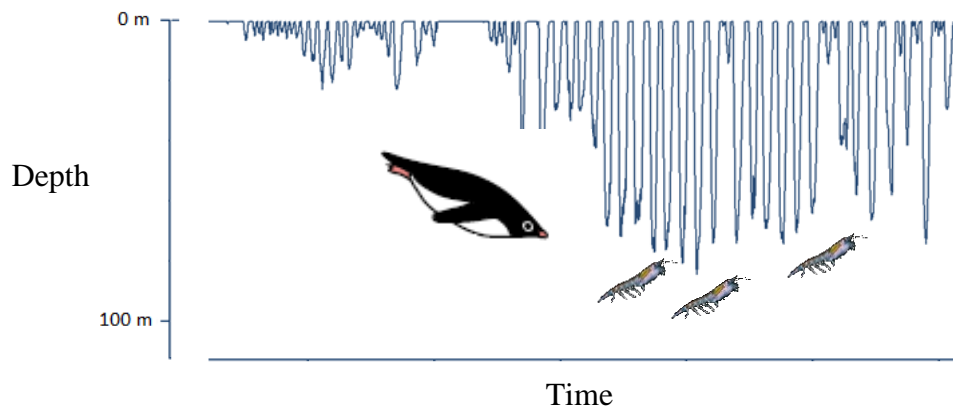


Figure 3: Diving profile of an Adélie penguin of the present study after ZOC.

2.4.3. Temporal organisation of dives : analyses of bouts, daily patterns and fractals

Marine mammals and seabirds dive in bouts, which correspond to sequences of multiple dives succeeding to each other over a certain period of time (Le Boeuf and Laws, 1994). Between two bouts, individuals can rest at the surface, on land, on sea ice or transit to other foraging areas (Le Boeuf and Laws, 1994). Bouts were defined here by a quantitative criterion based on post-dive intervals. A commonly used technique is the log survivorship analysis, which corresponds to a graphical method to specify the minimum interval separating bouts, also called the bout criterion interval (BCI) (Martin and Bateson, 1993).

Any gap less than BCI in length (short gaps) correspond to gaps between dives in a bout and all gaps greater than BCI are treated as between bouts intervals. In order to estimate the BCI, we plotted the cumulative frequency of gap lengths (surface duration) on a logarithmic scale against gap length. This technique is based on the assumption that both types of intervals are generated by two random processes with different rate constants. Basically, the log survivorship curve is supposed to have two portions: a rapidly declining part corresponding to the short gaps (between dives) and a slowly declining one representing longer gaps (between bouts). The point where these portions join can be considered as an objective quantitative criterion to specify the BCI (Martin and Bateson, 1993). To estimate the breakpoints, we used the ‘segmented’ package on R (Muggeo, 2015). From this bout definition, we could consider, for complete days only, the number of dives per day, the number of dives per bout, the number of bouts per day, the bout duration and the mean bottom duration per bout for each bird. Boxplots were firstly produced for each parameter of the bout analysis (number of bouts per day, number of dives per bout, mean bout duration, mean bout bottom duration, and number of dives per day). In order to compare the means for each parameter, as all samples were independent and come from normally distributed populations (Shapiro-Wilk test: $p\text{-value} > 0.05$), Student tests were used to compare the means of each parameter knowing that samples’ variances were unknown but equal (Fisher test: $p\text{-value} > 0.05$) and Welch tests were used in case of non-equal variances. The Bonferroni correction was applied to correct the level of significance because multiple comparisons were performed simultaneously. If an experimenter wants to do n comparisons and if the desired level of significance for the entire study is α , then the Bonferroni correction tests each comparison at a significance level of α/n (Bonferroni, 1935). Performing a bout analysis over the years permits to investigate changes in the organisation of the diving activity. In addition, some bout parameters have already been related to prey patch size and density and prey encounter rates (Boyd, 1996; Sommerfeld et al., 2015). Authors assumed that the prey patch is bigger when the number of dives within a bout increases. In the same way, small distances between dives within a bout are likely to reflect a higher prey patch density and the distance between bouts (i.e. the distance between two prey patches) can be linked to the prey encounter rate of the bird (Sommerfeld et al., 2015).

In parallel, we also examined the percentage of the number of dives and the mean depth reached during the day for each year using complete days only in order to investigate day/night patterns in diving behaviour. With diel migration, krill is known to come close to the surface at night (Kalinowski and Witek, 1980). Therefore, dives might be deeper during the day if they are targeting krill in open water. So, if the birds are foraging around ice, perhaps they might show shallower dives (targeting the krill near the underside of the ice), and maybe not show so much diurnal variation in their dive depth (because they are targeting krill at relatively constant depth under ice).

In addition, we used a fractal approach to measure the temporal complexity of dive sequences in relation with sea-ice conditions as an indicator of diving performance. A fractal is defined as a phenomenon that exhibits a repeating pattern at several scales (Mandelbrot, 1977). It is different from the other geometric figures because of the way in which it scales.

When zooming in, the same pattern appears over and over again as a reduced picture of the whole and each picture is connected to it by a scaling exponent, which is not necessarily an integer. Fractals are largely used in medical sciences (lungs and heart diseases, e.g. Shlesinger and West, 1991; Peng et al., 1993), geology (coastlines and rivers, e.g. Mandelbrot, 1977; Tarboton et al., 1988), astronomy (e.g. Heck and Perchang, 1991), meteorology (clouds and thunder structures, e.g. Lovejoy, 1985), but also in biology (plants, bacteria, e.g. Smith, 1984) and in various fields of ecology (study of corals, movement ecology and organization of behaviour, e.g. Bradbury and Reichelt, 1983; Riley and Turvey, 2002; Alados and Huffman, 2000). Fractal time series analyses concerning animal behaviour aim to describe the structure of behaviour as it occurs through time (Asher et al., 2009; MacIntosh, 2014). The resulting fractal index will be linked to the complexity of this behaviour. This approach helps to understand how interactions occurring between animal's behavioural strategies and their environmental conditions lead to the emergence of observed complexity signatures, which might reflect behavioural adaptations to environmental changes (Cribb and Seuront, 2016). We assume that when the environment changes towards greater heterogeneity, flexibility appears in the patterns of behaviour inducing a greater irregularity or stochasticity. This trend could show some adaptability of foraging strategies in relation with prey availability.

Following the method described by MacIntosh et al. (2013), we used the Detrended Fluctuation Analysis (DFA) approach to measure long-range dependence as an indicator of complexity in birds' diving sequences. We performed DFA using the 'fractal' package (Constantine and Percival, 2011) in R and this has been done in five main steps (Fig. 4).

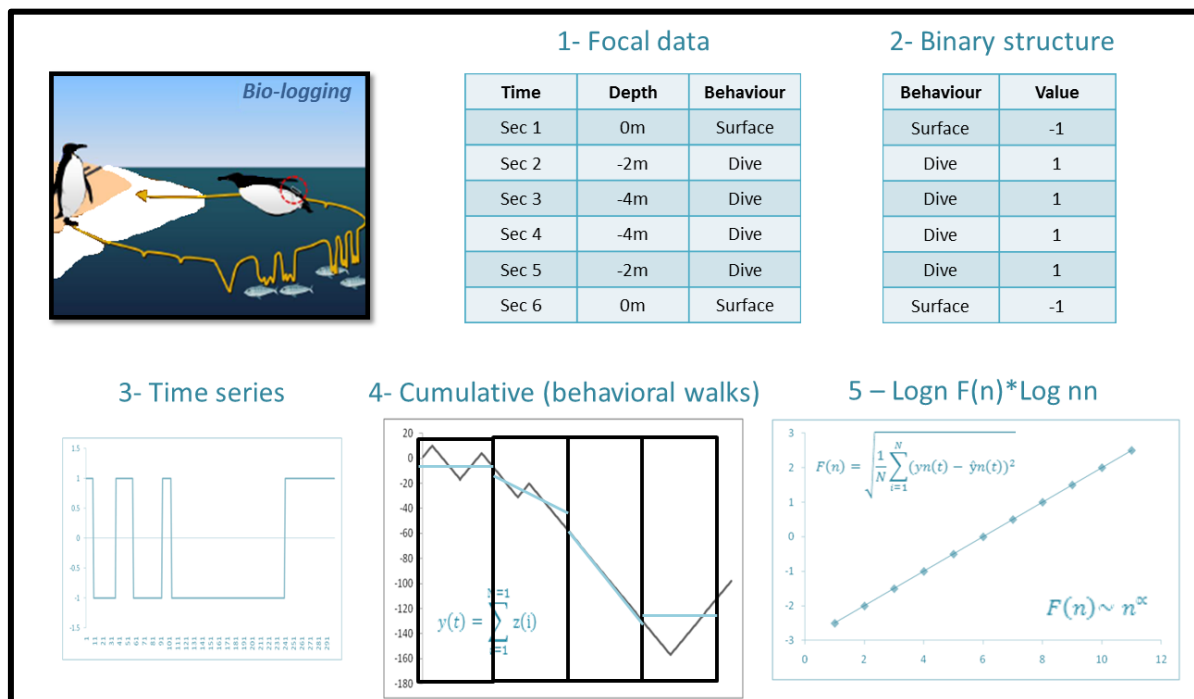


Figure 4: The calculation of the fractal index with the DFA method in five steps.

At first, dive sequences were coded as binary time series ($z(i)$) containing diving events (for which a value of 1 is attributed) and surface events (for which a value of -1 is attributed) (Fig. 4). Then, series were cumulatively summed ($y(t)$) (Fig. 4) meaning that for each second, we added $+1$ or -1 to the previous value. The next step consisted in estimating the scaling exponents (α DFA) of these sequences (Peng et al., 1992), which measures the degree to which time series are long-range dependent and statistically self-similar (Taqqu et al., 1995). In order to calculate this exponent, the cumulative curve of each bird was first divided into several time windows and for each segment, a local least-square regression line was fitted to the data by minimising the squared error (Fig. 4). Then the root-mean-square deviation (RMSE), the fluctuation, is calculated over each window (difference between predicted values and values actually observed). Different box sizes have been chosen and the previous process has been repeated over all window sizes. Then, a log-log graph of the fluctuation against the scale is constructed (Fig. 4). With the first scale (4s-window), the error is lower than with the next scale (8s-window) because the regression line best fits the data. This is why the relationship between the fluctuation F and the scale n is of the form: $F(n) \sim n^\alpha$, where α is the slope of the line on the double logarithmic plot of average fluctuation as a function of scale. When α DFA equals 0.5, this indicates a non-correlated, random sequence. As α DFA increases above 0.5, the diving sequence becomes more self-similar (indicating persistent long-range dependence) and the patterns over time are more predictable (Peng and Havlin, 1995). Theoretically, smaller values reflect greater complexity.

Values of α DFA are presented as mean \pm SE and a GAM was also performed to investigate the temporal variations in α DFA. The GAM was specified with a Gaussian family and 5 knots (121 values of α DFA).

2.4.4. Analysis of the diving parameters

From the dive profile, each dive was identified and different metrics were automatically calculated with a purpose-written macro in Igor Pro, for each dive deeper than 1m. Dives were cut into a descent phase, a bottom phase, where most of the prey hunting activity is known to occur in penguins (Kirkwood and Robertson, 1997; Ropert-Coudert et al., 2000; Ropert-Coudert et al., 2006), and an ascent phase (Fig. 5). Among the parameters automatically extracted by the macro, we principally investigated dive depth and duration, the two most basic parameters to study diving behaviour (Womble et al., 2013). However, other metrics were also calculated. The number of undulations, also called wiggles, is defined as the number of vertical undulations higher than 2m. Then, the bottom phase duration corresponds to the time spent between the first and the last time the depth change rate became <0.25 m/s during a dive (i.e. the time spent between the first and last wiggle). The post dive duration was also calculated, defined as the time at the surface (Fig. 5). The number of wiggles occurring during the bottom phase can be considered as a proxy of prey pursuit (Kirkwood and Robertson, 1997; Ropert-Coudert et al., 2001; Bost et al., 2007). This metric has been linked to foraging success and mass gain for king penguins (Hanuise et al., 2010).

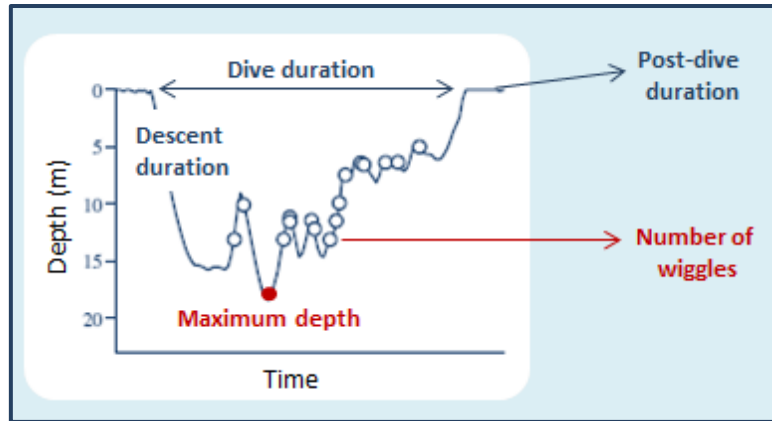


Figure 5: Presentation of the major diving metrics automatically extracted with IGOR Pro.

Indices can be developed as a combination of several of the basic, aforementioned diving metrics. A typical index, classically used in the literature, is the “diving efficiency” (Ydenberg and Clark, 1989) (Eq. 1). A second indicator was added, that we termed “TCPUE (Attempts of catch per unit effort)”, corresponding to pursuits per unit effort, an index which is close to the Catch per Unit Effort often used in fisheries science (Schaefer, 1954) (Eq. 2).

$$\text{Diving efficiency} = \frac{\text{Bottom duration}}{\text{Dive duration} + \text{Surface duration}} \quad (\text{Eq. 1})$$

$$\text{TCPUE} = \frac{\text{Number of wiggles}}{\text{Bottom duration}} \quad (\text{Eq. 2})$$

At first, a Principal Component Analysis (PCA) was performed to describe the relationships among diving parameters (Zimmer et al., 2011). PCA reduces the recorded variables to fewer ones in order to investigate the effects of sea ice only on these remaining variables. PCA corresponds to a multivariate technique in which observations are described by correlated quantitative variables (Husson et al., 2009). A principal axis corresponds to a linear combination of variables built on their correlation coefficients. On the variables factor map (variables represented by arrows), when the angle between variables is 180° , they are highly and negatively correlated, when it is $\pm 90^\circ$, the variables are totally independent from each other and when the angle is near 0° , they are highly and positively correlated. In addition, the higher a coordinate is (the closest to the circle), the better the variable is explained by the corresponding dimension. For all axes, the quality of representation of each variable can be assessed with the \cos^2 values, being higher with increasing \cos^2 values (in absolute values) (Husson et al., 2009). Diving metrics were analysed using the R package ‘FactoMineR’ with the function ‘PCA’ (Husson et al., 2009) on a dive-by-dive basis. The first thing to do was to decide which variable would be active or supplementary. Supplementary variables don’t take part in the distance calculations between individuals. They are included to illustrate the factorial axes. All the basic diving metrics were considered as active in this study as we are interested in diving profiles. The diving efficiency and the TCPUE indicators were set as supplementary variables but they indirectly take part in the construction of axes because they are a combination of basic metrics which are active. Sea-ice parameters truly constitute supplementary variables. All data were standardized because all variables were not stated in the same unit of measurement.

Then, boxplots were realized for each remaining diving parameters (maximum depth, descent rate, number of wiggles, post-dive duration, diving efficiency and TCPUE) and mean comparisons were performed using Welch tests (with the Bonferroni correction). Welch tests can also be used to compare the means of two groups under the assumption that both samples present a lot of observations ($n \gg 100$) and are random, independent and come from non-normally distributed populations (checked with a Shapiro-Wilk test). For all results, only the first trip of each bird was used and the overall significance level was set at 0.05.

In addition, linear mixed models (LMMs) were also performed on the diving metrics. The aim of a LMM is to study the connection between a dependent variable (response Y) and a set of explanatory variables (predictors $X_1 \dots X_k$) (Eq. 3).

$$Y = X.\beta + Z.\alpha + \varepsilon \quad (\text{Eq. 3})$$

where Y is the response vector, X is the matrix of covariates, β is a vector of unknown regression coefficients called the fixed effects, Z is a known matrix, α is the vector of random effects, and ε is a vector of errors (Jiang, 2007). Fixed effects factors have a finite number of levels that are well represented and random effects factors correspond to factors that include data which represent only a sampling of the possible levels of the factor (Zuur et al., 2007). A mixed model combines both fixed and random effects.

LMMs are particularly useful when the data have a hierarchical form, such as in longitudinal data, involving repeated observations of the same variables over long periods of time, with the possibility to include both fixed and random coefficients together with multiple error terms (Zuur et al., 2007). Longitudinal data have a hierarchical structure that can introduce correlations for the observations within a subject. Indeed, when measures are repeated for each individual, there might be some dependence between each observation. Random effects determine the structure of these correlations. The model offers the possibility to choose between a random intercept model (same slope for all birds) or a random intercept and slope model (both can vary among birds). For all diving parameters, a random intercept and slope model was performed assuming that the relationship between each metric and sea ice is different for each bird. Therefore, the effects of sea-ice parameters on each diving parameter could have been tested including the identification number of each bird in the random effect.

Several correlation structures could have been tested for each model in relation with the idea that a dive can impact the following ones, but R memory limitations prevented us from testing this. The compound symmetry and the first order auto-regressive (AR1) structures could have been chosen here, even if the first order auto-regressive structure seems more adapted to longitudinal data (Zuur et al., 2007). Compound symmetry refers to a special case of a variance covariance matrix (uniform correlation), assuming constant variance and that all within-subjects correlations are equal, and the AR1 structure is a model in which we use a linear model to predict the value at the present time using the values at previous time points: $x(t) = \phi_1 * x(t-1) + \delta + w$ (Appendix III).

When data were normally distributed, which was the case for most of the metrics, the estimation of the different parameters was done using the Maximum Likelihood method (ML) and the Restricted Maximum Likelihood method (REML). The method adopted here was: (i) search for the optimal random structure between a random intercept model or a random slope and intercept model (using the AIC criterion to compare models fitted on the same data) (ii) select the optimal fixed components (sea-ice variables) to consider in the model using the AIC criterion with the ML method (iii) present the estimated parameters and other results of the optimal model using the REML method. For mixed models, the R^2 can be divided in two components. The marginal R^2 (R^2_m) describes the proportion of variance explained by the fixed factor(s) and the conditional R^2 (R^2_c) the one explained by both the fixed and random factors. When data were not normally distributed (Generalized Linear Mixed Models GLMMs), we performed models using the *Bobyqa* optimizer. LMMs were performed using the *lme* function of the R package ‘nlme’ (Pinheiro et al., 2016) (Appendix IV).

Diving efficiency, descent rate and TCPUE were analysed in a LMM with a normal error distribution. To test for differences in the maximum depth and the post-dive duration between sea-ice conditions, a LMM with log10 transformed response values was applied. The number of wiggles was analysed in a GLMM with a Poisson error distribution.

2.4.5. Methodological comments on diving data

It is necessary to note the differences in sampling interval of the loggers used (5s in 1995 and 2007 and 1s for all other years) (Table 2). These differences introduce a bias in the analysis of the diving parameters, above all those that are using durations in their calculation. Measuring one value every 5s instead of 1s implies that the very short and very shallow dives are missed.

Because some analyses might not be reliable for these two years, we chose to adjust the protocol for each analysis. Two main options were adopted: (i) exclude 1995 and 2007 from the analyses and (ii) keep 1995 and 2007 in the dataset but only select the deep dives (>15m deep) because the diving parameters won't be too much affected by the differences in sampling interval for these dives. This 15 meters threshold was extracted from the dive depth – dive duration graph applied to all years. The cloud of points has two main portions and the technique assumes that deep dives (i.e. foraging dives) and surface dives (i.e. transit or resting dives) emerge from different processes.

This strategy to try both methods has been applied for all the diving metrics' analysis and the day/night patterns. The influence of different sampling intervals has been shown to have little, if no, influence on the DFA analysis (Macintosh et al., 2013). This is the reason why all years (9 years) have been considered in the fractal analysis (complexity of behavior). For the bout analysis, because considering deep dives only has no sense (just like for the fractals), the choice has been made to exclude 1995 and 2007 from the analysis. Options chosen for each analysis are presented in Table 3.

Table 3: Presentation of the methods chosen for each analysis.

Data	Analysis	Comments
Breeding success	GAM	-
Diving metrics	PCA (variables selection)	7 years all dives and 9 years deep dives
	Exploratory graphs	7 years all dives and 9 years deep dives
	Mean comparisons	7 years all dives and 9 years deep dives
	Mixed models	7 years all dives and 9 years deep dives
Fractals	DFA	9 years all dives (not biased)
Bout analysis	Exploratory graphs	7 years all dives
	Mean comparisons	7 years all dives
Day/night patterns	Exploratory graphs	7 years all dives and 9 years deep dives

3. Results

3.1. Temporal dynamics of sea ice in the Dumont D'Urville Sea

In this section, the different sea-ice conditions over the years will be examined. Sea-ice concentration changed drastically among years but also within year. A season starting with heavy ice can end up with no ice, which was for instance the case of the season 1995-1996 (Fig. 6).

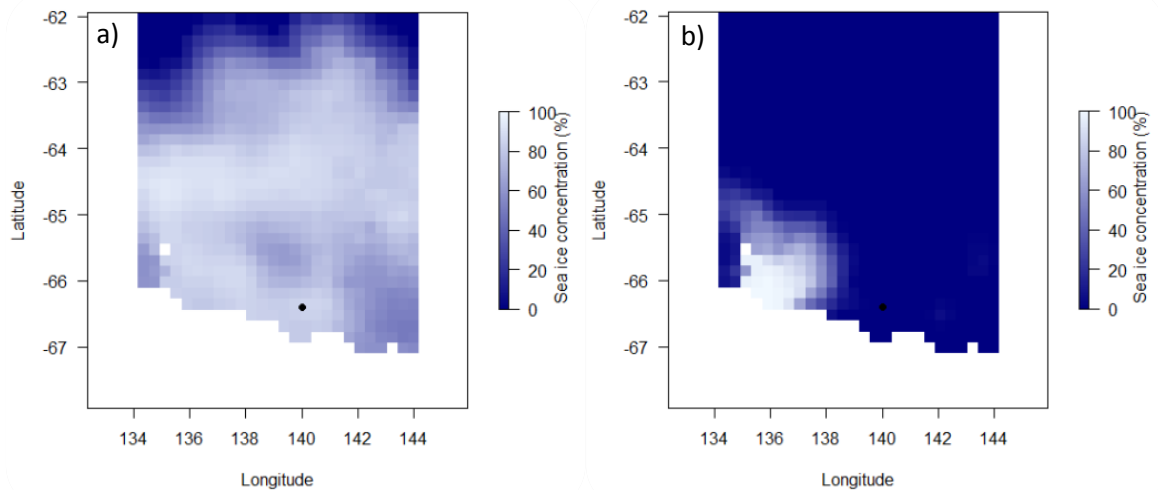


Figure 6: Maps of sea-ice concentration in the Dumont D'Urville area for two different days within the same season 1995-1996: a) 01/11/1995 and b) 31/01/1996. White represents sea ice and dark blue represents open water.

Daily sea-ice concentrations and sea-ice extents concerning the days when diving data were recorded showed very contrasted conditions among years (Fig. 7a). The evolution of the distance between the colony and the open water shows how far the ice edge was at the beginning of each season and how it decreased differently during the summer for each year (Fig. 7b).

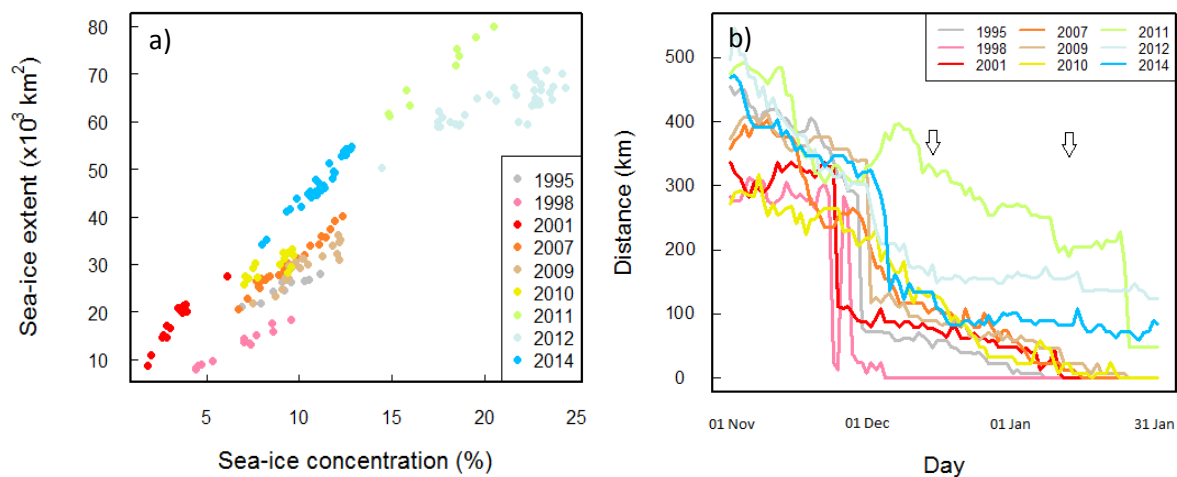


Figure 7: Sea-ice parameters over the years concerning a) the relationship between sea-ice extent (km^2) and sea-ice concentration (%) and b) the evolution of the distance colony-open water over the season (diving data concerning guard stage are available for the period between the two arrows).

The first graph permits to identify 1998 and 2001 as low sea-ice coverage years. In contrast, 2011 and 2012 were considered as years of high sea-ice coverage (Fig. 7a) with open water being far from the colony over the whole seasons (Fig. 7b). For all years, sea-ice concentration was strongly correlated with sea-ice extent (R^2 between $[0.508, 0.976]$, p-value $< 2.10^{-16}$) (Table 4).

Table 4: Correlation parameters of the relationship between SIE and SIC for all years.

Year	<i>SIE vs SIC (SIE=a*SIC+b)</i>			
	B	A	R^2	p-value (t)
1995	9740.38	1660.99	0.885	$< 2e-16$
1998	-834.11	2038.79	0.976	$< 2e-16$
2001	3560.00	4322.10	0.913	$< 2e-16$
2007	2065.50	2989.97	0.964	$< 2e-16$
2009	5718.00	2336.00	0.742	$< 2e-16$
2010	14123.40	1840.80	0.627	$< 2e-16$
2011	11508.12	3353.85	0.966	$< 2e-16$
2012	37452.00	1262.00	0.508	$< 2e-16$
2014	-3571.5	4514.7	0.908	$< 2e-16$

This strong positive relationship was observed only for these two sea-ice parameters. When the distance between colony and open water or polynyas was involved, the relationship was not that strong. Five polynyas were identified over the years. However, the resolution did not enable us to detect smaller polynyas that could be close to the colony, which could potentially contribute to the food availability of Adélie penguins.

3.2. Inter-annual variations in breeding success in relation with sea ice

For the whole period of interest (1995-2014), breeding success values were highly contrasted, ranging from 0 in 2013 to 1.336 in 1995. However, two seasons were very specific and deserved a closer inspection. The breeding season 2014 had intermediate sea-ice

concentration values but in January/February, sea ice took a long time to retreat. The distance between the colony and the open water was still around a hundred kilometers at the end of January (Fig. 7 b). In addition, there were a lot of snow events in December and only few sunny days (Reports from the overwintering teams of the Terres Australes et Antarctiques Françaises). All this can explain the relatively low breeding success in 2014 (around 0.3). Therefore, a generalized additive model (GAM) was fitted to the time series of breeding success with and without 2014 (Fig. 8 a and b). In addition, the low sea-ice value in 2001 resulted from the unusual presence of a huge iceberg in the Ross Sea, covering 11 000 km², that clearly affected Adélie penguins. As such, a GAM was also performed with and without 2001 because adding or not this year clearly changed the shape of the GAM (Fig. 8 a and c). Naturally, the model excluding both years (2001 and 2014) has also been done (Fig. 8 d).

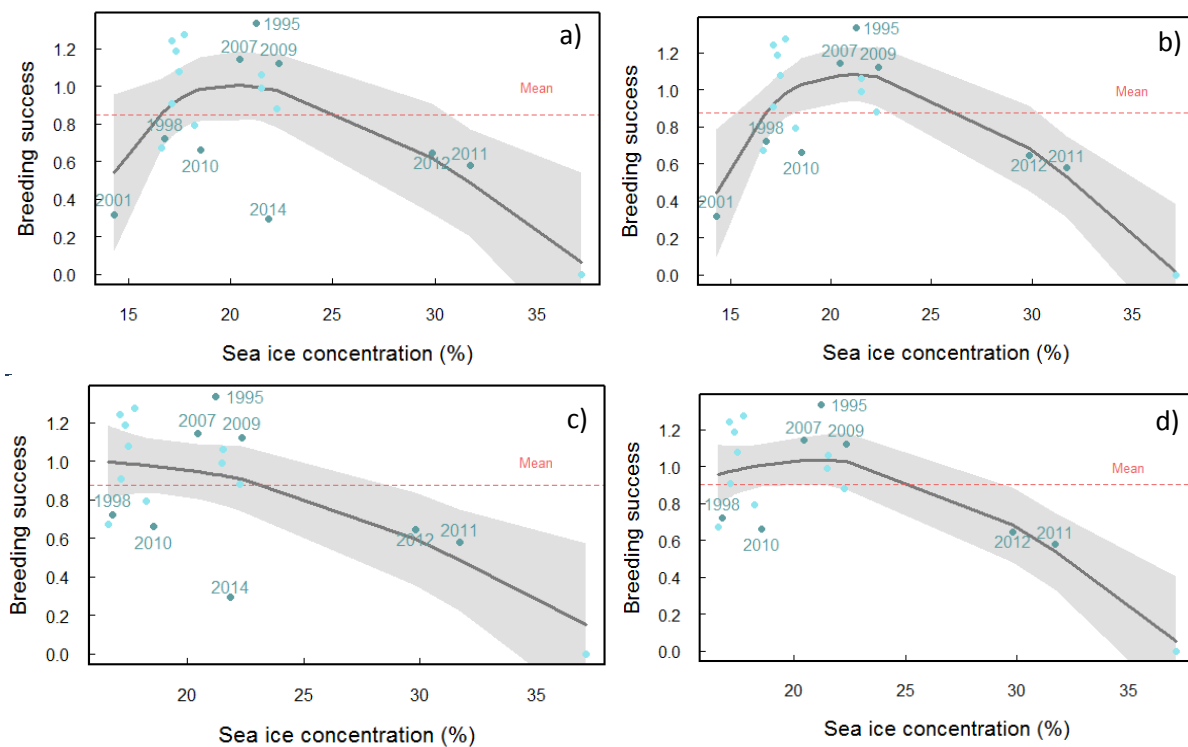


Figure 8: Fitted GAMs results concerning Adélie penguins' breeding success showing: a) the GAM fitted on all years, b) the GAM fitted on all years except 2014, c) the GAM fitted on all years except 2001 and (d) the GAM excluding both 2001 and 2014. Shades indicate 95% confidence intervals. Dark dots represent the studied years and light dots correspond to added data concerning the period of interest 1995-2014.

The effect of sea-ice concentration was significant for all models. The model excluding 2014 had the best fit (Adjusted $R^2 = 0.643$, p -value < 0.001) (Fig. 8 b; Table 5). In addition, the model including all years had nearly the same shape (Adjusted $R^2 = 0.426$ and p -value = 0.0119) (Fig. 8 a; Table 5). In contrast, the model excluding 2001 showed the lowest adjusted R^2 value (Adjusted $R^2 = 0.395$; p -value < 0.01) (Fig. 8 c; Table 5). The trend of this GAM suggests that the curve we observed with the two previous models is driven by a single point on the bottom-left corner, corresponding to the year 2001. Finally, the model excluding all years gives nearly the same shape (Adjusted $R^2 = 0.596$; p -value < 0.001) (Fig. 8 d; Table 5).

Table 5: Results of fitted GAMs on breeding success.

GAM (5 knots)	Gam fitted on breeding success		
	F-test	Adjusted R ²	p-value
All years	4.99	0.426	0.012
Without 2014	10.12	0.643	4.12*10 ⁻⁴
Without 2001	5.71	0.395	9.58*10 ⁻³
Without 2001 and 2014	11.48	0.596	5.91 * 10 ⁻⁴

3.3. Influence of sea ice on the diving activity

3.3.1. Modifications in diving rhythm

In total, the first trip of each bird across all years amounted to 180 000 dives being analysed. Investigating the effects of sea ice on the organisation of dives appears as the first step of the diving activity analysis. It concerns here the complexity of the behavior (at the scale of the foraging trip), the bout analysis (sequences of successive dives) and the organisation of dives during the day. Birds were expected to differ in temporal organisation of foraging behavior according to changes in the environment between years (Fig. 9).

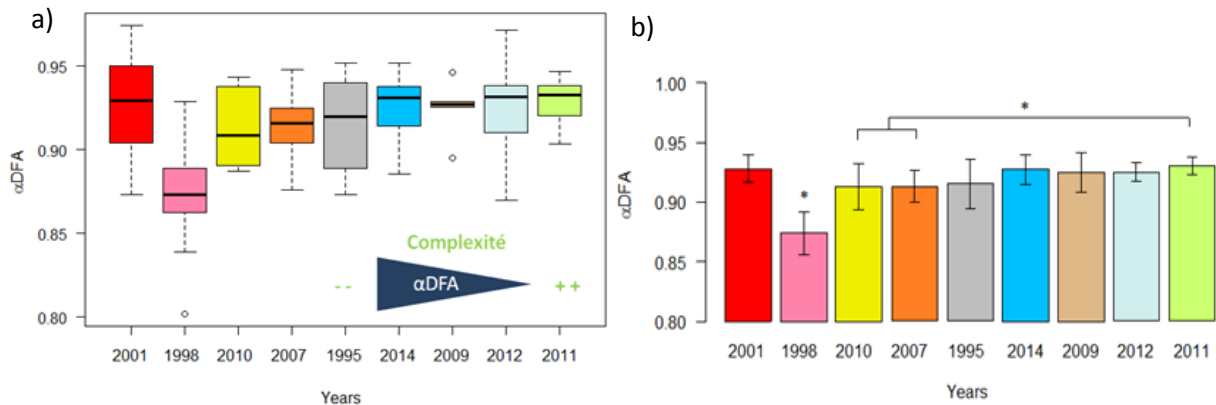


Figure 9: Results of the fractal analysis performed on all years considering all dives: a) boxplots of α DFA according to years classed by increasing sea-ice concentration and b) barplot for mean comparisons (t-test). Vertical bars height corresponds to the mean. Results are given for 9 years considering all dives.

Except for the year 2001, α DFA increases along the sea-ice concentration gradient, revealing a decrease in the complexity of the diving behavior (Fig. 9 a and b). In other words, diving sequences were characterized by higher degrees of long-range dependence when the sea-ice cover was important (i.e. dive and post-dive times of a given length are more likely to be followed by dive and post-dive times of a similar length). The highest value recorded was attributed to 2011 (0.9300 ± 0.0036) and the lowest one to 1998 (0.8739 ± 0.0090). The year 2001 presents values that significantly depart from this trend (0.9280 ± 0.0058) (t-test: p-value < 0.001) considering the low sea-ice concentration for this year. The global trend observed has been confirmed by the GAM performed on α DFA values (Fig. 10).

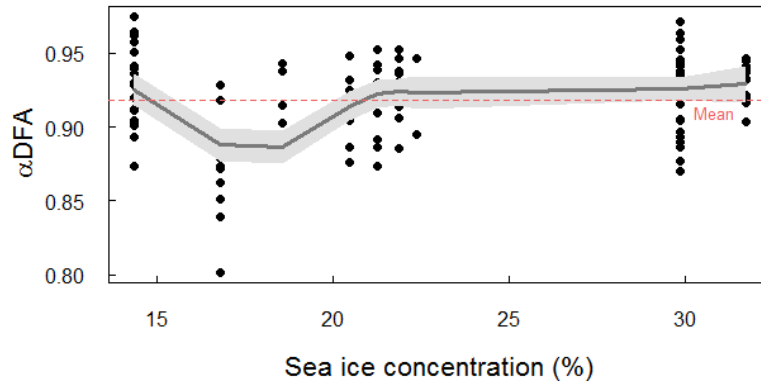


Figure 10: GAM performed on α DFA values according to sea-ice concentration concerning all years.

Results have shown that the effect of sea-ice concentration is significant (F-test=10.09, Adjusted $R^2=0.322$, p-value <0.001). Findings confirm the increase in α DFA from the year 1998 (around 17% of SIC) and the presence of high values for the year 2001 (around 14.30% of SIC).

Concerning the bout analysis, a total of 3310 bouts were identified over the nine years, according to the BCI values, which are ranged between 168.2s and 247.5s. Years with intermediate sea-ice concentrations, i.e. around 20%, were characterized by lower number of dives per day and lower number of bouts per day (Student test: p-value > 0.05) (Fig. 11).

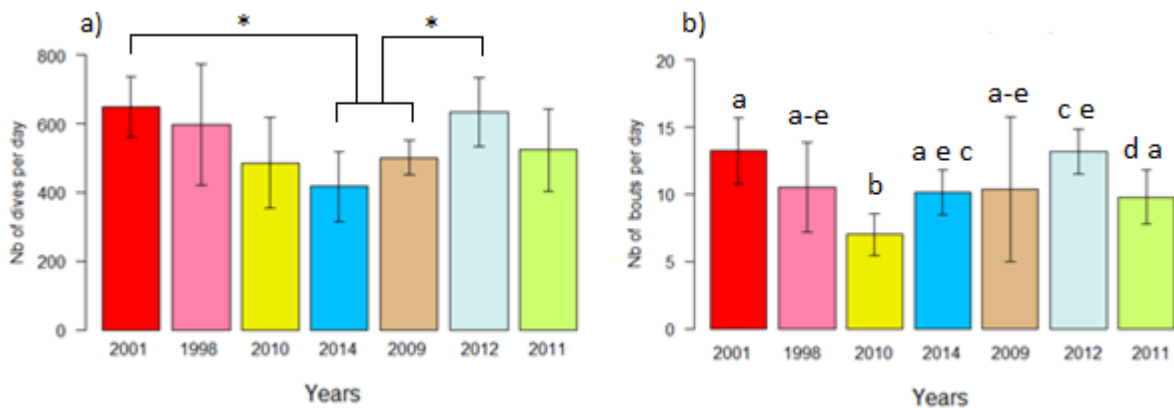


Figure 11: Barplots of a) the number of dives per day and b) the mean number of bouts per day, according to years classed by increasing sea-ice concentration. Vertical bars height corresponds to the mean. Results are given for 7 years considering all dives.

Concerning the number of dives per day, 2001 and 2012 showed the highest values (with 649.91 ± 43.93 and 633.70 ± 50.33 , respectively). The lowest number of dives per day was attributed to the year 2014 (417.22 ± 50.76). For the number of bouts per day, 2001 and 2012 possessed the most elevated values (with 13.22 ± 1.23 and 13.18 ± 0.85 , respectively) and the year 2014 showed the lowest value (6.99 ± 0.78). Concerning the number of dives per bout, some differences between years were significant but the trend observed is difficult to describe. However, no trend was observed for the bout duration and the bout bottom duration.

Finally, concerning the day/night analysis, during intermediate years (2007, 1995 and at a lesser extent 2014), birds performed dives at any time of the day, i.e. dives were homogeneously distributed over 24 hours (Appendix V). In addition, in 2011 and 2012 (years

of extreme sea-ice cover), birds dove deeper during night time (between 1900 and 0400 hours) but it was not statistically tested. In contrast, no daily pattern in dive depth was found for birds during years of low SIC and intermediate years. For deep dives (i.e. foraging dives), we observed that during intermediate sea-ice conditions, birds also dove at any time of the day. In contrast, for extreme sea-ice conditions, more foraging dives were performed during night time (Appendix V). However, no daily pattern was observed for maximum depth considering deep dives.

3.3.2. Variations in diving metrics

The next step consisted in analysing the diving metrics. Results of the PCAs performed on the diving metrics are given in Fig. 12.

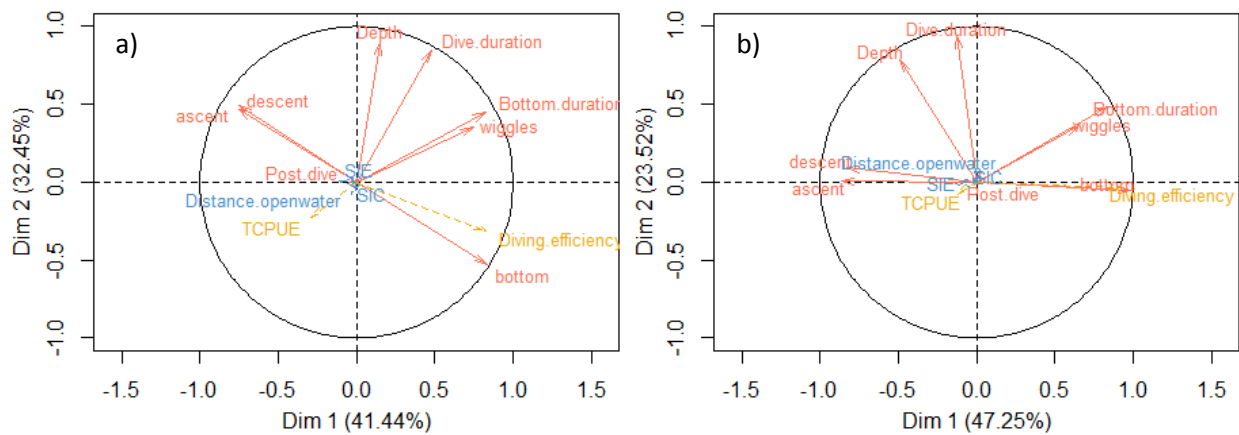


Figure 12: Variables factor maps of the PCAs performed on diving parameters for (a) 7 years all dives and (b) 9 years deep dives. Orange variables correspond to active variables; yellow variables refer to supplementary variables and the blue ones to supplementary sea-ice parameters.

Concerning the PCA performed on 7 years with all dives, the eigenvalues indicated that the first two axes accounted for 73.9% of the total variance, while the PCA performed on all years with deep dives only, the first two axes accounted for 70.77% (Fig. 12 a and b). As both PCAs gave similar results, the choice has been made to present the detailed results for the first PCA only (made on 7 years only). The bottom duration, the percentage of the bottom duration and the number of wiggles were the parameters the most involved in the construction of the first axis, with 0.83, 0.82 and 0.75 correlation coefficients respectively; accompanied by the percentages of the descent and ascent phases on the left side, presenting a correlation coefficient of 0.75 each. The parameters the most correlated to the second axis were the maximum depth and the dive duration, with a coefficient of correlation of 0.90 and 0.85, respectively. In addition, according to the length of arrows, the diving efficiency was quite well represented compared with the TCPUE ($\cos^2=0.688$ and $\cos^2=0.086$, respectively). The individuals showing higher diving efficiencies corresponded to birds that spent long periods at the bottom phase of dives, with a lot of wiggles, which is reflecting the way the diving efficiency is calculated (Eq. 1). On the opposite, TCPUE was associated with a lower number of wiggles and higher descent and ascent rates. Using the results of the PCAs (i.e. considering all correlation coefficients), some relevant metrics were chosen on an ecological basis to

investigate the effects of a sea ice only on these remaining variables. All further analyses were therefore conducted on the following selected variables only: maximum depth, number of wiggles, post-dive duration and descent rate, as well as diving efficiency and TCPUE. An example of a strong correlation between two variables is given for the relationship between dive depth and duration, for which a linear model was fitted for each year ($p\text{-values} < 2.10^{-16}$; $R^2 > 0.685$) (Appendix VI).

Then, an exploratory analysis was performed on this selection of variables in order to link the diving metrics with sea ice. The majority of dives were shallower than 5 meters and the maximum dive depth recorded was 139.7 meters. Results are indeed given for mean number of wiggles, mean of maximum depth, mean post-dive duration, percentage of descent phase duration, diving efficiency and TCPUE for both options : (i) considering 7 years with all dives (Fig. 13) and (ii) considering 9 years with deep dives only (Fig. 14).

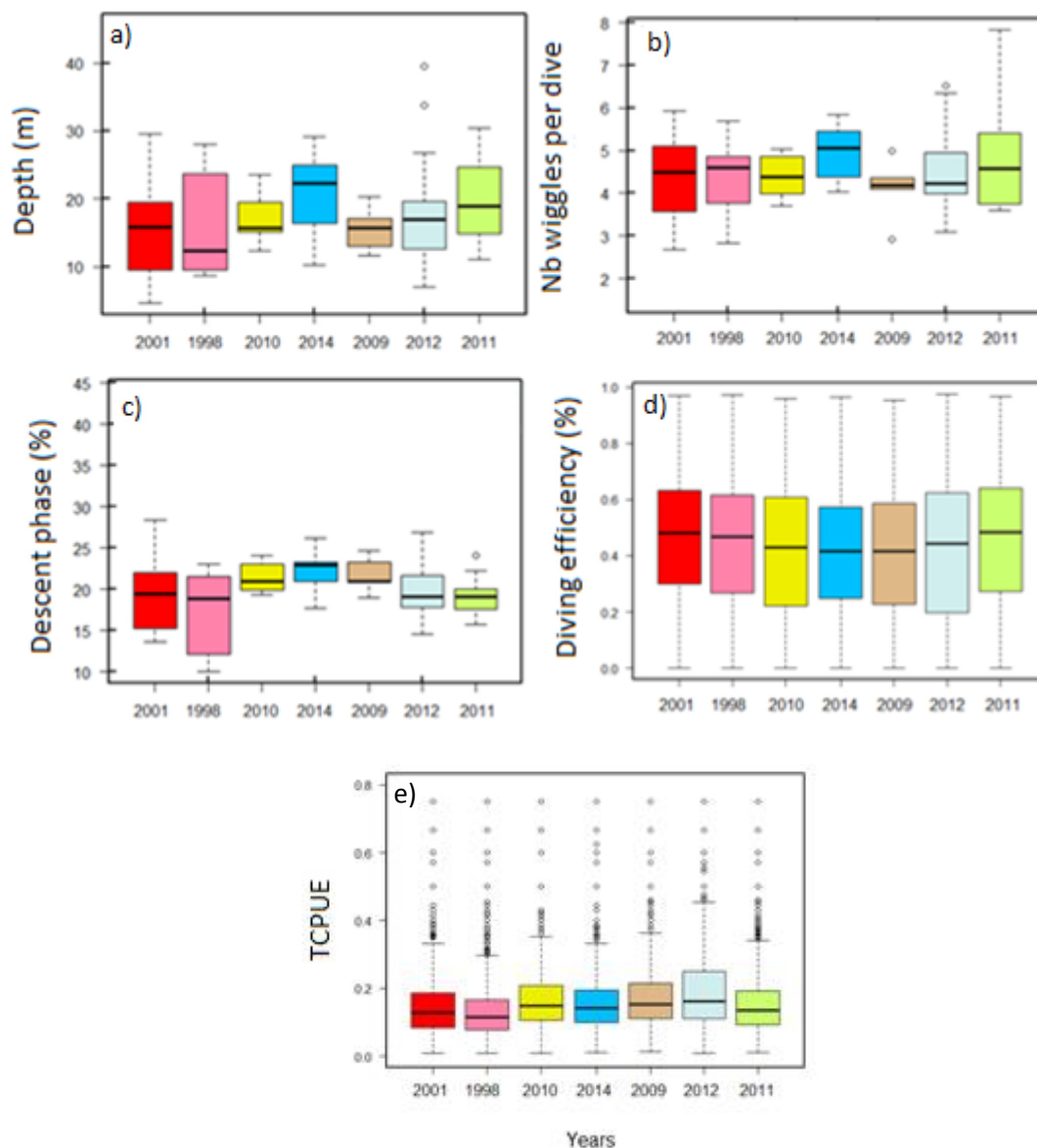


Figure 13: Boxplots of a) maximum depth, b) number of wiggles, c) descent phase, d) diving efficiency and e) TCPUE; according to years classed by increasing sea-ice concentration. These boxplots were made using 7 years and considering all dives.

For the maximum depth, the highest values have been recorded for intermediate years (2010, 2014 and 2009) with a mean of 17.26 m \pm 0.32, 20.00 m \pm 0.16 and 15.92 m \pm 0.32, respectively (Fig 13 a). The lowest values were attributed to the years 2001 and 2012, with a mean of 13.93 m \pm 0.12 and 13.83 m \pm 0.08, respectively. Welch tests revealed that the trends observed on the boxplots are significant. The same conclusions could be done for the descent rate, with a mean of 0.171 % \pm 0.002 in 2010, 0.203 % \pm 0.001 in 2014 and 0.179% \pm 0.002 in 2009 (Fig. 13 b). Concerning the number of wiggles, it looks like intermediate years are different but Welch tests revealed that there is no significant trend (Fig. 13 c). The difference between 2001 and 2010 was not significant ($t=-1.7908$, $df=8109.99$, $p\text{-value}=0.0734$), such as the difference between 2009 and 2012 ($t=-0.5818$, $df= 5991.92$, $p\text{-value}=0.5607$). Considering all dives, no trend could be confirmed for this parameter. The lowest diving efficiencies have been recorded for 2010, 2014 and 2009, with a mean of 0.454 \pm 0.003, 0.436 \pm 0.002 and 0.434 \pm 0.003, respectively (Fig. 13 d). The only comparisons which were not significant concerned the years 2001 and 2011 ($t=-0.8933$, $df=48385$, $p\text{-value}=0.3717$) and the years 2009 and 2010 ($t=-1.6458$, $df=11002.4$, $p\text{-value}=0.099$). Therefore, the trends observed were confirmed thanks to Welch tests. Finally, for the TCPUE, no trend could be found (Fig. 13 e).

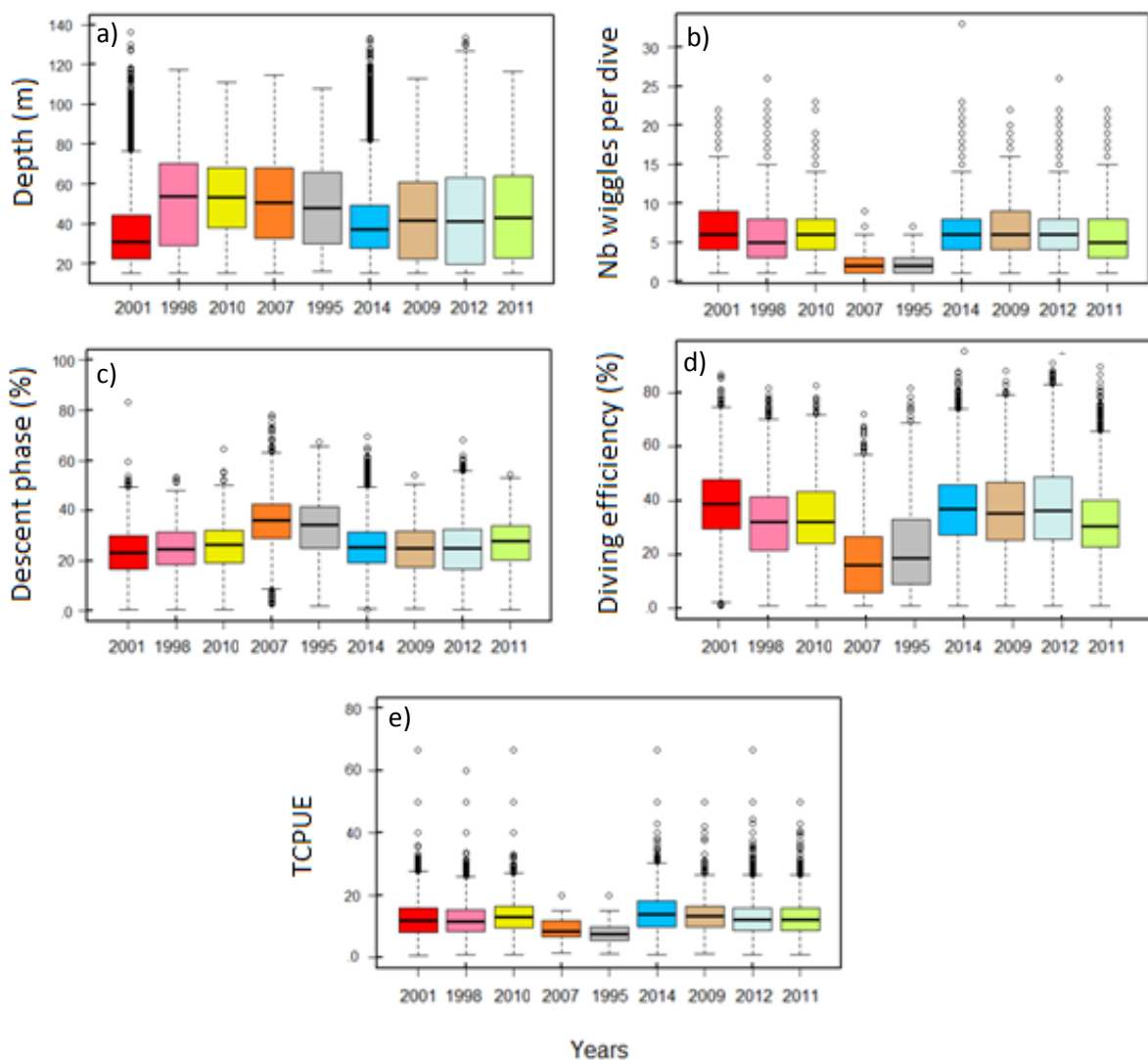


Figure 14: Boxplots of a) maximum depth, b) number of wiggles, c) descent phase, d) diving efficiency and e) TCPUE; according to years. Boxplots were made with 9 years considering deep dives only.

Considering all years with deep dives only, Welch tests showed that intermediate years (above all 1995 and 2007) were always significantly different from the others (p -values < 0.00139). This could be seen in terms of mean maximum depth ($50.62 \text{ m} \pm 0.56$ and $51.48 \text{ m} \pm 0.37$, respectively), mean number of wiggles per dive (2.18 ± 0.03 and 2.26 ± 0.02 , respectively) percentage of descent phase duration ($35\% \pm 0.002$ and $36\% \pm 0.002$, respectively), but also diving efficiency ($22\% \pm 0.003$ and $17\% \pm 0.002$, respectively) and TCPUE ($8.65\% \pm 0.1$ and $9.73\% \pm 0.1$, respectively) (Fig. 11). In other words, considering deep dives only (i.e. foraging dives), intermediate years were characterized by deeper dives, greater ascent, descent and post-dive durations and lower time spent at the bottom phase of the dives, lower number of wiggles, diving efficiency and TCPUE (Fig. 14).

The last parameter, which is the post-dive duration, needed closer investigation. This diving metric has been divided in two components: the post-dive duration considering dives within bouts only (post-dive duration $< \text{BCI}$) and the post-dive duration considering dives between bouts only (post-dive duration $> \text{BCI}$) (Fig. 15 a and b).

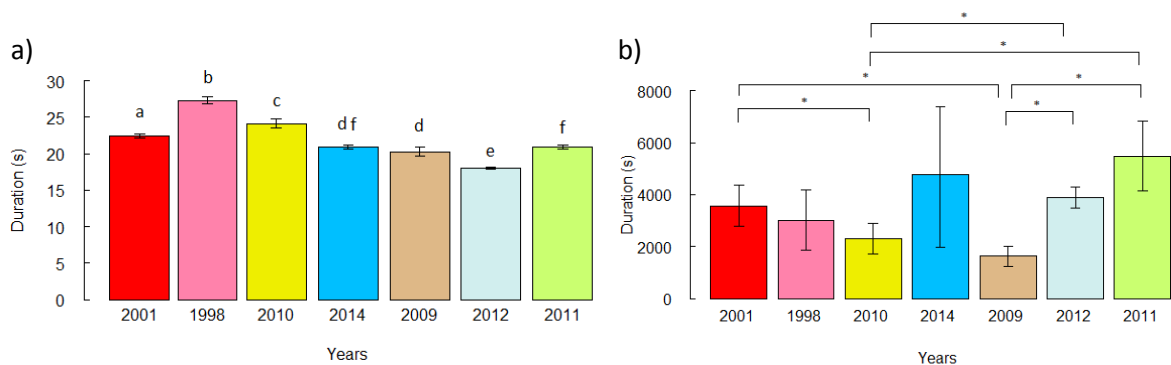


Figure 15: Barplots representing the post-dive duration across years considering a) dives within bouts only (post-dive duration < 207.7 s) and b) dives between bouts only (post-dive duration > 207 s).

Concerning the post-dive duration within bouts, the trend is difficult to describe (Fig. 15 a). The year 2010, as an intermediary year, is characterized by a high post-dive value compared to extreme years, with a mean of $24.13 \text{ s} \pm 0.32$). On the opposite, the year 2012 presents the lowest value for this parameter, with $18.07 \text{ s} \pm 0.07$). Results are more mitigated for 2014 and 2009, with a mean of $20.92 \text{ s} \pm 0.15$ and 20.28 ± 0.30 , respectively). However, for the post-dive duration between bouts, it appeared that lower values can be attributed to intermediate sea-ice conditions (Fig. 15 b). This is especially the case of 2009 and 2010 (with a mean of $1623.31 \text{ s} \pm 187.30$ and $2317.66 \text{ s} \pm 292.49$, respectively). These values are significantly different from the values obtained for extreme years (Welch test: p -value < 0.00238). The year 2011 present the highest value of high coverage years, with $5470.49 \text{ s} \pm 670.80$ and 2001 the highest value of low coverage years, with $3560.63 \text{ s} \pm 395.38$.

All mixed models tables and residuals are presented in [Appendix VII and VIII](#). In this section, the most relevant model for each parameter was selected (Fig. 16 and 17; Table 6). Because considering all dives for some parameters has no sense, the models selected for all parameters considered only the deep dives (i.e. foraging dives).

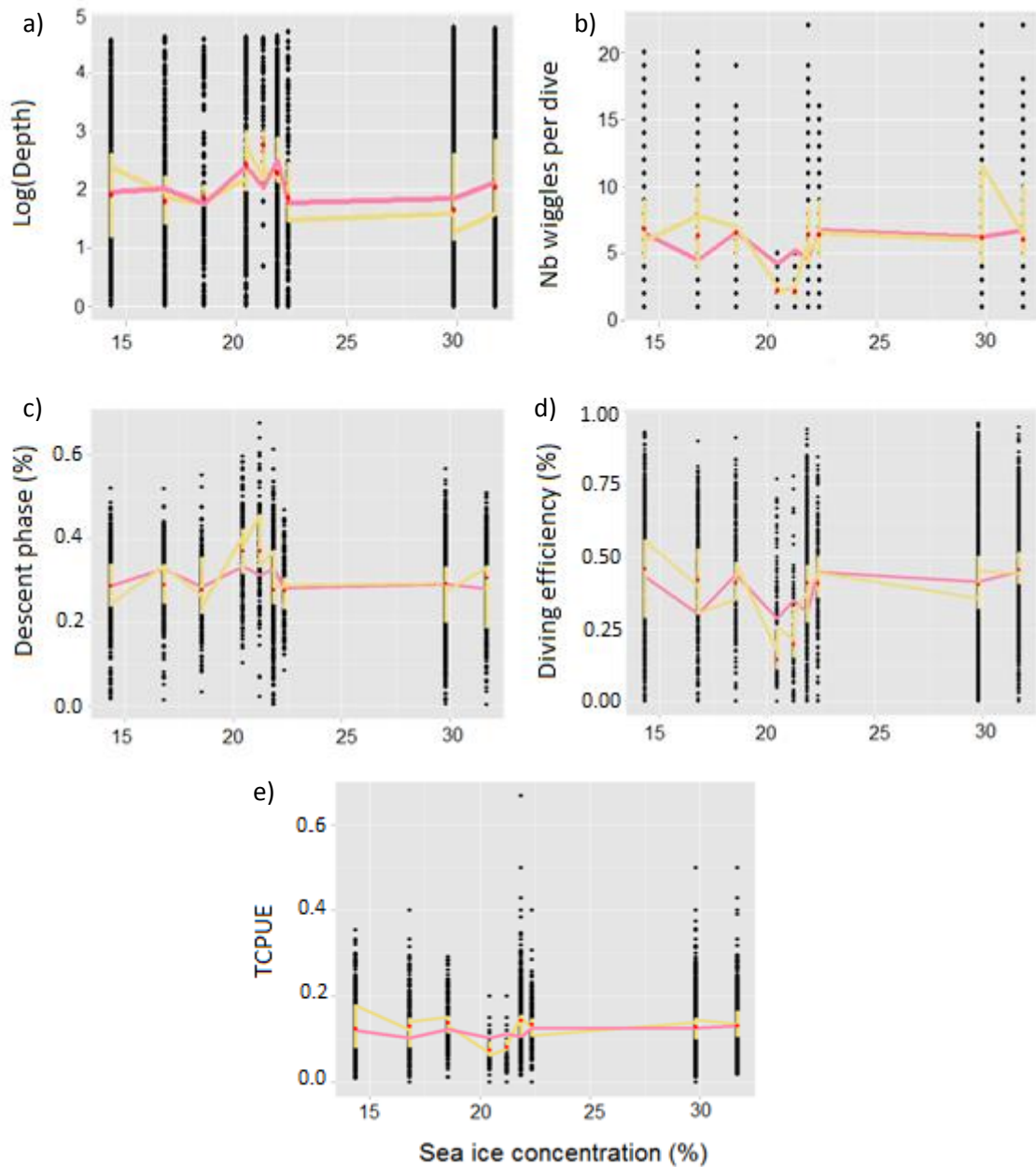


Figure 16: Results of the mixed models for each parameter according to sea-ice concentration: a) maximum depth (9 years deep dives), b) number of wiggles (9 years deep dives), c) descent rate (9 years deep dives), d) diving efficiency (9 years deep dives) and e) TCPUE (9 years deep dives). The fixed part is represented in pink and the random part in yellow.

All mixed models confirmed the findings revealed by the exploratory graphs and the mean comparisons, both with the fixed part (representing sea-ice parameters) and the random part (representing the individual variability) (Table 6).

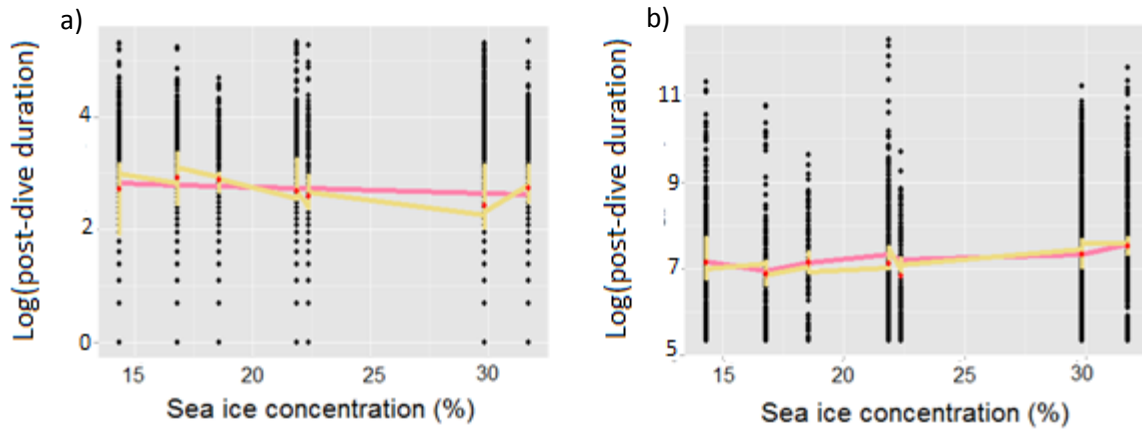


Figure 17: Results of the mixed models for the post-dive duration concerning: a) dives within bouts (post-dive duration <207.7 s), b) dives between bouts (post-dive duration >207.7 s), according to the sea-ice concentration gradient. The fixed part is represented in pink and the random part in yellow.

With the mixed model, we could not confirm the trend observed for the post-dive duration analysis which considers only the dives within bouts (Fig. 17 a). However, it looks like the trend observed for the post-dive duration considering the dives between bouts has been confirmed by the mixed model as well (Fig. 17 b).

Table 6: Results of the main mixed effects models for each metric.

Chosen models	Significant explanatory variables	R ² c	R ² m	AIC	p-values
Maximum depth					
9 years deep dives	SIC	0.417	0.0597	1442.75	0.0010
Diving efficiency					
9 years deep dives	SIC SIE	0.2780	0.0758	-8917.093	0.0094 <0.0001
Descent rate					
9 years deep dives	SIC SIE	0.2623	0.0463	-15540.09	0.0463 0.0001
TCPUE					
9 years deep dives	SIC SIE	0.1571	0.0287	-20224.61	0.0012 0.0034
Number of wiggles					
9 years deep dives	SIC SIE	0.4156	0.1133	35367.23	<0.0001 <0.0001
Post-dive duration					
7 years all dives within bout	SIC	0.101	0.006	19273.06	0.0301
7 years all dives between bouts	SIC Distance open water	0.1266	0.0091	10165.69	0.0027 0.0156

The trends observed with the boxplots and the mean comparisons were confirmed for all parameters except the post-dive duration (dives within bouts only) both with the random and the fixed part, showing different values for intermediate years. The sea-ice concentration

appears to be significant for all selected models (p-value<0.05) (Table 6). In addition, except for the post-dive duration, the fixed part largely contributed to the variability compared to the random part, which is however non-negligible.

4. Discussion

Our study showed that foraging strategies and breeding success of Adélie penguins changed according to a key environmental variable: sea ice. Guard stage is a critical breeding stage for adults because their foraging activity depends not only on their own energetic requirements (to forage, to ensure their basal metabolism and to restore their body condition from the long trips of incubation) but also on the energy demand of the chicks (Charrassin et al., 1998). Because at this stage, the extent of the foraging area is smaller (shorter trips) than during other stages, the foraging activity of Adélie penguins reflects local conditions.

4.1. An optimal range of sea-ice cover at the seasonal scale

Concerning breeding success, which is measured at the seasonal scale, our results corroborate those of Barbraud et al. (2015) and show that there is an optimal range of sea-ice concentration concerning Adélie penguins' breeding success. Ainley (2002) already suggested the idea that there could be a "perfect" sea-ice cover for Adélie penguins. On the one hand, as there is considerable evidence that krill feeds on under-ice communities (microalgae) but that its abundance is low where sea ice is at its maximal extent (Nicol, 2006), we can assume that there is an optimal density of krill in relation with sea-ice coverage (Flores et al., 2012). On the other hand, foraging costs of chick-rearing adults increase when sea-ice cover is extreme, forcing parents to walk longer distances on ice to reach the foraging areas (Davis, 1982). This may increase body mass loss for parents and as their foraging trips are longer, the frequency of meal deliveries to the chicks is reduced (Davis, 1982). In that case, the intermediate sea-ice conditions can be characterized by both prey presence and accessibility (Table 7).

Table 7: Table gathering main conclusions concerning Adélie penguins in relation with sea-ice cover.

	Low sea-ice cover	Intermediate sea-ice cover	High sea-ice cover
Prey presence	Krill not present	Krill present	Krill present
Prey accessibility	Accessible	Accessible	Not accessible (Long distances to reach the foraging areas)
Breeding success	Low (Low profitability of foraging trips and low chicks' body mass)	High	Low (Nest desertion and chicks' starvation)

Findings evidenced the importance of a synchronicity between breeding events and sea-ice retreat. However, two years deserved special inspection. Because sea ice took a long time to retreat in 2014 (the distance between the colony and the open water was still around a hundred kilometers at the end of January), the breeding success was quite low for this season. The year 2001 was also characterized by a low breeding success value. This may result from the unusual presence of a huge iceberg, which probably prevented ocean currents and winds from assisting the summer break-up of sea ice (that forms polynyas) in the Dumont D'Urville Sea (Comiso, 2010). This could affect Adélie penguins that needed to walk longer distances to reach the foraging areas in the open sea. If excluding 2001 changes the shape of the curve so dramatically, maybe the year 2001 deserves a close investigation in another study to see whether the hypothesis of higher travel times over fast is true. The breeding success for this year is not extremely low and does not correspond to an outlier either. This phenomenon is associated to a real sea-ice event. During guard stage, polynyas are indeed profitable foraging areas for two reasons: the high productivity and the reduced travel and search time required to reach them. Rain can also make the breeding success decreasing because the thermo-regulation capacities of the chicks weaken rapidly (Ropert-Coudert et al., 2015). The year 2013 (total breeding failure), with high sea-ice coverage, exemplifies this phenomenon, with chicks dying because of rain, starvation and predators.

4.2. Seabirds foraging response to changes in sea-ice distribution at finer scales

We observed an optimal range of sea-ice concentration that influenced most of the diving parameters studied. Our findings showed that differences in foraging strategies occurred at different temporal scales: foraging trip, day, bout and dive. Although inter-individual variability was strong and, consequently trends were not as visible as for breeding success, results on the foraging activity of penguins mirror those on breeding success. The link between foraging success and breeding success is due to the strong correlation between average meal size and quality delivered to a chick and its growth rate, regulated by the body condition of the parents (Lorentsen, 1996). As such the mirroring trends with sea ice could be expected and a “perfect” sea-ice cover for Adélie penguins had been suggested by Ainley (2002).

4.2.1. Adaptations in activity rhythm revealing the local conditions

At the foraging trip scale, fractal analysis has shown that an increase in behavioral complexity along the decreasing gradient of sea-ice concentration, suggesting higher degrees of long-range dependence when the sea-ice cover was important. This deterministic behavior occurring during high sea-ice coverage years could be due to the fact that birds are more constrained in their diving movements. The presence of polynyas in these conditions becomes crucial to explain the foraging activity of the birds: waters with more predictable prey fields should lead to more stereotyped foraging sequences (Meyer, 2016). In addition, following Reynolds et al. (2015), a greater determinism observed in diving sequences may result from a process that favours exploitation over exploration, which is once again more likely to occur

when the prey field is more homogeneous and confined like in polynyas. On the other side, the greater complexity in foraging behavior observed during low sea-ice coverage years could be explained by different theories. At first, several studies have already linked greater stochasticity in foraging behavior with greater heterogeneity in the vertical distribution of prey (Ropert-Coudert et al., 2009; Pelletier et al., 2012), which could be the case when birds are diving in deeper waters. In other words, according to the results of the present study, birds may target higher depths, inducing variability in dive durations and the associated post-dive durations. In addition, MacIntosh et al. (2011) suggested that individuals in more complex environments or exploiting prey that are harder to catch (i.e. mobile prey) foraged in a less deterministic way. To summarize this idea, complex behavioral sequences are more likely to occur when environments are less predictable in terms of prey type, density and distribution, probably offering mechanisms to enhance the foraging success. Other studies have highlighted that animals which favour the exploration of their environment were more likely to display complex behavior (Shimada et al., 1995; Kembro et al., 2009). The last mechanism that could be involved here concerns the fact that diving seabirds are physiologically constrained by their oxygen reserves (Wilson, 2003) during periods of heavy prey exploitation. The patterns of alternation between dive and post-dive times are thus much less periodic.

Then, concerning the daily scale, the fact that no daily pattern was observed during intermediary years concerning the frequency of dives (all dives and deep dives) could indicate that the density of krill was sufficient to satisfy the foraging activity of Adélie penguins all day long. In the same way, no daily patterns were observed for maximum depth considering deep dives and all dives for intermediary sea-ice conditions. As krill is generally more present in deep waters during the day and rises to the surface at night, in this case, diving patterns are not in relation with the known day/night vertical migration of krill (Croxall et al., 1988). These results could also indicate that the balance fish/krill in Adélie penguins has changed during these years, meaning that birds targeted different types of prey (probably more energetic prey when the cost of reaching the foraging grounds is higher). These findings corroborate the ones resulting from the fractal analysis. Furthermore, we observed that during extreme sea-ice conditions, more foraging dives were performed during night time. This can be linked to the diurnal vertical migration of krill, above all for low sea-ice coverage years, where birds forage in open water. These findings could suggest that birds adopt different foraging strategies to maximise the profitability of foraging trips by optimising the prey encounter rate and by reducing the diving effort.

In addition, the number of dives per day and the number of bouts per day were found to be negatively related to breeding success. This finding suggests that an increase in diving activity per time unit is associated with a lower abundance of prey (or non profitable distribution of prey) or a foraging behaviour applied on poor quality patches. Results concerning the post-dive duration revealed that for the dives between bouts, this parameter presents lower values for intermediate years. This suggests that birds could reach another prey patch in a shorter time (Sommerfeld et al., 2015). In other words, intermediate years are probably characterized by a higher prey encounter rate, suggesting a more favourable prey

availability. The competition between species or between conspecifics may also explain the increase in diving activity and the decrease in foraging success during extreme years because diving individuals are more constrained (Warwick-Evans et al., 2016).

4.2.2. *The flexibility of foraging strategies highlighted with diving metrics*

At the dive scale, our study showed that plasticity exists for most of the diving parameters in relation with changes in sea-ice distribution. At first, results revealed that birds dove deeper during intermediary years. The choice of diving deeper can be explained once again either by the quantity of prey (density and distribution) or the quality of prey (balance fish/krill) occurring in deep waters. These results confirm the findings obtained with the analyses of bouts and day/night patterns. Concerning the descent and ascent rates, it has been shown that during intermediate years presented higher values. Descent and ascent rates relate to the dive angle, a small angle suggesting a more exploratory dive. During high sea-ice coverage conditions, assuming that penguins are feeding in polynyas, dive profiles present a slow ascending phase probably because birds are looking for an access to the surface (Kato et al., 2009). Some researchers have also suggested that birds can adjust these phases according to previous dives (if successful or not) and future dives as well (Wilson, 2003; Sato et al., 2004). The high descent and ascent rates observed during intermediate years could be due to the high mean maximum depth. In other words, as birds have to go deeper, they spend more time for the ascent and decent phases, at the expense of the bottom phase duration. It seems that bottom duration is negatively correlated to foraging success. This finding suggests that Adélie penguins are able to adapt their diving activity to the prey patch encountered, tending to reduce the time spent at the bottom when successful. As wiggles occur during the bottom phase, the lower number of wiggles per dive observed during intermediate years can be explained by the low mean bottom duration associated. Indeed, the number of wiggles is also negatively correlated to foraging success. This finding is the opposite from other studies (Hanuise et al., 2010). Once again, this result suggests that for intermediate sea-ice conditions, the quantity of prey encountered for each patch was higher and that a lower number of undulations was required for each dive. This could also mean that the prey found at the bottom phase was not moving to deeper water to escape the penguins. However, successful foraging dives occurring during intermediary years are probably energetically more costly. Indeed, as birds dove deeper, longer post-dive durations (time at the surface) were observed as a behavioural response in order to maintain aerobic metabolism (to reduce the risk to have a large lack of oxygen). Post-dive duration actually contains a recovery phase, depending on the amount of oxygen used during previous dives (Wilson, 2003; Pütz and Chérel, 2005) and a preparatory phase for the next dive. Various studies have shown that birds are able to adjust their air volume for each dive depending on the target maximum dive depth in order to optimize the costs and benefits of buoyancy (Sato et al., 2002; Noda et al., 2016).

Predicting how changes in sea-ice conditions can affect this marine predator relies on our ability to assess the foraging success, which is a particularly difficult task (Viviant et al., 2014). In the present study, we have shown that only using diving patterns, we can tend to predict foraging success. The use of diving metrics permitted to highlight the adaptation of

Adélie penguins' activity patterns to the density and distribution of prey and we could show that there is flexibility in foraging strategies in relation with changes in sea-ice distribution.

4.3. Effect of foraging investment on breeding success in relation with sea ice

Our results did not show that parents with high foraging investment (high diving rhythm and bottom duration) induce higher breeding success. This can be explained by two main reasons: (i) a very low foraging success (due to a low prey availability or accessibility); (ii) a different allocation of food between parents and offspring (Takahashi et al., 2003). The second hypothesis could not be tested in the present study. The investment is expected to reflect breeding success only when they feed in good conditions. In the present study, it has been found that the diving efficiency (ratio between bottom duration and total dive cycle duration) seemed to be negatively correlated to the breeding success (Fig. 16). However, several studies have linked breeding success to foraging success (meal size provided to the chicks and their fledging mass) (Clarke et al., 2002).

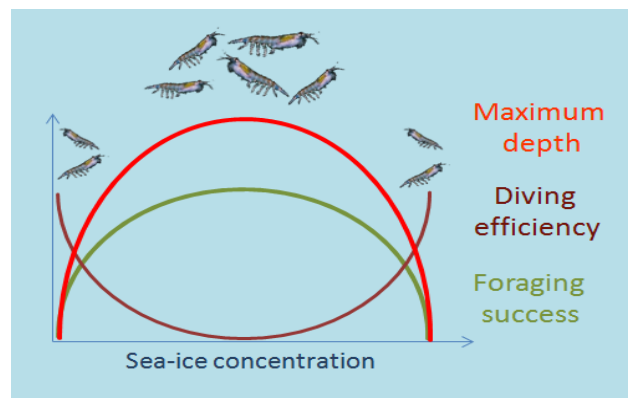


Figure 18: Schematic drawing representing the trends observed concerning breeding success, diving efficiency and foraging efficiency along the sea-ice concentration gradient.

Successful foraging is a determinant parameter involved in individual survival. But in the case of high diving efficiency values, the fact that birds spent a lot of time at the bottom phase of the dive doesn't necessarily mean they foraged successfully (Viviant et al., 2016) but they made more effort to find prey at the dive scale. Considering both the quality and the quantity of prey is necessary to understand the mechanisms involved. In the Southern Ocean, Antarctic krill (*E. superba*) density is not homogeneously distributed along the depth gradient. Indeed, krill density appears to be higher around 30-40 meters deep than around 10-20 metres (Godlewska et al., 1991). Even if little is known concerning the ice krill (*E. crystallophias*), as the Antarctic krill (*E. superba*) was well represented in stomach contents of Adélie penguins (Ridoux and Offredo, 1989), we could conclude that for intermediate sea-ice conditions, birds probably foraged on bigger krill patches by reaching higher depths. Moreover, the quality of krill could change with sea-ice conditions. Generally krill larvae are found just under sea ice, while juveniles and adults are a bit farther (both deeper and far from ice edge) (Nicol, 2006). When the sea-ice concentration is high, travel and access to open water is difficult, and presumably krill under the ice will be dispersed over much greater distances, making it more difficult for the penguins to find. In seasons with moderate amounts

of sea ice, travelling dives should be easy and the krill is not so dispersed, so maybe that supports the idea of an “optimum” amount of sea ice. In addition, the balance between krill and fish might be subject to change with sea-ice variations, forcing birds to adjust their diving depth (fish are more able to escape at higher depths).

The most obvious signal of optimality appears in breeding success. The optimal range of sea ice can be defined as the range of sea ice which is clearly enhancing the breeding. Meanwhile, foraging success couldn't be measured in this study but it has been shown that some foraging parameters peak for the same range of sea ice (around 20%). As such, it can be expected that these parameters are those that enhance foraging success, which is directly in relation with breeding success. However, it cannot be stated that the observed “optimal” values are the real optimal values that birds are able to perform. Penguins adjust their behavior to the different conditions in order to achieve high foraging success. This adjusted behavior is not necessarily “optimal”.

4.4. Methodological concerns and perspectives

This work could be complemented with more information about the individuals to highlight the response of a seabird to year-to-year variations of sea-ice conditions but the corresponding data doesn't exist for the years used in the present study. Coupling TDR data and GPS data may enable us to have a three-dimensional vision of the birds' habitat. In that way, we could investigate which areas seem more beneficial for the birds and know if penguins dive in polynyas or in open water. In addition, having more direct proxies of ingestion (such as data from accelerometers or oesophageal temperature measurements) and diet data could also enrich the discussion because we would be able to identify successful dives (Ropert-Coudert et al., 2001).

We could also investigate the influence of other environmental parameters, such as chlorophyll a concentration, meteorological parameters or data of currents. Indeed, in these ecosystems, eddies are known to be particularly important for predators, concentrating the food (Cottin et al., 2012). The strategy is energetically efficient as the birds are following the currents, at least during the first part of the trip (when they are in their lowest body condition). Note that some of these environmental parameters can be difficult to obtain with the presence of sea ice as they are depending on the remote sensing data obtained by satellites.

Furthermore, even if we worked on mean diving parameters, the fact that different spatial resolutions were used according to the different types of data can be a problem. Indeed, sea-ice concentration data were extracted at a large scale (25 km resolution) and diving data were recorded at a fine scale. However, the main limitation in this study is the differences in sample intervals. The differences between years were a real issue for analysing diving data. The bias emerging from differences in sampling intervals among years made the results hard to interpret. With the improvements made on bio-logging, the capacities of the electronic devices are subject to change but for long-term analyses, there is a real need to homogenise the protocol.

Long-term studies could arouse the interest of international institutions such as the Ecosystem Monitoring Program (CEMP) of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) which aims to detect changes in critical components of this marine ecosystem and to distinguish them between changes due to environmental variability and other changes. Even if working with 121 birds over 9 years is already acceptable, working over a longer period could enable researchers to better characterize the optimal range of sea ice (i.e. to identify if it is narrow or not) both in terms of foraging performance and breeding success. Long-term studies on this species should be done for several colonies because the trends observed for all colonies are not the same. In the Dumont D'Urville area, the last years were characterized by high sea-ice cover. As a consequence, the trends observed for this colony might not reflect the overall trend for this species, especially in a context of global warming.

Still considering that having a larger view is necessary, different breeding stages (incubation and chick-rearing) could be compared (Widmann et al., 2015). In the same way, coupling summer and winter studies would be judicious because the responses of birds to changes in sea-ice conditions can be different among stages. Winter studies could be particularly useful to better understand a second fundamental biological trait: the adults' survival. In addition, low food availability in winter can delay the arrival of birds to the colony. Therefore, events occurring in winter can have an influence on the foraging behaviour of parents during the summer.

4.5. Relevance of this marine predator as an eco-indicating species

Through this study, the ultimate aim was to assess if this marine predator can be a relevant eco-indicating species. Seabirds are known to be good eco-indicators of the environment (Furness and Camphuysen, 1997). The first main reason for which seabirds are largely used as eco-indicators is due to the fact that the study of central-place foragers is facilitated because the access to the different colonies is quite easy. In addition, the concept of using characteristics from upper trophic levels to bring information on ecosystem structure and functioning (including lower trophic levels) is interesting.

By its abundance and its circumpolar distribution, the Adélie penguin appears as a key species of the Southern Ocean ecosystem, subject to the full range of environmental changes. Populations' trends are very different among regions. For instance, in the Antarctic Peninsula area, corresponding to the fastest-warming place on Earth (Bromwich et al., 2013), populations have been decreasing during the past decades (Fraser and Patterson, 1997), whereas those in the Ross Sea increased (Taylor et al., 1990; Wilson et al., 2001). It appears that declining populations experienced several years with high sea surface temperature compared to those that are increasing (Cimino et al., 2016). The increase in Ross Sea populations might be due to an increase in wind strength and warmer winter temperatures that have resulted in thinner sea-ice cover and a more important presence of polynyas (Lyver et al., 2014). These changes in sea ice probably enhanced the foraging efficiency of foraging trips. Thus, breeding success has increased and populations have grown. Another factor that

has facilitated the increase in Adélie Penguin colonies in this area is the extraction by whalers of the penguins' main competitor for food, the Antarctic minke whale (*Balaenoptera bonaerensis*) (Lyver et al., 2014). In addition, this increase can be explained by the arrival of a commercial fishery which targets a fish species that competes for food with the penguins: the Antarctic toothfish (*Dissostichus mawsoni*), feeding mainly on Antarctic silverfish (Lyver et al., 2014). Meteorological factors and anthropogenic pressures (fishery development) also play a major role in population trends. To summarize, various factors can affect Adélie penguins' survival and fitness, two fundamental biological traits.

Global warming appears as the main factor affecting this long-lived marine predator, in relation with sea-ice retreat that causes habitat loss. A recent study has shown that Antarctica will potentially be responsible for sea-level rise of more than one metre by 2100 and more than 15 metres by 2500 (DeConto and Pollard, 2016). Adélie penguins depend on ice for foraging, resting, avoiding predators (leopard seals *Hydruga leptonix* and killer whales *Orcinus orca*), moulting, migrating and therefore breeding. To use Adélie penguins as indicators of the environment, we must consider relevant parameters that can be easily measured, sensitive to environmental change and integrative (Iverson et al., 2007). Among these, foraging behaviour parameters appear as an obvious choice. Indeed, the present study has shown that there might be an optimal range of sea ice (around 20%) in terms of foraging efficiency and breeding success, meaning that this species represents a great indicator of rising global warming. But this is not the only factor associated with global warming that is impacting this species. Because their spatial distributions are dependent on the matching between their physiological optima and biotic and abiotic conditions, marine invertebrates and fish species are known to respond to increasing water temperatures through distribution shifts (Cheung et al., 2013). With global warming, these species are susceptible to migrate toward poles. The arrival of new species might modify the structure and the functioning of the food web in the Southern Ocean, bringing new potential prey for Adélie penguins and their competitors. Therefore, top-down and bottom-up forces might be modified and the Southern Ocean's ecosystem will therefore experience major changes.

Other disturbances are also referred for this species. Adélie penguins populations are affected by krill fisheries in the Southern Ocean (Trathan et al., 2015). Even if the CCAMLR (fisheries management authority) regulates the Antarctic krill fishery, we are in a context of increasing krill harvesting because of the increasing population trend (Cury et al., 2011). Because they need to maintain their plumage in a good condition (Trathan et al., 2015), Adélie penguins can also be affected by another non-negligible anthropogenic factor: water pollution (García-Borboroglu et al., 2008).

It can be highlighted that the Adélie penguin is a species that can give an exhaustive picture of what is happening in term of sea-ice variability. Other species present in Adélie Land with a circumpolar distribution are also of particular interest to many researchers. This is the case of the South Polar skua (*Catharacta maccormicki*), the Emperor penguin (*Aptenodytes forsteri*), the Weddell seal (*Leptonychotes weddellii*), the Snow petrel (*Pagodroma nivea*) or other petrels. Being a diving marine predator (such as the Emperor penguin and the Weddell seal) and not a flying bird, the Adélie penguin is more constrained

and dependent on sea ice. As they breed in winter (Wilson, 1907), emperor penguins are really hard to work on (researchers need to work in extreme cold, wind and dark). In addition, it is difficult to follow the same individuals because they don't make any nest. Furthermore, the Emperor penguin is a protected species (BirdLife International, 2012b), making difficult to get a permit to work on it. Finally, unlike the Weddell seal, which is a coastal species, Adélie penguins can give relevant information concerning the “entire” ecosystem.

5. Conclusion

The Adélie penguin is one of the species monitored by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). It takes part of its CCAMLR Ecosystem Monitoring Program (CEMP) to detect anthropogenic impacts on Antarctic marine ecosystems.

Thanks to a multi-scale approach confronting breeding success and diving data concerning Adélie penguins with sea-ice data, this work allowed us to provide evidence that birds can adjust their foraging strategies according to sea-ice variations, suggesting that there could be an optimal range of sea-ice concentration for this species (around 20%). Therefore, we gave new clues for taking into account Antarctic marine predators when investigating the effects of global warming on the Southern Ocean's ecosystem. However, the work has to be complemented with long-term studies conducted on more individuals that could highlight the responses of this marine predator to year-to-year variations of environmental variables and thus contribute to refine the predictions made on this species in relation with global warming.

The Adélie penguin is a long-lived species whose breeding success depends on several environmental and anthropogenic pressures. In a context of predicted alteration of sea-ice cover, it is timely to better investigate the optimal range of sea ice in relation to behavioral flexibility.

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Appendices

Appendix I: Simplified R-Script: The extraction and calculation of sea-ice parameters for one year.

```
#### Camille Le Guen - February 2016 - PCA on diving data Adélie penguins DDU
```

```
### Data and packages
```

```
library(raster)
```

```
library(devtools)
```

```
library(rgdal)
```

```
ice1995 <- brick("seacedaily_NDJ_1995.grd")
```

```
# The .grd file contains 92 layers: one layer for each day of the season (from 01-nov to 31-jan).
```

```
### Plot a map of sea-ice concentration for each day
```

```
mapLL <- projectRaster(ice1995, crs = "+proj=longlat +ellps=WGS84")
```

```
# Plot for the first day (01-nov)
```

```
# The navyblue colour corresponds to open water and aliceblue to sea ice.
```

```
plot(mapLL[[1]], xlim=c(134,144), ylim=c(-68,-62), col=colorRampPalette(c("navyblue",  
"aliceblue"))(100), zlim = c(0, 100) , xlab="Longitude", ylab="Latitude", main= "Sea ice  
concentration")
```

```
# Plot for the last day (31-jan)
```

```
plot(mapLL[[92]],xlim=c(134,144), ylim=c(-68,-62), col=colorRampPalette(c("navyblue",  
"aliceblue"))(100),zlim = c(0, 100) , xlab="Longitude", ylab="Latitude", main= "Sea ice  
concentration")
```

```
mapLL<-trim(mapLL) # isolates the map from the background of the plot
```

```
text(locator(1),"Sea ice concentration (%)", cex=1, srt=90, xpd=T)
```

```
points(140.01,-66.40,col="black",lwd=1,pch=16) # indicates the location of the colony on the map
```

```
#### Calculation of mean sea-ice concentration for each day
```

```
daymean1995<-data.frame(date=getZ(ice1995),meanice=cellStats(ice1995, mean,na.rm=T))
```

```
# Calculates a single mean value of SIC for each day
```

```
write.csv2(daymean1995$meanice, file='daymean1995.csv')
```

```
# Creates a file gathering the 92 values of SIC (one value for a day)
```

```
#### Calculation of sea-ice extent (area covered by sea ice)
```

```
# Define our region of interest
```

```
mapLL <- projectRaster(ice1995, crs = "+proj=longlat +ellps=WGS84")
```

```
roi=raster(xmn=134,xmx=144,ymn=-68,ymx=-62) # Define our region of interest in long/lat
```

```
lonlatproj="+proj=longlat +ellps=WGS84" # Define the projection
```

```
projection(roi)=lonlatproj
```

```

# Check that everything has worked as expected doing daily plots (not presented here)
# Extract the sea ice in our region of interest

for (x in 1:92) {
ice_roi=intersect(mapLL[[x]],roi) # Select the cells of the region of interest
icegrid_cellarea=area(ice_roi) # Calculate the area of every grid cell in the region of interest
# !!!!! All the cells don't have the same area!!!!!!
area<-sum(values(icegrid_cellarea),na.rm=T) # Calculate the total area of the region of interest

# We need to select the cells which are covered by sea ice. Usually a concentration of 15% is used as
the cutoff to define open water

ice_mask=ice_roi>=15 # This will have values of 1 where ice was >=15%, and 0 otherwise

# Now mask out the area information with the sea ice information
temp=ice_mask*icegrid_cellarea # values will be 0 for open-water cells and 1 when sea ice covered
ice_area=sum(values(temp),na.rm=TRUE) ## total area of ice-covered grid cells in region of interest

# or, to calculate total sea ice area
a<-sum(values(ice_roi*icegrid_cellarea/100),na.rm=TRUE)
print(a)
}

### Distance colony - open water

map<-crop(mapLL[[1]], extent(134,144,-67,-62))
plot(map,xlim=c(134,144), ylim=c(-68,-62),col=rainbow(20),zlim = c(0,100) , xlab="Longitude",
ylab="Latitude", main= "Sea ice concentration")
points(140.01,-66.40,col="black",lwd=1,pch=16) # indicates the location of the colony
a<-click(map,n=1, id=FALSE, xy=TRUE) # Select the closest cell of open water with the computer
mouse. A contains two values: a$x and a$y, its two coordinates.
pointDistance(c(140.01,-66.40),c(a$x,a$y),lonlat=TRUE) # use its coordinates to calculate the
distance between the colony and this point (in meters)

### Distance colony - polynya

```

The same process was applied for polynyas, meaning that we use the coordinates of the closest point with 15% of SIC or less to calculate the distance between the colony and the first polynya.

Appendix II: Simplified R-Script: GAM performed on Adélie penguins' breeding success.

```
#### Camille Le Guen - April 2016 - Breeding success Adélie Penguins
```

```
## Data and packages
```

```
repro.all<-read.table("breeding success all years.csv", sep=";", header=TRUE)
head(repro.all)
library(mgcv)
```

```
## Choice to consider all years or not
```

```
repro.all<-subset(repro.all, subset=c(repro.all$Year!=2014))
repro.all<-subset(repro.all, subset=c(repro.all$Year!=2001))
```

```
## Flexible way of specifying the colouring
```

```
tracking_years <- c(1995,1998,2001,2007,2009,2010,2011,2012,2014) # 9 years for tracking data
plot_colour <- rep("cadetblue2",nrow(repro.all)) # colour by default
plot_colour[repro.all$Year %in% tracking_years] <- "cadetblue" # colour for tracking data
```

```
# Visualisation of data
```

```
plot(repro.all$SIC.global, repro.all$Breeding.success, tck=0.02, cex.lab=1.3, pch=16, las=1,
xlab="Global sea ice concentration (%)", cex.axis=1,ylab="Breeding success", col=plot_colour,
main="Breeding success of Adélie penguins")
box(lwd=2)
legend("topright", cex=0.7, legend=c("Data - study period","Data - added"),
col=c("cadetblue","cadetblue2"), pch=16)
```

```
###Modelling part
```

```
# One issue in using the cubic regression spline basis for the smooth term (bs="cr") is that the results can be sensitive to where the knots are placed (and how many knots), and choosing these values is not always obvious. By default, k=10 knots and they are placed evenly throughout the values of SIC.global. In this case, we have a small data set (20 rows = 20 years) and the SIC.global values are not evenly spaced (there are a lot of values around 17-22%). So by default, bs="cr" will tend to place multiple knots around 17 and 22. This will tend to overfit in these regions, which explains why the curve using 10 knots looks too wiggly.
```

```
# Deal with overfitting
```

```
# Test 1: amount of smoothing not fixed with cubic regression spline
```

```
model.test<-gam(Breeding.success ~ s(SIC.global, fx=F, k=-1, bs="cr"), data=repro.all)
plot(model.test)
```

```
place.knots(repro.all$SIC.global,10) ## to see where R will place the knots with
```

```
# It gives [1] 14.33 16.79 17.14 17.46 18.22 20.46 21.49 22.26 29.84 37.15 so, yes, it is putting multiple knots around 17 and 22. One way to avoid this is to reduce the number of knots (e.g. k=5) as Zuur et al. (2009) suggested it, but in doing this the result might still be sensitive where those knots are placed.
```

```
model.test2<-gam(Breeding.success ~ s(SIC.global,k=5, bs="cr"), data=repro.all)
```

```
If you look at gam.check(model.test2) below it is suggesting that k=5 may not be enough knots. Another way to get around the overfitting seen in model.test is to use the default 10 knots but place them evenly between the minimum and maximum values of SIC.global.
```

```
kn <-list(SIC.global=seq(from=min(repro.all$SIC.global),to=max(repro.all$SIC.global),
length.out=10))
```

```

fit10 <-
gam(Breeding.success~s(SIC.global,bs="cr",k=length(kn$SIC.global)),data=repro.all,knots=kn)
# However, this looks pretty similar to model.test2. If we reduce the number of knots (but still keeping
them evenly spaced) we get largely the same result
kn <- list(SIC.global=seq(from=min(repro.all$SIC.global),to=max(repro.all$SIC.global),
length.out=8))
fit8 <- gam(Breeding.success~s(SIC.global,bs="cr",k=length(kn$SIC.global)),
data=repro.all,knots=kn)
# AIC-based model selection says they are equally good
AIC(fit8,fit10)
# However, evenly-spaced knots is perhaps not a great idea, because it places knots at values where
there are no data points. It might be better to put the knots near data points, but just make sure that we
don't put multiple knots close to each other. What if we choose knots at unique values of SIC after first
rounding the SIC values to the nearest multiple of 2
kn <- list(SIC.global=sort(unique(round(repro.all$SIC.global/2)*2)))
fit <- gam(Breeding.success~s(SIC.global,bs="cr",k=length(kn$SIC.global)),data=repro.all,knots=kn)
# another way to avoid the overfitting is to use the default thin-plate spline basis for the smooth. This
doesn't require knot placement (it places one knot at each data point) and the smoothness penalty
works differently (and seems to be more reliable in this case). This gives the same smooth fit as we are
seeing previously. But tp splines are harder to explain than cubic regressions, so if you want to stay
with bs="cr" I would use evenly-placed knots. We are getting basically the same curves for all of these
options, so we can be fairly confident that these are reasonable fits.

```

```

# Should the year 2001 be included in the analysis or not?

```

```

# If we look at the plot of breeding success against SIC, the far-left point has very low breeding
success as well as very low sea ice. This was year 2001, which was a very unusual year for sea ice
(Iceberg B15). We could try to perform the GAM with and without 2001 to see if this point is having a
large effect on the fit.This is what we get with 2001:
repro.all<-read.table("breeding success all years.csv", sep=";", header=TRUE)
fit_tp <- gam(Breeding.success ~ s(SIC.global),data=repro.all)
plot(fit_tp)
# In this plot (and all the previous smooth fits) the breeding success starts low for SIC around 15%,
then peaks at SIC around 22%, then drops again. Here is what we get without 2001:
fit_tp2 <- gam(Breeding.success ~ s(SIC.global),data=subset(repro.all,Year!=2001))
plot(fit_tp2)
# Now, breeding success does not drop for low SIC. That trend is being driven by the 2001 season.

```

```

# Example of graph of a chosen model

```

```

model<-model.test2

```

```

fit <- predict(model ,se = TRUE)$fit
se <- predict(model ,se = TRUE)$se.fit
lcl <- fit - 1.96 * se
ucl <- fit + 1.96 * se
plot(repro.all$SIC.global, repro.all$Breeding.success, tck=0.02, cex.axis=1, cex.lab=1.3, pch=16,
las=1, xlab="Sea ice concentration (%)", ylab="Breeding success",
col=c("cadetblue","cadetblue2","cadetblue2","cadetblue","cadetblue2","cadetblue2","cadetblue","c
adetblue2","cadetblue2","cadetblue2","cadetblue2","cadetblue2","cadetblue","cadetblue2","c
adetblue","cadetblue","cadetblue","cadetblue2","cadetblue"),main="Breeding success of Adélie
penguins all years - 5 knots")

```

```

i.for <- order(repro.all$SIC.global )
i.back <- order(repro.all$SIC.global , decreasing = TRUE )
x.polygon <- c(repro.all$SIC.global[i.for] , repro.all$SIC.global[i.back] )
y.polygon <- c( ucl[i.for] , lcl[i.back] )

polygon( x.polygon , y.polygon , col = "gray88" , border = NA )
lines(repro.all$SIC.global[i.for] , fit[i.for], col = "gray48" , lwd = 3 )

abline(h=mean(repro.all$Breeding.success) , lty = 2, col="indianred2" )
text(35, 0.93,labels="Mean", cex=0.8, col="indianred2")
axis(side=2,lwd=2,lwd.ticks = 2,labels=F,tck=0.02)
axis(side=1,lwd=2,lwd.ticks = 2,labels=F,tck=0.02)
box(which="plot",lty="solid",lwd=2)
legend("topright", cex=0.8, legend=c("Data - study period", "Data - added"),
col=c("cadetblue","cadetblue2"), pch=16)

```

Appendix III: Presentation of two correlation structures applicable to the mixed models: the compound symmetry and the first order autoregressive structure.

$$\sigma^2 \begin{pmatrix} 1 & \rho & \rho \\ \rho & 1 & \rho \\ \rho & \rho & 1 \end{pmatrix}$$

Compound symmetry

$$\sigma^2 \begin{pmatrix} 1 & \rho & \rho^2 \\ \rho & 1 & \rho \\ \rho^2 & \rho & 1 \end{pmatrix}$$

AR1

Appendix IV: Simplified R-Script: mixed model applied on diving efficiency for all years including all dives at the seasonal scale.

```
#### Camille Le Guen - May 2016 - Script mixed models - Adélie P data DDU 1995-2014
```

```
### Data and packages
```

```
library(nlme) ; library(lme4) ; library(lattice) ; library(MASS) ; library(MuMIn) ; library(mgcv) ;  
library(ggplot2) ; library(car) ; library(MASS) ;library(plyr)  
test3<-read.table("Multiyear diving data first trip.csv",header=T,sep=";")  
test3$Year<-as.factor(test3$Year)  
head(test3)  
str(test3)
```

```
### Subset required (because of R memory issues)
```

```
test3 <- test3[sample(1:nrow(test3),7000),]
```

```
### Fraction of zero
```

```
temp<-ddply(test3,.(Year), function (z)data.frame(fraction_with_zero=sum(z$Bottom.duration<1e-  
06)/nrow(z)))
```

```
ggplot(temp,aes(Year,fraction_with_zero))+
```

```
  geom_bar(stat="identity")+
```

```
  labs(y="Fraction of dives with a bottom duration of zero")
```

```
# There are a lot of zero in the dataset. That is why we tried delta modelling (script not presented  
here). We need to find a probability distribution that can handle this.
```

```
### Rescaling variables for convergence purposes
```

```
test3$SIC.global.demeaned<-test3$SIC.global-mean(test3$SIC.global)
```

```
test3$SIC.global.rescaled<-test3$SIC.global.demeaned/sd(test3$SIC.global)
```

```
test3$SIE.global.demeaned<-test3$SIE.global-mean(test3$SIE.global)
```

```
test3$SIE.global.rescaled<-test3$SIE.global.demeaned/sd(test3$SIE.global)
```

```
test3$dOW.global.demeaned<-test3$dOW.global-mean(test3$dOW.global)
```

```
test3$dOW.global.rescaled<-test3$dOW.global.demeaned/sd(test3$dOW.global)
```

```
### Modelling part
```

```
## Random intercept model (RI) or random slope and intercept model (RS)? Comparison using the  
ML method.
```

```
m2.ri.ML<-lme(Dive.intensity ~ SIC.global.rescaled + SIE.global.rescaled + dOW.global.rescaled +  
SIC.global.rescaled:SIE.global.rescaled, control=list(niterEM=100000), random=~1|Bird.ID,  
method="ML",data=test3)
```

```
m2.rs.ML<-lme(Dive.intensity ~ SIC.global.rescaled + SIE.global.rescaled + dOW.global.rescaled +  
SIC.global.rescaled:SIE.global.rescaled, control=list(niterEM=100000),  
random=~SIC.global.rescaled|Bird.ID, method="ML",data=test3)
```

```
AIC(m2.ri.ML,m2.rs.ML)
```

```
model<-m2.rs.ML
```

```
summary(model)
```

```
anova(model)
```

```
## In favour of the random intercept and slope model (RS)
```

```
## Selection of variables
```



```

m3.rs.a.ML<-lme(Dive.intensity ~ SIC.global.rescaled + SIE.global.rescaled,
               control=list(niterEM=100000),
               random=~SIC.global.rescaled|Bird.ID, method="ML",data=test3)

AIC(m2.rs.ML,m3.rs.a.ML)
#better AIC for m3.rs.a.ML

## Estimation of the different parameters using the REML method.

m3.rs.a.REML<-lme(Dive.intensity ~ SIC.global.rescaled + SIE.global.rescaled,
                  control=list(niterEM=100000),
                  random=~SIC.global.rescaled|Bird.ID, method="REML",data=test3)

r.squaredGLMM(m3.rs.a.REML)
summary(m3.rs.a)
anova(m3.rs.a)
AIC(m2.rs,m3.rs.a)
#both parameters are significant

## Hypothesis testing for the chosen model

model<-m3.rs.a.REML
plot(resid(model))
hist(resid(model))
qqnorm(resid(model))
qqline(resid(model), col="red")

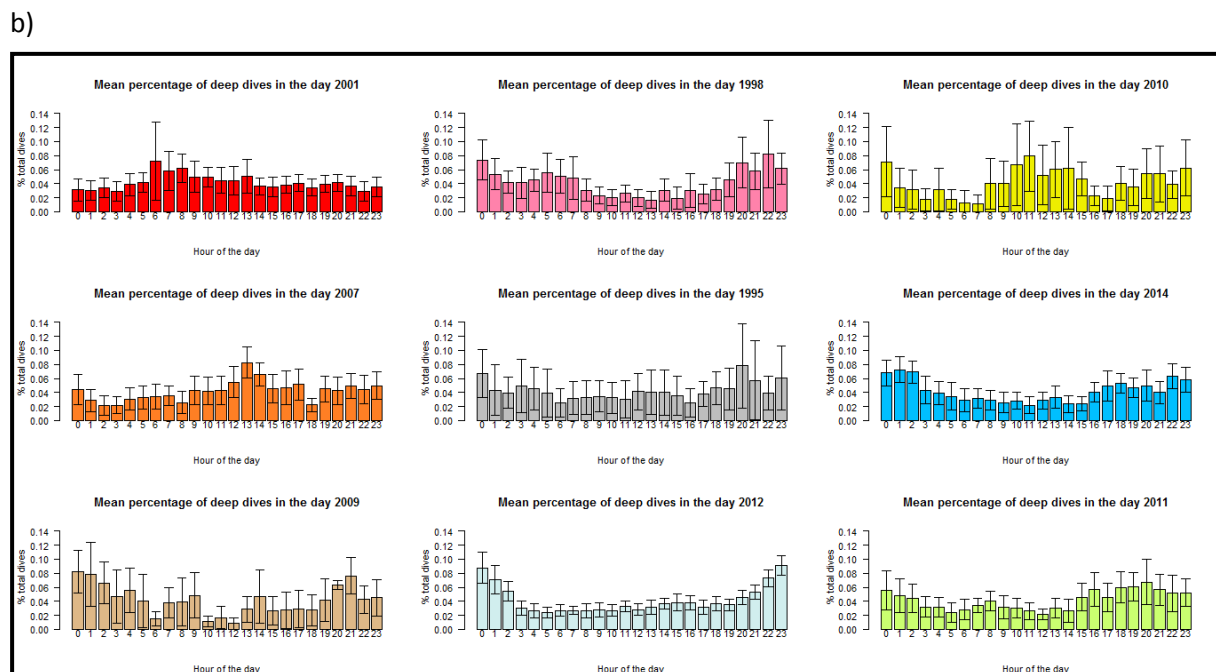
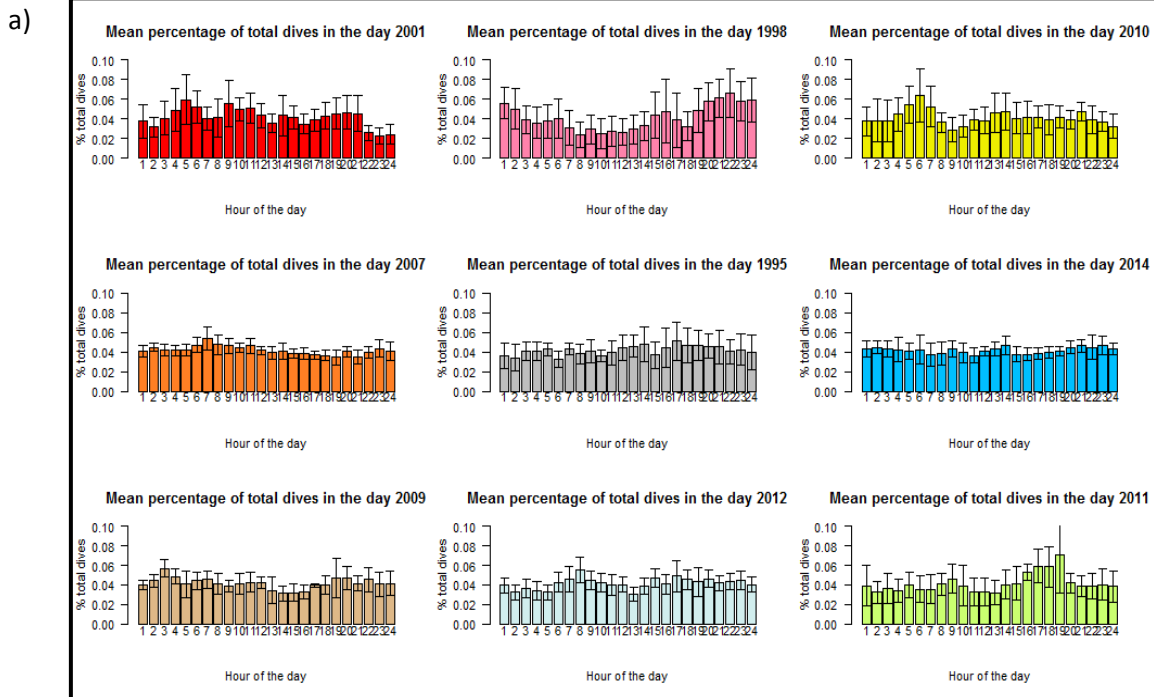
## Making graphs

new.dat<-data.frame(Dive.intensity=test3$Dive.intensity, Year=test3$Year,
                    SIC.global=test3$SIC.global,SIC.global.rescaled=test3$SIC.global.rescaled,
                    SIE.global=test3$SIE.global, SIE.global.rescaled=test3$SIE.global.rescaled,
                    dOW.global=test3$dOW.global, dOW.global.rescaled=test3$dOW.global.rescaled,
                    Bird.ID=test3$Bird.ID)
ggplot(data=new.dat, aes(x=SIC.global, y=Dive.intensity))+
  geom_point(size=2)+
  geom_line(aes(y=predict(model), group=Bird.ID),colour="orange")+
  geom_line(data=new.dat,aes(y=predict(model,level=0,newdata=new.dat)),colour="palevioletred1",
            lwd=2)+

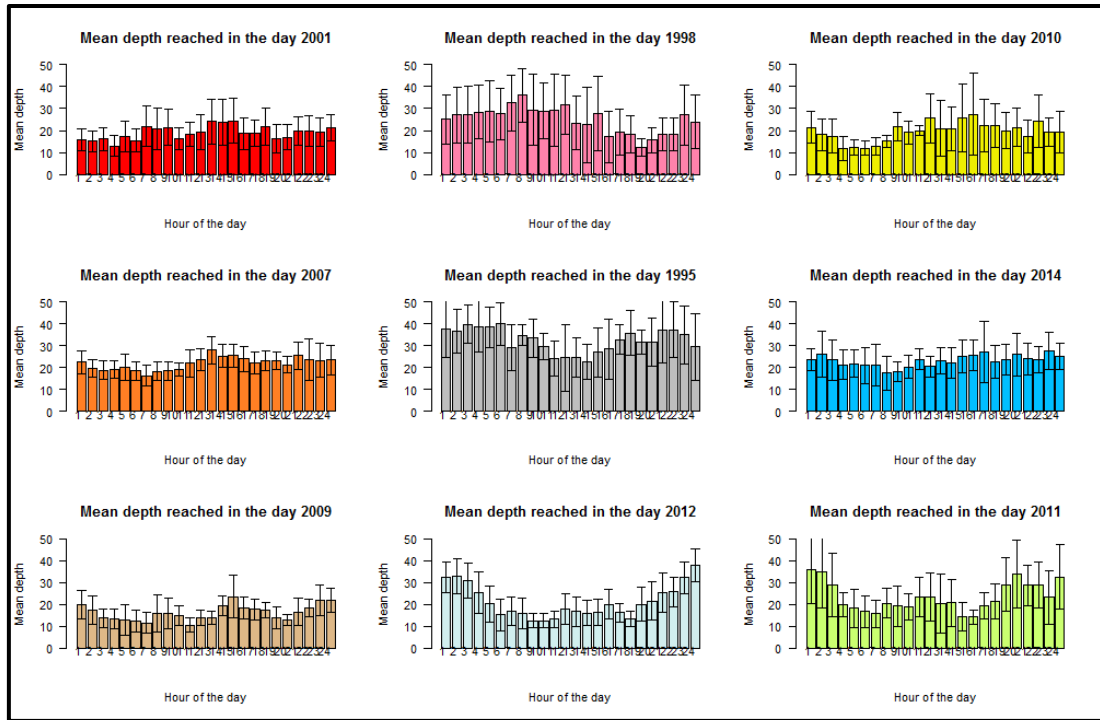
  geom_line(data=new.dat,aes(y=predict(model,level=1,newdata=new.dat)),colour="lightgoldenrod2",l
            wd=2)+
  stat_summary(data=new.dat, fun.data=mean_se, geom="pointrange", color="red")
  geom_smooth(color="skyblue3", lwd=2, se=T, method=loess)

```

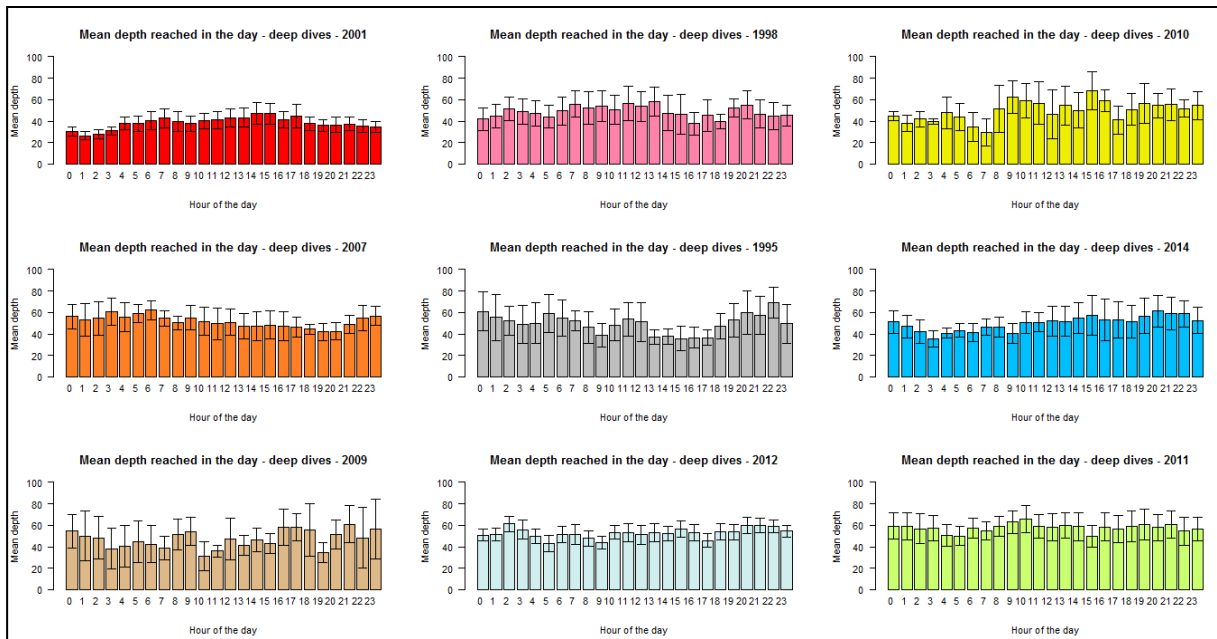
Appendix V: Day/night analysis performed on a) the frequency of dives considering all dives, b) the frequency of dives considering deep dives only, c) the mean maximum depth considering all dives and d) the mean maximum depth considering deep dives only. Plots are organised according to an increasing gradient of sea-ice concentration. Values for each year are grand mean of all birds + SE.



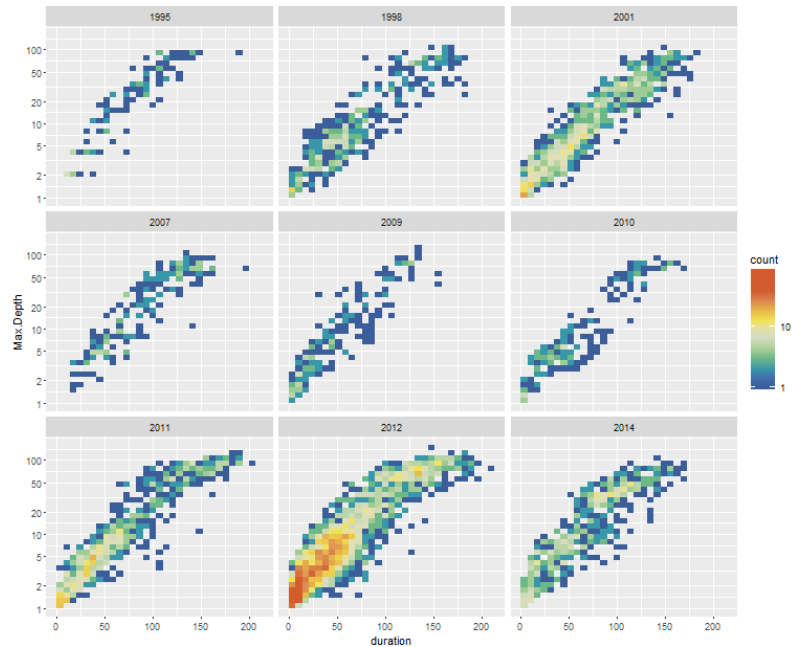
c)



d)



Appendix VI: Study of the relationship between dive depth and dive duration for all years.



Density plot representing the relationship between dive duration and maximum depth for each year

Results of correlation parameters concerning the relationship between depth and duration for each year.

Year	<i>Depth vs Duration (Depth=a*Duration+b)</i>			
	B	a	r ²	p-value (t)
1995	-7.60	0.569	0.795	***
1998	-9.10	0.417	0.685	***
2001	-5.66	0.332	0.691	***
2007	-10.59	0.500	0.785	***
2009	-5.73	0.464	0.769	***
2010	-6.59	0.441	0.741	***
2011	-10.55	0.502	0.788	***
2012	-6.20	0.448	0.748	***
2014	-7.22	0.436	0.740	***

*** <2e-16

Appendix VII: Results of mixed models for each diving parameter.

Maximum depth	Significant explanatory variables	R²c	R²m	AIC	p-values
7 years all dives					
By season	SIE. Distance open water	0.1376	0.0212	16639.27	0.0010 0.0002
By day	Polynya	0.1255	0.0295	16807.88	<0.0001
9 years deep dives only					
By season	SIC	0.417	0.0597	1442.75	0.0010
By day	Polynya	0.499	0.01	1292.87	0.0053

Post-dive	Significant explanatory variables	R²c	R²m	AIC	p-values
7 years all dives (dives within bouts)					
By season	SIC	0.101	0.006	19273.06	0.0301
By day	SIC SIE	0.0859	0.0141	18977.17	0.0150 0.0199
7 years all dives (dives between bouts)					
By season	SIC Distance open water	0.1266	0.0091	10165.69	0.0027 0.0156
By day	SIC	0.1391	0.0170	11526.54	0.0021

Diving efficiency	Significant explanatory variables	R²c	R²m	AIC	p-values
9 years deep dives only					
By season	SIC SIE	0.2780	0.0758	-8917.093	0.0094 <0.0001
By day	SIE	0.3237	0.0293	-8695.841	0.0032

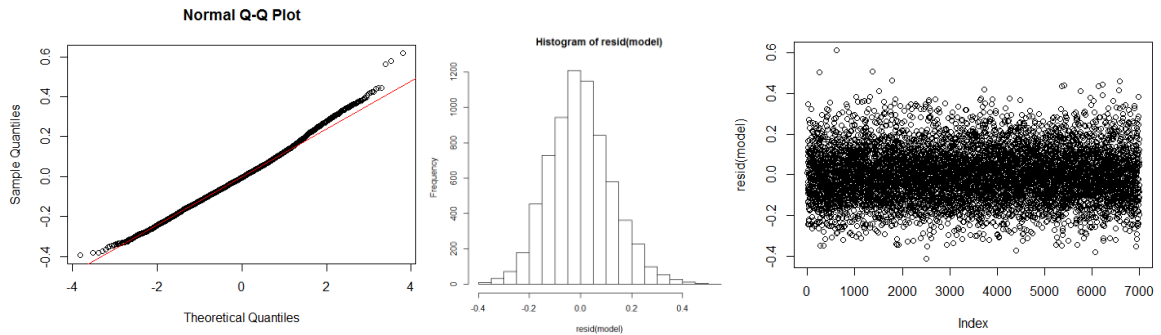
Descent rate	Significant explanatory variables	R²c	R²m	AIC	p-values
7 years all dives					
By season	SIC SIE	0.1590	0.0391	-5769.58	0.0076 <0.0001
By day	SIE Distance.open water Polynya	0.1295	0.0194	-5637.723	0.0062 0.0103 0.0031
9 years deep dives only					
By season	SIC SIE	0.2623	0.0463	-15540.09	0.0463 0.0001
By day	SIE	0.2799	0.0231	-15309.61	9.10 ⁻⁴

TCPUE	Significant explanatory variables	R²c	R²m	AIC	p-values
9 years deep dives only					
By season	SIC SIE	0.1571	0.0287	-20224.61	0.0012 0.0034
By day	SIC	0.1881	0.0231	-20342.81	2.10 ⁻⁴

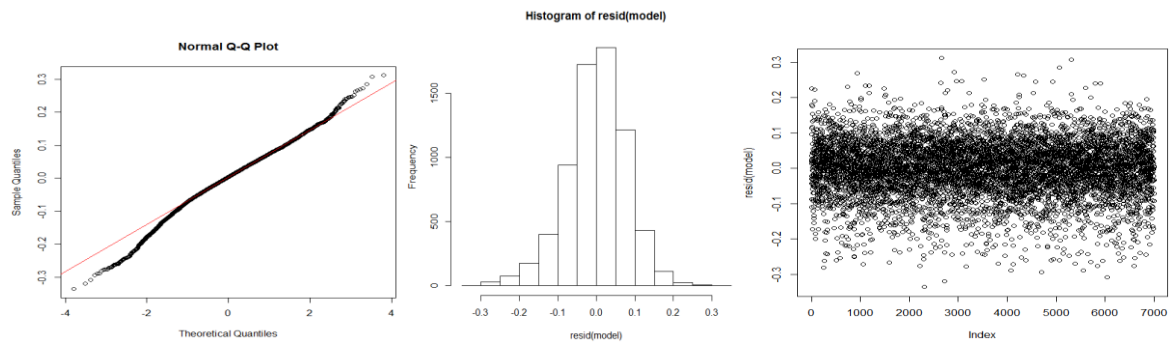
Nb wiggles	Significant explanatory variables	R²c	R²m	AIC	p-values
9 years deep dives only					
By season	SIC SIE	0.4156	0.1133	35367.23	<0.0001 <0.0001
By day	SIE	-	0.0744	33258.95	5.06*10 ⁻⁶

Appendix VIII: Residuals of the chosen mixed model of each diving parameter.

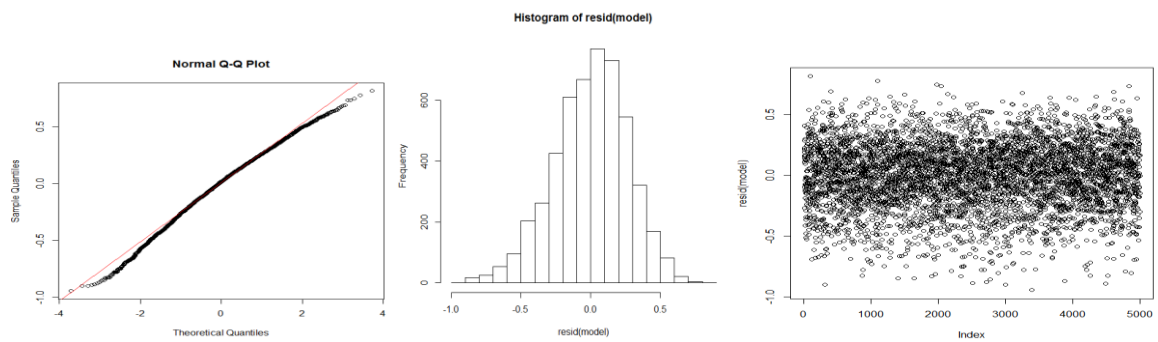
a) Diving efficiency



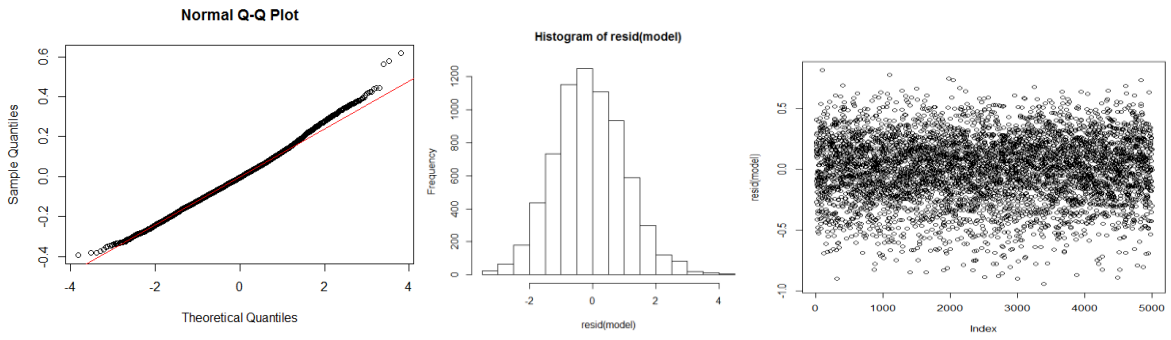
b) Descent rate



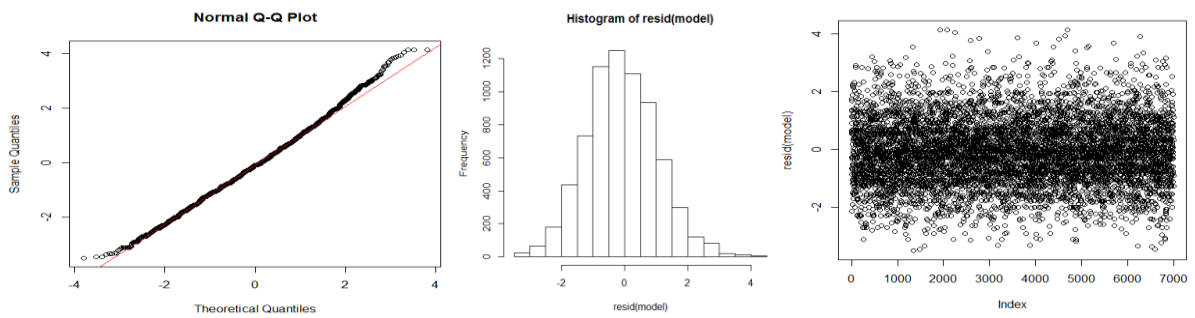
c) Maximum depth



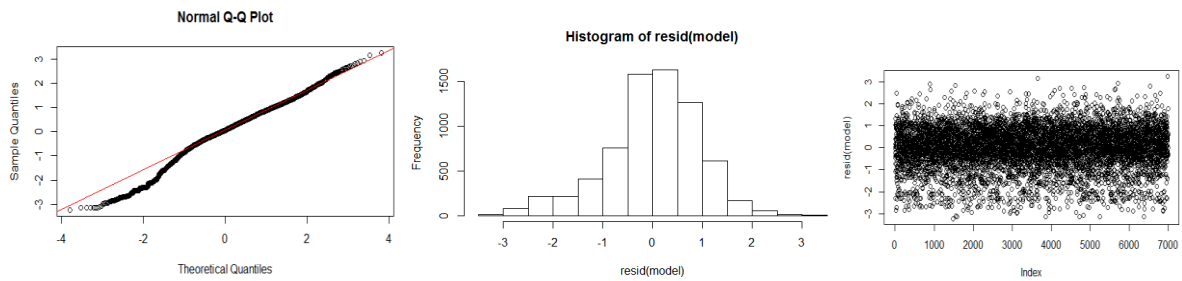
d) TCPUE



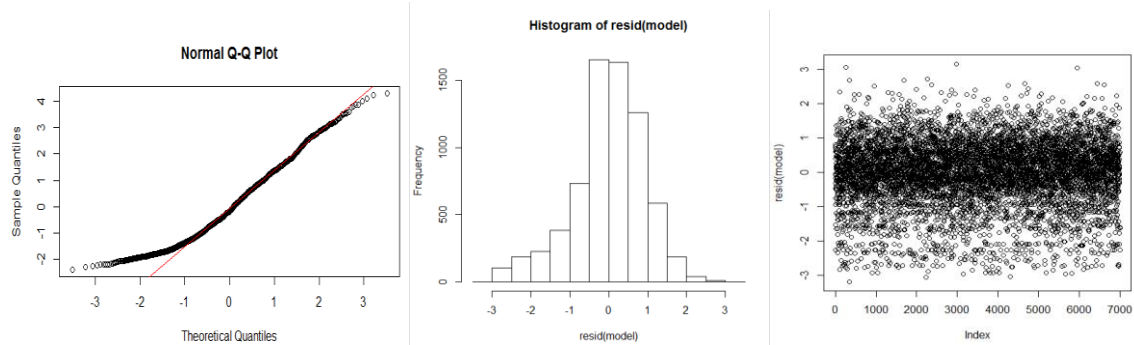
e) Number of wiggles



f) Post-dive duration (dives within bouts)



g) Post-dive duration (dives between bouts)





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Spécialisation / option : Sciences Halieutiques et Aquacoles (option REA)
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Titre français : Influence des conditions de glace de mer sur l'activité de plongée d'un prédateur marin: le manchot Adélie (*Pygoscelis adeliae*)

Titre anglais : Influence of sea ice conditions on the diving activity of a marine predator: the Adélie Penguin (*Pygoscelis adeliae*)

Résumé :

L'océan Austral fait l'objet de changements environnementaux majeurs, notamment concernant la glace de mer, connue pour influencer la structure et le fonctionnement de l'écosystème et pour affecter la survie et la reproduction des oiseaux marins en conditionnant la disponibilité et l'accès à la ressource. Le succès reproducteur du Manchot Adélie varie selon la couverture de glace, présentant un pic dans la gamme intermédiaire. Pour comprendre cette relation entre la glace de mer et le succès reproducteur, l'activité de plongée a également été étudiée. Cette étude a été menée sur 9 années aux conditions de glace contrastées, à différentes échelles temporelles (saison, voyage alimentaire, journée et plongée). L'étude de l'organisation des plongées (analyses des fractales, des séquences de plongées et du rythme jour/nuit) a révélé que pour une gamme de glace moyenne, les oiseaux sont contraints dans leur comportement, avec une activité plus régulière et moins intense. L'analyse des paramètres de plongée a montré que lors des années intermédiaires, les individus ajustent leurs stratégies alimentaires pour maximiser la profitabilité des voyages alimentaires. Ils semblent cibler des zones plus profondes et ajuster leur effort de plongée pour rencontrer des proies de meilleure qualité ou en plus grande quantité. Ceci suggère l'existence d'une gamme optimale de glace chez ce prédateur marin longévif (autour de 20%). Le manchot Adélie étant considéré comme un bon éco-indicateur de l'Océan Austral, une étude à plus long terme est nécessaire pour mieux caractériser cette gamme optimale.

Abstract :

The Southern Ocean experiences major environmental variations, including changes in sea-ice cover, which is known to influence the ecosystem structure and functioning and to affect the survival and the reproduction of seabirds by limiting the availability and the access to food resources. Adélie penguins' breeding success varies according to sea ice with a peak at intermediate sea-ice coverage. To better understand this relationship, the diving activity was also investigated. This study was conducted over 9 contrasted years in term of sea ice using a multi-scale approach (season, foraging trip, day and dive). The analysis of the temporal organisation of dives (fractal analysis, bout analysis and day/night patterns) revealed that for intermediary sea-ice conditions, birds are less constrained in their behavior, having a more regular and less intense activity. The analysis of the diving metrics has shown that during intermediary years, individuals adjust their foraging strategies to maximize the profitability of foraging trips. They target higher depths and adjust their diving effort to encounter different prey of higher quality or quantity. However, during extreme years, the availability or the accessibility of prey can be limited. This suggests the existence of an optimal range of sea ice for this long-lived marine predator (around 20%). As the Adélie penguin can be considered as good eco-indicator of the Southern Ocean, working on a longer time-series is required to better characterize this optimal range.

Mots-clés : Océan Austral, glace de mer, succès reproducteur, activité de plongée, efficacité alimentaire, stratégie alimentaire, optimum écologique, manchot Adélie.

Key Words: Southern Ocean, sea ice, breeding success, diving activity, foraging efficiency, foraging strategies, ecological optimum, Adélie penguin.