The foraging behaviour and range of little penguins (*Eudyptula minor*) at two neighbouring colonies

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Abstract

Differences between colonies in foraging behaviour have been reported for little penguin colonies in New Zealand and Australia. The differences between colonies are generally attributed to different environmental conditions at the colonies. However, no New Zealand study has compared the foraging behaviour of two neighbouring little penguin colonies that share the same marine environment.

The current study compared the foraging behaviour of birds from two colonies in Oamaru, New Zealand, during the guard stage of the 2016 breeding season. These colonies were the Oamaru Blue Penguin Colony (OBPC) and the Oamaru Creek Penguin Refuge colony (Creek). These colonies are less than 1 km apart, so individuals have access to the same marine environment. Data loggers were used to assess at-sea behaviour and to determine the foraging range of little penguins at each colony.

All recorded foraging trips during the guard stage were single day trips and which penguins departed from their colony early in the morning and return to their colony in the evening. There were no consistent differences between colonies in foraging and diving behaviours. The mean maximum distance from each colony was < 25 km. There was a difference between colonies in the mean duration of trips, with a longer mean trip duration for Creek colony birds than OBPC birds. The mean return time to the colony was later for Creek individuals. The mean foraging range per trip was greater for Creek individuals than for OBPC birds. This difference in mean values was attributed to a higher proportion of wide-ranging trips by Creek individuals. Practical limitations for the study meant that the sample sizes were smaller than those of some other studies. It is considered likely that if a larger sample size had been possible then the results would have shown no difference between

colonies in the mean foraging range per trip during the guard stage in 2016. There were no differences between colonies in diving behaviour variables.

The total foraging areas for individuals from each colony were compared between colonies to determine if there were distinct foraging areas for birds from each colony. Distinct foraging areas have been observed for neighbouring populations of conspecifics for many seabird species. However, the foraging areas for little penguins from the OBPC and Creek colony is overlapped and were not distinct. Distinct foraging areas for seabirds from neighbouring colonies is thought to be driven by intra-specific competition, so competition between colonies for foraging areas appears to have been low for Oamaru little penguins during the 2016 guard stage.

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1. General introduction

1.1 Introduction

Little penguins are the smallest penguin species. They live around the New Zealand coastline and in Australia. The biology of little penguins is introduced in this general introduction, with a description of their morphology and taxonomic classification. Little penguins are classified by the Department of Conservation as at risk and declining. Their population status and current threats to survival are described, followed by a consideration of little penguin life history traits and their annual cycle.

Seabird foraging patterns are discussed in section two, including central place foraging theory, environmental and oceanographic patterns that influence foraging behaviour, and morphological and physiological constraints that different species, sexes, and age-classes face when foraging.

Little penguin foraging behaviour is then considered. Little penguins are central place foragers that are limited in their foraging range during chick rearing. Foraging during the breeding season is discussed and compared with foraging behaviour during the non-breeding winter period, followed by discussion on little penguin diving behaviour. Spatio-temporal variation in foraging behaviour between and amongst colonies is highly influenced by oceanographic features and temporal changes in the environment. Ocean productivity influences food availability for little penguins. Relationships between ocean productivity and foraging behaviour are described. Subsequently, variability in foraging behaviour with regard to sex or age is discussed. The last topic in the general introduction relates to conspecific interactions, with both the effects of group foraging and intra-specific competition discussed.

1.2 Little penguin biology

1.2.1 General description

Little penguins (*Eudyptula minor*), also known as kororā, little blue penguins and blue penguins, are the smallest living penguin species, weighing approximately 1 kg and measuring 40 cm in height (Marchant and Higgins, 1990; Salton *et al.*, 2015). One of three penguin species found on mainland New Zealand, they are distributed throughout the New Zealand coastline, including both Stewart and the Chatham islands. In addition, they are present along the south Australian coastline and parts of the western and eastern coast (Marchant and Higgins, 1990). Whilst males and females are generally monomorphic, there is minor sexual dimorphism in bill dimensions, with bills generally wider and longer in male than female penguins (Arnould *et al.*, 2004).

1.2.2 Taxonomy

The current classification of little penguins in New Zealand recognises a single species (*Eudyptula minor*), whereas an earlier classification recognised five subspecies (Gill, 2010). It has recently been proposed, on the basis of analysis of mitochondrial DNA, that there are two clades of little penguins. One clade is suggested to be Australian penguins and little penguins present on the south-east coast of the South Island of New Zealand, whilst the second clade is proposed to comprise other populations along the New Zealand coast (Peucker *et al.*, 2009). Multi-locus genetic analysis has provided support for recognition of the Australian and New Zealand clades as separate species, *Eudyptula novaehollandiae* and *E.minor* respectively (Grosser *et al.*, 2015). Osteological analysis has revealed differences in morphology between these clades as well, with differences in scores derived from principal components analysis of skeletal elements. However, comparison of individual skeletal

elements reveals no difference between these clades (Grosser *et al.*, 2017). The New Zealand and the historically Australian clade may have diverged somewhat since separation, although this may not represent a speciation event as interbreeding between these clades still does occur in New Zealand. In addition, evidence of behavioural divergence is weak and currently little penguins in New Zealand are still recognised a single species, *Eudyptula minor*.

1.2.3 Population status and threats

Little penguins are classified as 'at risk and declining' by the Department of Conservation and are expected to undergo a population decline of 10-30% over the next 10 years (Robertson *et al.*, 2017). Little penguin decline is attributed to a number of factors. These include predation, specifically from dogs and mustelids (Challies, 2015), and human disturbance, often by encroachment on penguin habitat through development. Increased human activity has resulted in a high number of road deaths in some colonies (Heber *et al.*, 2008; Braidwood, 2009). Furthermore, little penguins are vulnerable to threats at sea. Little penguins are often caught in near-shore set nets (Taylor, 2000). However, the greatest human induced at-sea threats are those that alter the marine environment. Oil spills pose as a major threat for little penguins with mass mortality events occurring in both New Zealand and Australia in recent history (Goldsworthy *et al.*, 2000; Sievwright, 2014). Further at-sea threats may include long term changes in foraging habitat resulting from climate change (Perriman *et al.*, 2000; Agnew *et al.*, 2015).

1.2.4 Annual cycle

Little Penguins are nocturnal while on land. Adults depart from colonies before dawn and return to their nests after dusk. Little Penguins will nest in a range of habitats, including

burrows, dense vegetation (Johannesen *et al.*, 2002a), and artificial structures such as nest-boxes. Little penguins will nest in areas with high levels of disturbance and there are anecdotal accounts of little penguins nesting under houses. Furthermore, penguins nesting in boxes close to walking tracks did not have lower breeding success than birds nesting further away from tracks (Braidwood *et al.*, 2011). Nest density in colonies with nest boxes is often very high and breeding birds may occupy nest boxes within 1 metre of each other (personal observation). However, nest density varies greatly between colonies, with densities between 0.01 nests/100 m^2 and 9-12 nests/100 m^2 having been observed (Fortescue, 1999; Lowe, 2009). Little penguins are highly philopatric and generally return to their natal colony. In addition, they also exhibit high nest site fidelity. If breeding is successful, it is likely that individuals will return to the same nest the following breeding season (Johannesen *et al.*, 2002a). Successful breeding season is also highly correlated with mate fidelity. Pairs that are successful in fledging chicks in a given season are more likely to reunite the following season compared to those that are not successful breeders (Johannesen *et al.*, 2002a; Rogers and Knight, 2006).

The timing and duration of the breeding season is highly variable across different years and between different colonies. Furthermore, breeding success is highly variable between colonies. This may be attributed to climatic conditions or whether a colony has a high proportion of 'double-brooders' (Perriman *et al.*, 2000; Agnew *et al.*, 2014). Breeding usually occurs between July and February in New Zealand, egg laying may occur over a range of months as pairs are not particularly synchronous (Gales, 1985; Heber *et al.*, 2008; Agnew *et al.*, 2015). The breeding season may be divided into 3 distinct periods: incubation, guard, and post-guard. Parents will lay 2 eggs in a clutch, and the eggs are incubated for approximately 35 days (Reilly and Cullen, 1981; Agnew *et al.*, 2014). During this period the

male and female take turns incubating the egg, while the other parent leaves to forage. Foraging trips are generally less than 5 days during incubation. However, longer trips have been recorded but they are generally associated with poor foraging conditions and colonies with lower breeding success (Fortescue, 1999; Numata *et al.*, 2000; Saraux *et al.*, 2016). Following hatching, brooding is shared between parents in a similar way to incubation. Foraging trips are generally restricted to one day during this period as parents alternate daily between nest attendance and foraging (Numata *et al.*, 2004). The chick guard period varies between colonies and years. The average guard stage lasts 14-20 days (Chiaradia and Kerry, 1999; Numata *et al.*, 2004; Chiaradia and Nisbet, 2006). Following the guard stage chicks are left alone during the day while both parents forage. This occurs until fledging, approximately 8 weeks after hatching.

Following fledging of chicks, parents return to sea to build fat reserves before fasting during moult (Gales and Green, 1990). Penguins undergo a 'catastrophic moult', in which all feathers are lost in one period (Brasso *et al.*, 2013). Moult last approximately 15-20 days during which time birds remain ashore and cannot feed (Reilly and Cullen, 1983). Following this period, birds return to sea to forage and will return to the colony periodically over the winter.

1.3 Drivers of seabird foraging patterns

1.3.1 Central place foraging

Seabirds breed on land and forage at sea, so their foraging range is constrained during the breeding season to areas around the breeding colony that are close enough for parents to regularly return to feed their young. Animals that return to a central place after each foraging bout are called central place foragers (Elliott *et al.*, 2009), so breeding seabirds are

considered to be central place foragers. Some seabirds are central place foragers for most of the year as they return to land for moulting and to rest as well as for breeding. Seabirds are limited to foraging around their central place and hence are affected by changes in prey availability within their foraging area. Populations confined to foraging zones with lower prey density show greater foraging effort or may have lower reproductive success than other populations (Jakubas *et al.*, 2013). Furthermore, because central place foragers are highly constrained in where they can forage these species cannot avoid anthropogenic threats such as oil spills or trawl net fishing within their foraging zone (Trathan *et al.*, 2015). Central place foraging theory predicts that animals will minimise their travel time by selecting foraging areas close to the breeding colony and will travel by the most direct path to and from the central place. The distance that an individual must travel generally depends on how far away suitable prey patches are located (Orians and Pearson, 1979). For central place foragers this distance is often related to three factors:

1) the distance between suitable breeding habitat and suitable prey habitat
2) depletion of nearby food sources over time
3) intra-specific competition reducing forging efficiency near to the colony

Seabirds require distinct habitats for foraging and for breeding (ocean for feeding and a terrestrial site for breeding). Both habitats must be suitable, so populations may breed some distance from suitable prey patches, in which case individuals are required to 'commute' from their colonies to foraging sites (Weimerskirch, 2007). Furthermore, because locations that have suitable terrestrial habitat with adjacent oceanic habitat are rare, the breeding locations can become densely populated. Dense colonies are particularly vulnerable to prey depletion within their foraging zone. This may occur due to high levels of predation locally or may be the result of prey species actively moving further from the colony to reduce

predation pressure (Hemerik *et al.*, 2014). This is referred to as Ashmole's halo and it is predicted that a halo of low food availability will occur around a colony due to food resource depletion. A larger colony will have a larger 'halo' (Birt *et al.*, 1987), so individuals must forage further from larger than from smaller colonies. Furthermore, high intra-specific competition near the colony may reduce foraging efficiency within nearby prey patches, resulting in individuals foraging further from the colony. Seabirds have been observed bypassing large foraging flocks in favour of foraging at more distant prey patches (Irons, 1998; Davoren *et al.*, 2003). This is perhaps related to high competition experienced in flocks. However, whether an individual forages in prey patches distant from colonies where there is reduced competition for food or forages in large flocks closer to colonies may be dependent on behaviours that are species specific. Both solitary and group foraging has been observed among little penguins, with the effectiveness of each behaviour depending on prey type (Sutton *et al.*, 2015). In contrast to the little penguin, most seabirds do forage in flocks (Shealer, 2002). Group foraging may result from coarse-scale aggregations where individuals group together because of high prey density at a specific location or from fine-scale processes where birds may undertake co-operative foraging (Pöysä, 1992). Foraging patterns that further mitigate intra-specific competition include both age or sex segregation, whereby individuals of differing age classes or sex may forage in different locations or have different prey preferences (González-Solís *et al.*, 2000; Pelletier *et al.*, 2014).

In addition, prey depletion and intra-specific competition can be exacerbated by the presence of conspecifics from other colonies within the same foraging range (Furness and Birkhead, 1984). Foraging patterns may alter due to inter-colony competition. Colonies that have theoretically overlapping foraging ranges may show some form of segregation whilst foraging. Cape gannets (*Morus capensis*) from neighbouring breeding colonies had very

little overlap in their foraging areas. Colonies that were 110 km apart with foraging zones that were predicted to overlap by to 89% had only 13-14% overlap (Grémillet *et al.*, 2004). Similar observations were recorded for Northern gannets (*Morus bassanus*) (Wakefield *et al.*, 2013). Colonies of Cory's shearwaters (*Calonectris borealis*) within 2 km of each other also had partial spatial segregation during foraging trips (Ceia *et al.*, 2015a). Colonies that overlap in foraging locations may vary in other feeding behaviours. Little penguins that have broadly overlapping foraging ranges during the pre-laying and incubation stages have been shown to vary in prey species taken for birds from different colonies. Anchovies formed the majority of the diet for penguins at one colony, while birds at a neighbouring colony fed on a diverse range of prey (Chiaradia *et al.*, 2012).

During the breeding season birds undergo a trade-off between foraging strategies that benefit offspring and strategies that benefit the adults. Longer trips are thought to benefit the adult because they may forage in more distant and productive areas, and birds may forage for longer (Ropert-Coudert *et al.*, 2004). Conversely, shorter foraging trips will benefit offspring because parents will return more often to feed them. Many species undertake long foraging trips for most of the year, and then reduce trip duration during chick rearing. However, changes in environmental conditions that may reduce foraging efficiency can cause adults to revert back to longer foraging trips at the expense of their chicks. For example, stormy conditions can cause little penguins to forage for longer and penguins in poor body condition more frequently engage in long foraging trips (Numata *et al.*, 2000; Agnew *et al.*, 2015).

1.3.2 Environmental and oceanographic processes

Seabird foraging patterns are often highly correlated with environmental and oceanographic variables. Although central place foraging theory highlights how individuals are bound to

forage within a certain range, specific foraging locations are often closely associated with oceanographic characteristics (Hunt, 1999; Weimerskirch, 2007). The marine environment is far from uniform. Prey are often patchily distributed and certain oceanographic features that favour high prey abundance are often associated with the presence of seabirds. Seabirds inhabit a highly heterogeneous environment with a range of underlying physical processes that act at range of spatial scales. This results in hierarchical prey distribution, where prey patches are often nested in larger areas of prey abundance (Kotliar and Wiens, 1990). Therefore, if seabirds are to exploit areas with the greatest abundance of prey, they must respond to oceanic processes at multiple scales. Major physical processes that control prey distribution include large oceanic gyres and circulation systems. These systems act at a 'mega-scale' and influence ocean productivity by controlling the distribution and assemblages of planktonic species over large biogeographical regions. Within these regions are 'macro-scale' processes that result in lesser or greater productivity in a given area (Hunt, 1987). Global seabird distribution and abundance are associated with processes that act at the mega-scale. Greater seabird density is typically observed at ocean margins and avifauna may vary on each side of large oceans (Hunt, 1987). Because mega-scale processes act at very large spatial scales (thousands of kilometres), they do not influence daily seabird foraging patterns. However, the scale at which oceanic features can influence a species' foraging behaviour will depend on the foraging range of the species and on their preferential prey species. For example, wandering albatrosses (*Diomedea exulans*) forage for widely dispersed prey and therefore cover an extensive area while foraging (Weimerskirch *et al.*, 2005), whereas grey-headed albatrosses (*Thalassarche chrysostoma*) tend to concentrate their feeding activity around physical features that aggregate prey due to meso-scale processes (Nel *et al.*, 2001). In addition, many penguin species are also constrained in the scales they can exploit prey at because they are limited in their daily foraging range (Cotté *et al.*, 2007).

Smaller scale processes, those acting at a ‘meso-scale’ or ‘coarse-scale’, form prey patches that may influence daily seabird foraging patterns. These physical processes usually result from interactions between adjacent water bodies and may include eddies, bathymetric gradients, upwelling zones, fronts and fresh-water plumes at river outlets (Hunt, 1987). These meso-scale features are associated with high biological production (Martin *et al.*, 2002) and often create distinct aggregations of prey species which seabirds can exploit. Meso-scale features may also cause prey aggregation due to physical forcing. For example, strong tidal upwelling may force fish to the surface where seabirds may feed on them (Hunt, 1999). As a result, seabirds are thought to concentrate their foraging efforts within these areas because it is where prey biomass is likely to be highest. There are numerous examples of seabirds aggregating or showing increased foraging activity at mesoscale features (Hunt, 1987; Weimerskirch, 2007). For example, shelf edges, eddies and fronts are popular foraging locations for various seabird species including gannets, penguins, petrels and terns (Cotté *et al.*, 2007; Weimerskirch, 2007; Sabarros *et al.*, 2014; Bon *et al.*, 2015). The physical features that are correlated with increased foraging activity may vary between species. For example, within the Mozambique Channel, sooty terns (*Onychoprion fuscatus*) commonly associate with cyclonic eddies; red-footed boobies (*Sula sula*) concentrate at divergent zones; and frigate birds (*Fregata spp*) are found in frontal zones (Jaquemet *et al.*, 2014).

Foraging patterns may also be influenced by fine scale processes. At fine spatial scales physical processes that influence how seabirds select foraging sites may include water temperature or the presence of thermoclines. In addition, biological factors such as olfactory cues or visual information may help individuals locate prey patches. For example, procellariforms are able to locate prey by using olfactory cues (Nevitt *et al.*, 2008). Local

enhancement may also influence fine-scale foraging decisions among seabirds. This occurs when individuals observe conspecifics as indicators of prey presence (Thiebault *et al.*, 2014). This often results in seabirds aggregating in large flocks over relatively small spatial scales.

1.3.3 Physiological and morphological constraints

Inter-specific differences in physiology and physical traits may also cause variation in foraging behaviour between species. Divergence in body form among marine species is reflected in the various foraging modes that have been observed. Among flying species, feeding methods may vary with differences in wing morphology. For example, the wandering albatross has a high aspect ratio wing and low wing loading, which are suited to using wind to glide over long distances, so they can forage over a very large range (Jouventin and Weimerskirch, 1990; Shaffer *et al.*, 2001). Alternatively, birds with wing morphology that are not suited to soaring will expend greater energy foraging over a large range and differ in feeding methods. For example, sooty terns and brown noddies (*Anous stolidusare*) are similar in body mass but differ in wing morphology. Sooty terns have a higher wing aspect ratio and longer wingspan than brown noddies. These morphological differences are reflected in their foraging behaviour, with sooty terns foraging over much greater distances and for longer durations than brown noddies (Hertel and Ballance, 1999). Conversely, some seabirds are adapted to diving and their wing morphology is suited to this rather than to long distance flight. Penguins for example, being obligate divers, have relatively large wing bones, reduced wingspan and greater muscle myoglobin concentration (Kooyman and Ponganis, 1998; Ksepka and Ando, 2011), which help them to pursue prey underwater. Furthermore, diving ability is often correlated with body mass; larger species can dive deeper and for a greater duration. This is because larger species generally have a greater oxygen store relative to their oxygen usage (Mori, 2002). For example, emperor penguins

(*Aptenodytes forsteri*), Adélie penguins (*Pygoscelis adeliae*) and little penguins can dive to depths over 500, 150 and 60 m respectively (Sato *et al.*, 2002; Ropert-Coudert *et al.*, 2006a; Wienecke *et al.*, 2007). Diving behaviour may also be influenced by physiological parameters relating to oxygen storage. Oxygen may be stored in the lungs as respiratory oxygen, bound to haemoglobin in the blood, or bound to myoglobin in the muscle. Feeding strategies may vary depending on how oxygen is stored during a diving bout. For example, haematological parameters in three procellariform species vary in relation to their diving parameters. The relatively deep diving sooty shearwater (*Puffinus griseus*) has a higher blood volume and red blood cell count than grey-faced petrels (*Pterodroma macroptera gouldi*) and common diving petrels (*Pelecanoides urinatrix urinatrix*) (Dunphy *et al.*, 2015). However, respiratory oxygen stores are higher among the shallow diving species. This likely reflects buoyancy costs that a deep diving species would encounter with high respiratory oxygen stores. Furthermore, this relationship has been noted among diving Alcids. Thick-billed murres (*Uria lomvia*) have lower respiratory stores per kg than the shallow diving Cassin's auklets (*Ptychoramphus aleuticus;* Elliott *et al.*, 2010). Similarly, penguins that exhibit shallower dives store a greater percentage of total oxygen as respiratory oxygen. Adélie penguins have a respiratory oxygen volume of 73 ml out of 217 ml of total oxygen volume available for diving (33.6%). In contrast, little penguins store 42.6% of total oxygen as respiratory oxygen (Hansen and Ricklefs, 2004). Furthermore, the deep diving emperor penguin stores only 19% of total body oxygen within the respiratory system, with 47% stored in muscle (Ponganis *et al.*, 2010).

Variation in foraging and diving behaviour also exists within species. This is often related to variation in environmental parameters between colonies or over seasons. For example, birds may adjust their foraging behaviour in response to changes in prey distribution, presence of

dependent offspring, or changes in weather (Phillips *et al.*, 2017). However, individuals within a single colony often vary in foraging behaviour over a single season. Such variation often correlates with demographic parameters such as gender or age. Much like inter-specific differences in foraging behaviour, this may relate to morphological or physiological differences between individuals. It has been argued that differences in foraging behaviour between sexes are related to body size, thus dimorphic species will exhibit greater inter-sexual variance. Foraging differentiation between sexes has been identified in number of dimorphic species (Lewis *et al.*, 2002). Trip range and duration are positively correlated with wingspan for lesser black-backed gulls (*Larus fuscus*) and larger males can forage much further from the colony than females (Camphuysen *et al.*, 2015). Similarly, red-footed boobies exhibit reverse sexual dimorphism, and larger females forage farther, can dive to a greater depth, and fly faster than their male counterparts (Weimerskirch *et al.*, 2006). Inter-sexual differences in foraging behaviour have also been observed among Spheniscidae. Among African penguins (*Spheniscus demersus*), males on average dive significantly deeper than females. However, maximum dive depth does not vary between sexes (Pichegru *et al.*, 2013). Furthermore, male and female Adélie and Magellanic penguins (*Spheniscus magellanicus*) feed at different trophic levels. Male Adélie penguins feed at a higher trophic level and in the pelagic zone, whereas females feed coastally (Beaulieu *et al.*, 2010). This may reflect differences in foraging ability between the sexes due to sexual dimorphism. However, differences in foraging behaviour have been noted among monomorphic species also. For example, female northern gannets dive deeper and for greater duration than males. This species is monomorphic, so body size does not contribute to this variation (Lewis *et al.*, 2002). Alternate foraging behaviour may reflect niche partitioning to reduce intra-specific competition, or different nutritional requirements for each sex.

Foraging behaviour often varies between individuals of different ages. Differences in foraging efficiency, explorative behaviour, and age-related spatial segregation during foraging bouts have been observed. Middle aged thick-billed murres (*Uria lomvia*) have lower activity levels per dive than either young or old birds, indicating greater foraging efficiency per dive (Cunningham *et al.*, 2017). Similarly, king penguins (*Aptenodytes patagonicus*) adjust their diving behaviour as they age. Older king penguins exert greater effort than juveniles in the initial stages of descent but show less effort at the bottom stages and diving ascent (Le Vaillant *et al.*, 2012). As individuals grow, they may improve their foraging ability due to having greater experience, individuals will learn how best to acquire resources as they age. Alternatively, physiological and anatomical changes that occur while aging may improve foraging efficiency. For example, older king penguins may have greater pectoral muscle mass, therefore dives will require less effort overall. In contrast, older penguins may have learned to position themselves in a more hydrodynamic posture while diving, reducing dive effort. In addition to diving, learned behaviour may also influence foraging range. Younger birds tend to be more explorative, while adults often show greater fidelity to productive foraging zones. Relative to immatures, adult northern gannets show high foraging site and route fidelity. In addition, immatures showed great variation in distal locations between foraging trips (Votier *et al.*, 2017). Juvenile exploration possibly occurs because immatures, unlike adults, have not yet learned of productive foraging sites surrounding the colony. Similarly, wandering albatross juveniles infrequently used 'restricted foraging' behaviour compared to adults. Restricted foraging behaviour for albatrosses involves repeated searching for prey within a confined area typically less than 100 km in diameter. Juveniles performed prey searching behaviour over areas greater than 1000 km in diameter. Furthermore, juvenile and adult foraging zones were spatially segregated (Riotte-Lambert and Weimerskirch, 2013). Juveniles were restricted to deep waters in sub-

tropical zones, whereas adults foraged at shelf edges, sub-Antarctic and sub-tropical deep waters. The authors suggest that juveniles gain an advantage foraging in the lighter winds of the sub-tropical zone compared to adults, and that this segregation could reduce intra-specific competition between the age classes. Similar patterns have been observed among emperor penguins; while adults forage within the Ross Sea, juveniles forage further from the coast and over a much larger area (Kooyman *et al.*, 1996). Although observations suggest there is a general trend for foraging skills to increase as birds age, this may be exacerbated by selection against individuals that are poor foragers over time. Therefore, adults will have a greater proportion of poor foragers removed from their age-class compared to juveniles (Orgeret *et al.*, 2016). Differences in foraging behaviour are also present between middle aged and older age classes, with foraging ability reducing with age due to senescence. Old male grey-headed albatrosses perform longer foraging trips during the incubation period than their middle-aged counterparts, and middle-aged individuals have a 65% greater mass gain per trip compared to old males. This suggests that foraging is much less efficient for older males during this stage (Catry *et al.*, 2006). Catry *et al.* (2011) also suggests Cory's shearwaters decline in their ability to perform spontaneous bouts of activity as they age. Older individuals perform less 'take-offs' during a foraging bout. However, this may also indicate that older individuals are foraging more efficiently, thus do not need to 'take-off' and search for prey as often as middle-aged birds.

Understanding variation in foraging behaviour between different sexes and age-classes has important demographic implications. For example, different groups of individuals may be more prone to anthropogenic threats or changes in oceanographic processes such as fisheries bycatch or climate change respectively. Furthermore, if a specific gender or age-class exhibits higher foraging site fidelity, they will be vulnerable to changes in resource

availability within their foraging zone. In addition, individuals that require greater foraging effort to meet nutritional demands may struggle during seasons of low resource availability or in the face of environmental change. This variation can result in differential survival rates between sexes or age classes which can have implications for population demography.

1.4 Little penguin foraging behaviour

1.4.1 General description

Little penguins are inshore foragers that typically feed in shallow coastal waters. They usually depart from the colony before sunrise to undertake foraging trips and return after sunset. In the evening, penguins may form groups called rafts offshore from the colony, then arrive on land in rafts. Rafting has been observed at large nest box colonies in New Zealand, although rafting has not often been observed on coastlines where there are natural nest sites at much lower densities. Although it has been suggested that this behaviour is unique to Australian clade individuals (Grosser *et al.*, 2015), rafting has been observed in penguins that would not be classified as Australian clade. Little penguins are classified as central place foragers as they must return to their nest site on land to engage in breeding behaviours such as nest building or courtship. Little penguins can undertake single day trips or forage for multiple days. When foraging for a single day, penguins usually remain within 25 km of the colony. Typically, little penguins are pelagic foragers, diving to the upper parts of the water column. The foraging behaviour of little penguins is variable between locations, years and across breeding stages. Little penguin foraging behaviour has been studied widely throughout their range (Fig. 1.3), although detailed reports of foraging behaviour in New Zealand are limited to only a few colonies (Fig. 1.4).

This review highlights the foraging capability of little penguins and considers how their behaviour and foraging success can change through time and space. Behavioural change may be related to demands imposed by breeding or could be influenced by environmental variables. Little penguins are highly plastic in their foraging behaviour, altering their diet and behaviour in relation to environmental conditions. As environmental conditions are dynamic, little penguins vary in foraging behaviour between colonies, and between years at the same colony. However, some evidence suggests that behaviour may be influenced by sex or age. In addition, intra-specific interactions may influence behaviour, both through the effects of group foraging and the general influence of intra-specific competition.

1.4.2 Foraging constraints

As the smallest of all penguin species, little penguins are limited to a relatively small foraging area due to physiological and morphological constraints. In general, penguin foraging ranges are related to body size. Larger species can swim faster, thus they can cover a larger area during a foraging trip (Sato *et al.*, 2010). Average horizontal travel speeds for little penguins have been reported at 1.1 ms^{-1} (Bethge *et al.*, 1997a; Zhang *et al.*, 2015). However, true swim speeds average 1.8 ms^{-1}, with maximum speeds of 3.3 ms^{-1} reported by Bethge *et al.* (1997a). When travelling to foraging sites and searching for prey, penguins typically travel at a speed which minimises the cost of transport (Wilson *et al.*, 2002; Sato *et al.*, 2010). The relatively slow travel speeds, in conjunction with the limited thermoregulatory and fasting ability of little penguin chicks, means that during the chick-rearing period, adults can only cover a small distance before returning to the colony (Hoskins *et al.*, 2008). The mean foraging range for little penguins conducting single day trips is therefore typically limited to within 25 km of their colony. However, single day trips with maximum distances from the colony of 36 and 35.2 km have been recorded for Australian and New Zealand birds

respectively (Hoskins *et al.*, 2008; Agnew, 2014). In addition to provisioning chicks, birds are also constrained by having to replace incubating partners on the nest so the partner can go to sea to forage. In addition to limitations in their foraging range, little penguins cannot dive as deep or for as long as large penguin species (Bethge *et al.*, 1997a). The deepest recorded dive for a little penguin is 66.7 m, but they typically do not dive deeper than 30 m (Ropert-Coudert *et al.*, 2006a). These constraints make little penguins particularly sensitive to variations in prey availability near the colony. However, outside of the breeding season, penguins are not restricted by some of these factors, and may forage for multiple days and travel greater distances. Because of these seasonal limitations, foraging behaviour varies throughout the year and is often studied during four stages: incubation, guard stage, post-guard, and non-breeding. Trips are often classified as short (single day trips) or long (multiple days at sea). The likelihood of a trip being short or long varies depending on the breeding stage.

1.4.3 Diving behaviour

While little penguins are capable of diving to depths of more than 60 m, the majority of dives are markedly shallower than this (Ropert-Coudert *et al.*, 2006a). Mean diving depths for little penguins have been reported from 3.4 to 17.8 m (Bethge *et al.*, 1997b; Ropert-Coudert *et al.*, 2007), with mean dive durations from 7.7 to 38.6 s (Zimmer *et al.*, 2011a; Wiebkin, 2012). These two parameters are usually correlated, with dives of longer duration typically being deeper (Chilvers, 2017). The profile of individual dives can be split into multiple phases: descent, bottom and ascent. Where descent is the period when individuals are diving to the deepest section of the dive, bottom is the phase that is spent around the deepest area of the dive, and ascent is the return to the surface. The bottom phase is typically associated with prey pursuit. Ropert-Coudert *et al.* (2006b) reported that prey pursuit, as indicated by brief

bursts of increased flipper beating, did occur primarily at the bottom of a dive, with 75.4% of prey pursuit events happening in the bottom phase. In addition, little penguins may capture prey from above, as most prey pursuit events were associated with downwards travel. Among diving mammals and seabirds, dives have been further categorised as U, V, or W shaped (Fig. 1.1). V dives typically have no or a very brief bottom phase and are thought to be primarily exploratory dives, while U or W dives are associated with prey capture (Wilson, 1995). The U shape represents a flat bottom phase, while W dives represent wiggles or undulations occurring during the bottom phase. Among little penguins, it has been suggested that U shape dives could represent exploratory movements as well. Mattern (2001) reported a high proportion of dives as U shape at both Motuara Island and Oamaru (80.3 and 73.2%, respectively), while 84.6% of dives from St Kilda breakwater penguins had a bottom phase (Preston *et al.*, 2008). Mattern (2001) suggests that U dives with undulations (W dives) are more likely to represent prey pursuit. More recently, a metric for prey pursuit involves accelerometer data, whereby surges of acceleration can produce a signature distinctive of a prey capture or prey pursuit (Carroll *et al.*, 2014).

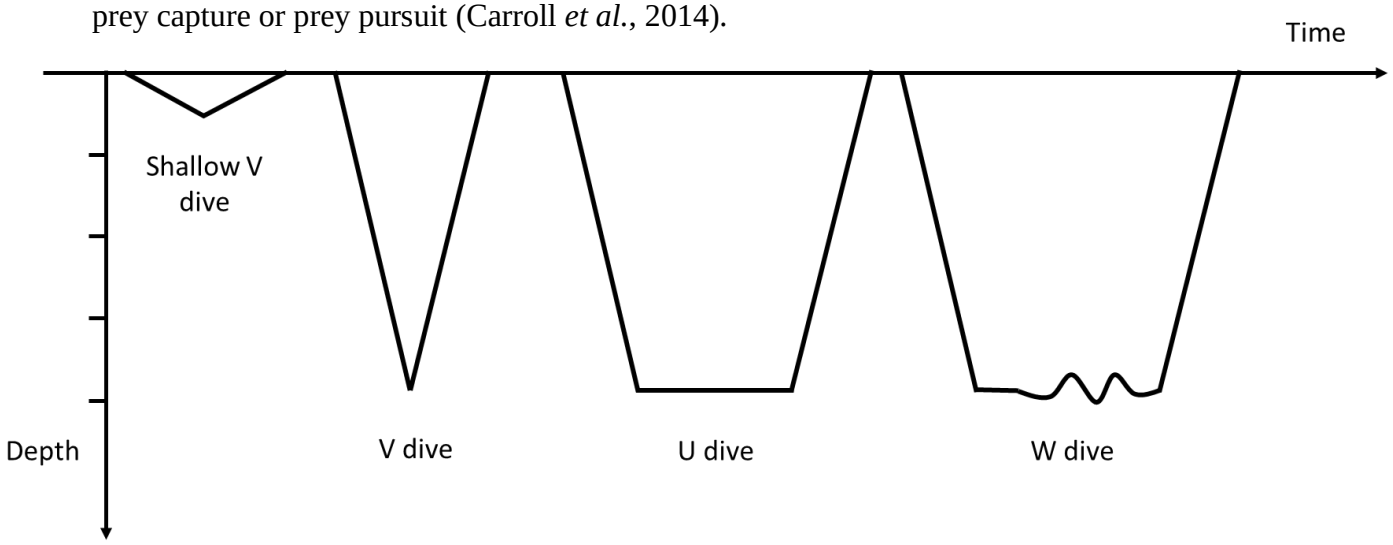

Fig. 1.1. Dive diagram to show dive shapes of penguins. Shallow V-dives (to less than 1 m) are often associated with travel rather than prey searching or pursuit and are typically excluded from diving analyses. V-dives are thought to be exploratory, while U and W- dives are associated with prey pursuit or capture.

At many colonies the foraging range of little penguins includes a substantial area where water depth is greater than 30 m; despite this the vast majority of dives do not reach these depths (Chiaradia *et al.*, 2007b). Little penguins are primarily pelagic divers, with most dives occurring within the first 20 m of the water column. Although physiologically able to dive deeper, shallower diving may represent a more optimal foraging strategy**.** As visual predators, penguins are dependent on light to locate and capture prey. Little penguins held in pools pursued prey more often when light levels were higher (Cannell and Cullen, 1998). As light does not penetrate deeper waters as well, little penguins may forage less effectively at greater depths. Furthermore, multiple studies have shown dive depth is greater near midday, when ambient light would penetrate deeper water (Mattern, 2001; Ropert-Coudert *et al.*, 2006b). In addition, given that the oxygen stores of little penguins are estimated at 45 ml/kg before a dive, the aerobic dive limit (ADL) for little penguins has been calculated at 44 seconds (Bethge *et al.*, 1997a). Dives that go beyond the ADL result in an increase in blood lactate levels, which can induce muscle fatigue and are associated with long post-dive intervals. Repeatedly diving beyond this limit may reduce foraging ability by reducing time available for diving.

In response to low prey availability, penguins may increase their foraging effort through increasing foraging duration and range or increasing their diving effort. Diving effort is often calculated as the total time or proportion of a trip spent diving (Agnew, 2014; Berlincourt and Arnould, 2015). The total vertical distance travelled during a trip has also been used as a measure of diving effort (Hoskins *et al.*, 2008; Pelletier *et al.*, 2014). Total diving time is a function of dive duration and the number of dives. The mean number of dives per day has been reported as 391 to 2119 (Wiebkin, 2012; Sánchez *et al.*, 2018), although the number of dives per day is typically between 600 and 900 (Table 1.1). Little penguins only dive during

daylight. Usually, little penguins will dive for 4 to 6 hours within a day, and this typically represents about 30 – 60 % of total trip duration.

However, as little penguins depart and return to the colony under darkness, when they do not dive, the total time spent diving will represent a larger portion of their active foraging time. Furthermore, little research has been done on winter foraging and diving time likely contributes to a greater proportion of the day during this period, as the daylight period is shorter. The number of dives per day is often correlated with mean or median dive depths. Generally, when little penguins conduct shallow dives throughout the day, they dive more often (Mattern, 2001; Amélineau *et al.*, 2021). Diving effort can remain unchanged as dive depth and diving rate changes. For example, individuals from Phillip Island dived twice as deep as Kanowna Island individuals while each colony had similar vertical travel distance per hour. This occurred because Kanowna Island individuals dived twice as often (Hoskins *et al.*, 2008). Generally higher foraging effort is associated with deeper diving (Chiaradia *et al.*, 2007b). However, an increase in the number of dives can mediate greater foraging effort (Agnew, 2014; Amélineau *et al.*, 2021). For example, total daily diving time increased during the 2010 breeding season at Oamaru with more and shallower dives (Agnew, 2014). Diving behaviour is often visually depicted as a dive profile with depth on the x axis and time on the y axis. Variability in diving behaviour throughout a trip can be observed from such profiles (Fig 1.2).

Diving behaviour can be characterised with calculated variables. For example, foraging efficiency is often defined as the proportion of dives which involve a prey pursuit. If penguins are pursuing prey more often, their foraging behaviour is assumed to be more efficient. Diving efficiency has been calculated as:

$$\text{Dive efficiency} = \frac{\text{Bottom duration}}{\text{Dive duration + post dive duration}}$$

As the bottom phase is associated with prey pursuit, this calculates the theoretical proportion of time spent foraging during a dive (Ydenberg and Clark, 1989).

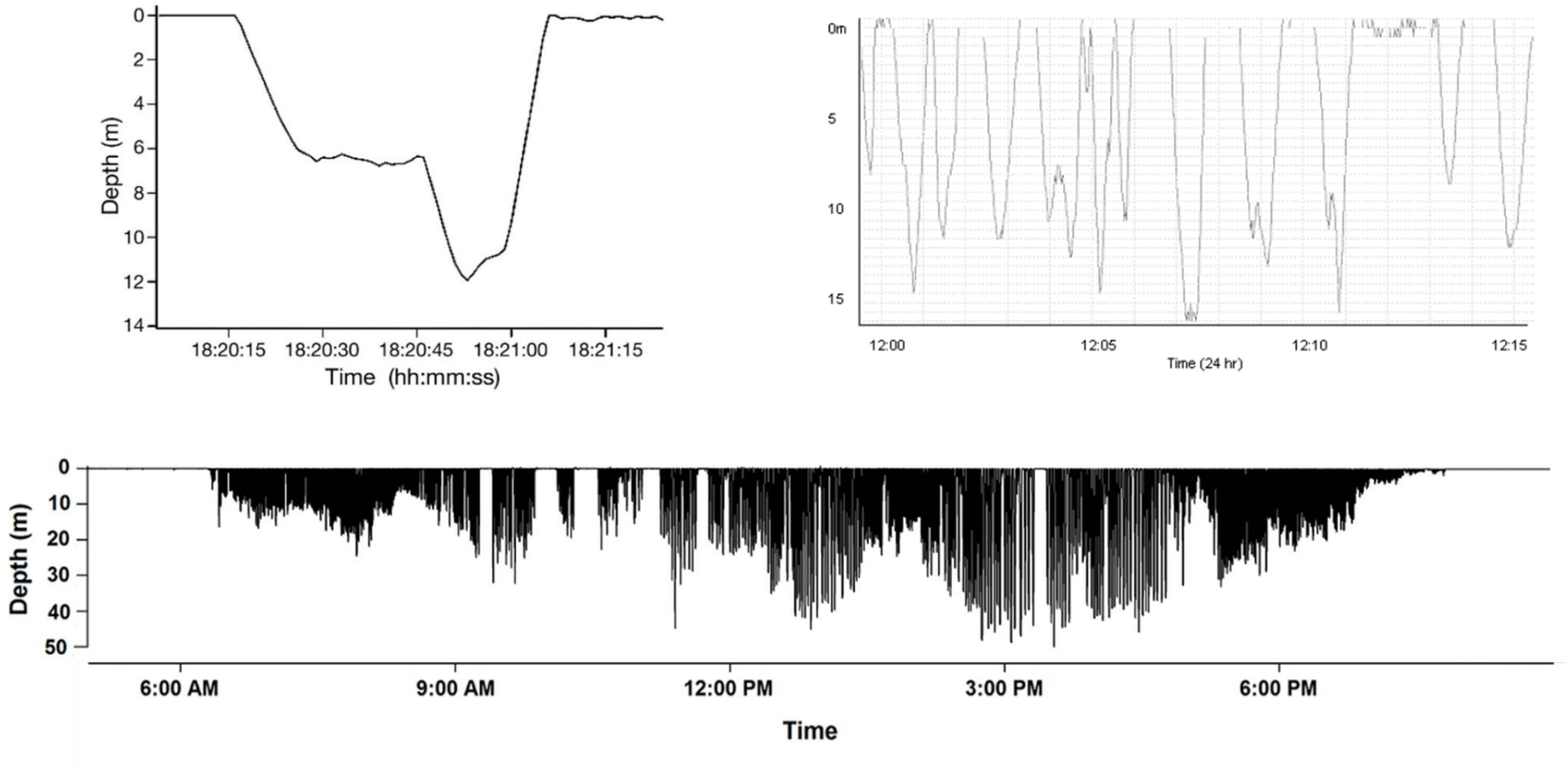

Fig. 1.2. Examples from the literature of little penguin dive profiles, illustrating a single dive (Preston *et al.*, 2008), a series of dives (Wiebkin, 2012), and all dives throughout a foraging trip (Sánchez *et al.*, 2018).

Table 1.1. Summary of previous research on little penguin diving behaviour[1]. Values are presented as mean ± S.D.

Mean diving time (h)	Mean diving time (% of trip)	Mean depth (m)	Mean duration (s)	Mean bottom time (s)	Mean bottom time (% of dive)	Mean dive efficiency	Mean number of dives	Number of trips	Location	Year	Notes	Reference
	62 ± 0.2	6.4 ± 0.6	24.6 ± 0.3		20.3 ± 0.6		1447 ± 220	4	Adele Is.	2012	G	Chilvers (2017)
	34.8 ± 11.1	12.7 ± 7.7				0.17 ± 13.0		32	Gabo Is	2013	G	Berlincourt and Arnould (2015)
	38.4 ± 7.9	11.4 ± 7.9				0.14 ± 0.12		16	Gabo Is	2013	PG	Berlincourt and Arnould (2015)
	35.2 ± 12.4	8.8 ± 5.9				0.27 ± 0.17		27	Gabo Is	2012	G	Berlincourt and Arnould (2015)
	28 ± 8.7	10.3 ± 7.7				0.22 ± 0.16		12	Gabo Is	2012	PG	Berlincourt and Arnould (2015)
	27.9 ± 7.1	9.8 ± 6.8				0.22 ± 0.16		17	Gabo Is	2011	G	Berlincourt and Arnould (2015)
	32 ± 13.8	9.5 ± 8.2				0.26 ± 0.17		10	Gabo Is	2011	PG	Berlincourt and Arnould (2015)
		7.1 ± 0.1						6	Gabo Is.	2014	G, Males	Sutton *et al.* (2015)
		5.7 ± 0.2						5	Gabo Is.	2014	G, Females	Sutton *et al.* (2015)
		5.4 ± 2.3	13.2 ± 12.4				1402 ± 418	8	Kanowna Is.	2005	G	Hoskins *et al.* (2008)
	71 ± 0.4	6.1 ± 2.7	20.1 ± 5.8		16 ± 4.5		1750 ± 562	14	Leisure Is.	2014	I	Chilvers *et al.* (2015)
		12.3 ± 0.2						5	London Bridge	2014	G, Males	Sutton *et al.* (2015)

Mean diving time (h)	Mean diving time (% of trip)	Mean depth (m)	Mean duration (s)	Mean bottom time (s)	Mean bottom time (% of dive)	Mean dive efficiency	Mean number of dives	Number of trips	Location	Year	Notes	Reference
		5.7 ± 0.1						5	London Bridge	2014	G, Females	Sutton *et al.* (2015)
	27.2 ± 13.2	9.2 ± 5.4				0.14 ± 0.11		26	London Bridge	2013	G	Berlincourt and Arnould (2015)
	30.4 ± 17.5	6.8 ± 4.1				0.18 ± 0.11		7	London Bridge	2013	PG	Berlincourt and Arnould (2015)
	22 ± 15.2	7.1 ± 4.6				0.21 ± 0.16		25	London Bridge	2012	G	Berlincourt and Arnould (2015)
	21 ± 13.8	6.8 ± 5.2				0.21 ± 0.17		17	London Bridge	2012	PG	Berlincourt and Arnould (2015)
	42.3 ± 8.5	11 ± 6				0.18 ± 0.15		17	London Bridge	2011	G	Berlincourt and Arnould (2015)
	25.8 ± 4.8	10.1 ± 6.1				0.17 ± 0.15		4	London Bridge	2011	PG	Berlincourt and Arnould (2015)
	60	3.4 ± 3.9	21.3 ± 8.42				500	12	Marion Bay	1993	B	Bethge *et al.* (1997b)
		13.9	23.6	23.3			711	5	Matiu / Somes Is.			Chilvers (2017)
		7.6	25.9	14.1				23	Montague Is.	2013	B, *, Dives with prey capture	Carroll *et al.* (2014)
		2.6	6.9	4				23	Montague Is.	2013	B, *, Dives with no prey capture	Carroll *et al.* (2014)

Mean diving time (h)	Mean diving time (% of trip)	Mean depth (m)	Mean duration (s)	Mean bottom time (s)	Mean bottom time (% of dive)	Mean dive efficiency	Mean number of dives	Number of trips	Location	Year	Notes	Reference
	60 ± 22	11.5 ± 0.3	31.7 ± 0.5		16 ± 0.5		1014 ± 357	7	Motuara Is.	2014	Unknown breeding state	Chilvers (2019)
8.6		11 ± 2.7			32 ± 6	0.21 ± 0.05		4	Motuara Is.	2000	G	Chiaradia *et al.* (2007b)
	61.3 ± 4.9	6.0 ± 3.7	22.4 ± 12.9	12.3 ± 7.8			1165 ± 137	5	Motuara Is.	2000	G	Mattern (2001)
4.89		9.74		0.47			620	6	Oamaru	2012	Pre egg, median	Agnew (2014)
5.31		8.28		0.44			754	17	Oamaru	2012	I, median	Agnew (2014)
6.26		9.8		0.42			898	13	Oamaru	2012	CR, median	Agnew (2014)
3.38		6.31		0.44			597	9	Oamaru	2012	I, 2nd brood, median	Agnew (2014)
3.9		5.06		0.42			838	7	Oamaru	2012	CR, 2nd brood, median	Agnew (2014)
4.94		8.49		0.47			584	9	Oamaru	2011	Pre egg, median	Agnew (2014)
7.05		10.27		0.46			836	15	Oamaru	2011	I, median	Agnew (2014)
4.17		6.66		0.44			727	13	Oamaru	2011	CR, median	Agnew (2014)
4.18		11.6		0.42			461	7	Oamaru	2010	Pre egg, median	Agnew (2014)
4.9		9.99		0.41			566	9	Oamaru	2010	I, median	Agnew (2014)
6.11		12.67		0.41			696	8	Oamaru	2010	CR, median	Agnew (2014)

Mean diving time (h)	Mean diving time (% of trip)	Mean depth (m)	Mean duration (s)	Mean bottom time (s)	Mean bottom time (% of dive)	Mean dive efficiency	Mean number of dives	Number of trips	Location	Year	Notes	Reference
5.78		7.31		0.44			874	6	Oamaru	2010	I, 2nd brood, median	Agnew (2014)
8.59		7.91		0.46			1264	4	Oamaru	2010	CR, 2nd brood, median	Agnew (2014)
4.4		5 ± 0.9			34 ± 6	0.16 ± 0.04		4	Oamaru	2000	G	Chiaradia *et al.* (2007b)
	29.8 ± 5.3	10.1 ± 5.6	29.5 ± 12.9	15.0 ± 7.6			809 ± 87	6	Oamaru	2000	CR	Mattern (2001)
	43 ± 0.2	5.2 ± 0.8	19.6 ± 0.2		9.6 ± 0.4		1283 ± 416	4	Pearl Is.	2011	G	Chilvers (2017)
5.8 ± 1.0		13.4 ± 3.6	38.6 ± 4.0	10.9 ± 0.6	0.29 ± 0.03		534 ± 91	3	Pearson Is.	2004	G	Wiebkin (2012)
5.5	38.7	10.4	37.7		52.6		516 ± 128	4	Penguin Is.	2002	CR	Ropert-Coudert *et al.* (2006b)
	30	1.9					1430	4	Penguin Is.	2001	B, "Shallow divers"	Cannell *et al.* (2020)
	57	8.1					679	2	Penguin Is.	2001	Breeding, "Deep divers"	Cannell *et al.* (2020)
5.2		6 ± 3.5			47 ± 4	0.32 ± 0.06		8	Penguin Is.	2001	G	Chiaradia *et al.* (2007b)
5.1 ± 1.3		7.7 ± 3.9	10.3 ± 5.1	5.2 ± 2.8				7	Phillip Is	2005	G, young	Zimmer *et al.* (2011a)
		10.4 ± 8.0						9	Phillip Is.	2016	I, Sub colony 1	Gómez (2019)
		13.1 ± 10.2						10	Phillip Is.	2016	I, Sub colony 2	Gómez (2019)
		17.8 ± 14.9						12	Phillip Is.	2016	G, Sub colony 1	Gómez (2019)

Mean diving time (h)	Mean diving time (% of trip)	Mean depth (m)	Mean duration (s)	Mean bottom time (s)	Mean bottom time (% of dive)	Mean dive efficiency	Mean number of dives	Number of trips	Location	Year	Notes	Reference
		16.5 ± 15.5						13	Phillip Is.	2016	G, Sub colony 2	Gómez (2019)
		13.9 ± 9.8						8	Phillip Is.	2016	PG, Sub colony 1	Gómez (2019)
		11.0 ± 12.0						10	Phillip Is.	2016	PG, Sub colony 2	Gómez (2019)
		5.4 ± 0.1					1557 ± 1284	5	Phillip Is.	2015	I, Sub colony 1, males	Sánchez *et al.* (2018)
		5 ± 0.2					698 ± 179	5	Phillip Is.	2015	I, Sub colony 1, female	Sánchez *et al.* (2018)
		5.4 ± 0.2					1040 ± 774	5	Phillip Is.	2015	I, Sub colony 2, males	Sánchez *et al.* (2018)
		9.4 ± 0.2					2119 ± 1768	4	Phillip Is.	2015	I, Sub colony, females	Sánchez *et al.* (2018)
		10.2 ± 0.4					827 ± 220	7	Phillip Is.	2015	G, Sub colony 1, males	Sánchez *et al.* (2018)
		11 ± 0.4					707 ± 83	6	Phillip Is.	2015	G, Sub colony 1, females	Sánchez *et al.* (2018)
		16.7 ± 0.6					564 ± 71	8	Phillip Is.	2015	G, Sub-colony 2, males	Sánchez *et al.* (2018)

Mean diving time (h)	Mean diving time (% of trip)	Mean depth (m)	Mean duration (s)	Mean bottom time (s)	Mean bottom time (% of dive)	Mean dive efficiency	Mean number of dives	Number of trips	Location	Year	Notes	Reference
		18.1 ± 0.5					624 ± 169	6	Phillip Is.	2015	G, Sub colony 2, females	Sánchez *et al.* (2018)
		15.4 ± 0.5					607 ± 125	5	Phillip Is.	2015	PG, Sub colony 1, males	Sánchez *et al.* (2018)
		13.1 ± 0.4					790 ± 295	5	Phillip Is.	2015	PG, Sub colony 1, females	Sánchez *et al.* (2018)
		15.8 ± 0.3					1532 ± 1042	4	Phillip Is.	2015	PG, Sub colony 2, males	Sánchez *et al.* (2018)
		15.4 ± 0.3					1477 ± 902	3	Phillip Is.	2015	PG, Sub colony 2, females	Sánchez *et al.* (2018)
	37 ± 12						667 ± 146	4	Phillip Is.	2010	Middle-aged males	Pelletier *et al.* (2014)
	36 ± 9.8						634 ± 118	6	Phillip Is.	2010	Old females	Pelletier *et al.* (2014)
	41 ± 6						696 ± 177	9	Phillip Is.	2010	Old males	Pelletier *et al.* (2014)
	34 ± 10.5						613 ± 122	7	Phillip Is.	2010	Middle-aged females	Pelletier *et al.* (2014)
		19	40	12		0.17			Phillip Is.	2008	I, male, *	Amélineau *et al.* (2021)
		17.5	37	10.5		0.16			Phillip Is.	2008	G, male, *	Amélineau *et al.* (2021)

Mean diving time (h)	Mean diving time (% of trip)	Mean depth (m)	Mean duration (s)	Mean bottom time (s)	Mean bottom time (% of dive)	Mean dive efficiency	Mean number of dives	Number of trips	Location	Year	Notes	Reference
		14.5	33	11.1		0.2			Phillip Is.	2008	PG, male,*	Amélineau *et al.* (2021)
4.2 ± 2.3		5.8 ± 1.1	17.8 ± 1		34 ± 2		568 ± 274	5	Phillip Is.	2006	G, males	Ropert-Coudert *et al.* (2009)
5.1 ± 0.6		8 ± 1.1	18.1 ± 1		31 ± 2		611 ± 81	5	Phillip Is.	2006	G, females	Ropert-Coudert *et al.* (2009)
4.7 ± 1.3		10.1 ± 4.6	24.0 ± 9.8	8.04 ± 2.71		0.19 ± 0.04	811 ± 392	14	Phillip Is.	2005	G	Fallow *et al.* (2009)
		10.9 ± 4.4	28.5 ± 24.35				735 ± 403	10	Phillip Is.	2005	G	Hoskins *et al.* (2008)
6.6 ± 0.98		10.9 ± 0.24			35.2 ± 4.4		892 ± 311	6	Phillip Is.	2005	G	Pelletier *et al.* (2014)
4.4 ± 1.0		10.9 ± 0.35			28.3 ± 4.8		600 ± 128	12	Phillip Is.	2005	G	Pelletier *et al.* (2014)
4.8 ± 1.9		8.2 ± 0.32			34.2 ± 7.6		979 ± 443	10	Phillip Is.	2005	G	Pelletier *et al.* (2014)
4.9 ± 1.6		6.3 ± 0.26			35.7 ± 5.8		1165 ± 370	7	Phillip Is.	2005	G	Pelletier *et al.* (2014)
5.8 ± 0.8		6.1 ± 0.28			37 ± 2.0		1441 ± 421	8	Phillip Is.	2005	G	Pelletier *et al.* (2014)
5.9 ± 1.7		8.4 ± 1.1	22.2 ± 1		37 ± 2		609 ± 195	5	Phillip Is.	2005	G, males	Ropert-Coudert *et al.* (2009)
4.8 ± 1.7		8.5 ± 1.2	16.3 ± 1.1		26 ± 3		591 ± 166	5	Phillip Is.	2005	G, females	Ropert-Coudert *et al.* (2009)
4.8 ± 1.3		8.5 ± 3.9	7.7 ± 2.7	4.5 ± 2.8				7	Phillip Is.	2005	G, middle aged	Zimmer *et al.* (2011a)
6.5 ± 1.3		10.6 ± 3.9	10.8 ± 2.0	6.0 ± 1.3				5	Phillip Is.	2005	G, old	Zimmer *et al.* (2011a)
5.4 ± 1.4				8.1 ± 1.5			1058 ± 486	19	Phillip Is.	2005	G	Zimmer *et al.* (2011b)

Mean diving time (h)	Mean diving time (% of trip)	Mean depth (m)	Mean duration (s)	Mean bottom time (s)	Mean bottom time (% of dive)	Mean dive efficiency	Mean number of dives	Number of trips	Location	Year	Notes	Reference
5.7 ± 0.9		14.8 ± 2.9	35.6 ± 5.2				585 ± 99	5	Phillip Is.	2004	I, males	Kato *et al.* (2008)
5.5 ± 0.7		11.3 ± 2.4	26 ± 4.1				775 ± 139	5	Phillip Is.	2004	I, females	Kato *et al.* (2008)
5.9 ± 0.4	40.3 ± 3.0		34.3 ± 2.0		0.29 ± 0.02		617 ± 34		Phillip Is.	2004	G	Ropert-Coudert *et al.* (2007)
8		13 ± 3.9			22 ± 5	0.14 ± 0.04		22	Phillip Is.	2002	G	Chiaradia *et al.* (2007b)
		8.1 ± 1.2	28.6 ± 9				881 ± 153	9	Rabbit Is.	2005	G	Hoskins *et al.* (2008)
		7.7 ± 1.6			46.1 ± 3.7		825 ± 117	17	St Kilda Breakwater	2008	B	Preston *et al.* (2010)
		8.6 ± 1.8			44.6 ± 4.0		776 ± 131	5	St Kilda Breakwater	2007	B	Preston *et al.* (2010)
		8.4 ± 1.8	28.5 ± 3.8		49.7 ± 7.3		681	12	St Kilda Breakwater	2006	B	Preston *et al.* (2008)
3.8 ± 1.2		12.0 ± 2.4	36.4 ± 8.1	13.7 ± 1.6	0.35 ± 0.05		391 ± 139	9	Troubridge Is.	2004	G	Wiebkin (2012)

[1]The table includes data from papers which report diving depths, duration, bottom duration, total diving time or proportion of a trip spent diving (a measure of foraging effort), proportion of a dive at the bottom, or a proportion of the dive cycle at the bottom (a measure of diving efficiency), and the number of dives in a day. Results are from single colonies in a single season or breeding stage. Results are presented alphabetically by colony location and breeding stage (incubation (I), guard (G), post-guard (PG), chick-rearing (CR; sampling either occurred through both guard and post-guard or the stage of chick-rearing was not stated), and breeding (B; studies during incubation, guard or post-guard or did not state the breeding stage). The sex or age of birds is indicated when this was reported. Results estimated from graphs are indicated by asterisk in the notes column. Sample size (number of trips), and standard deviations of mean values are reported when available.

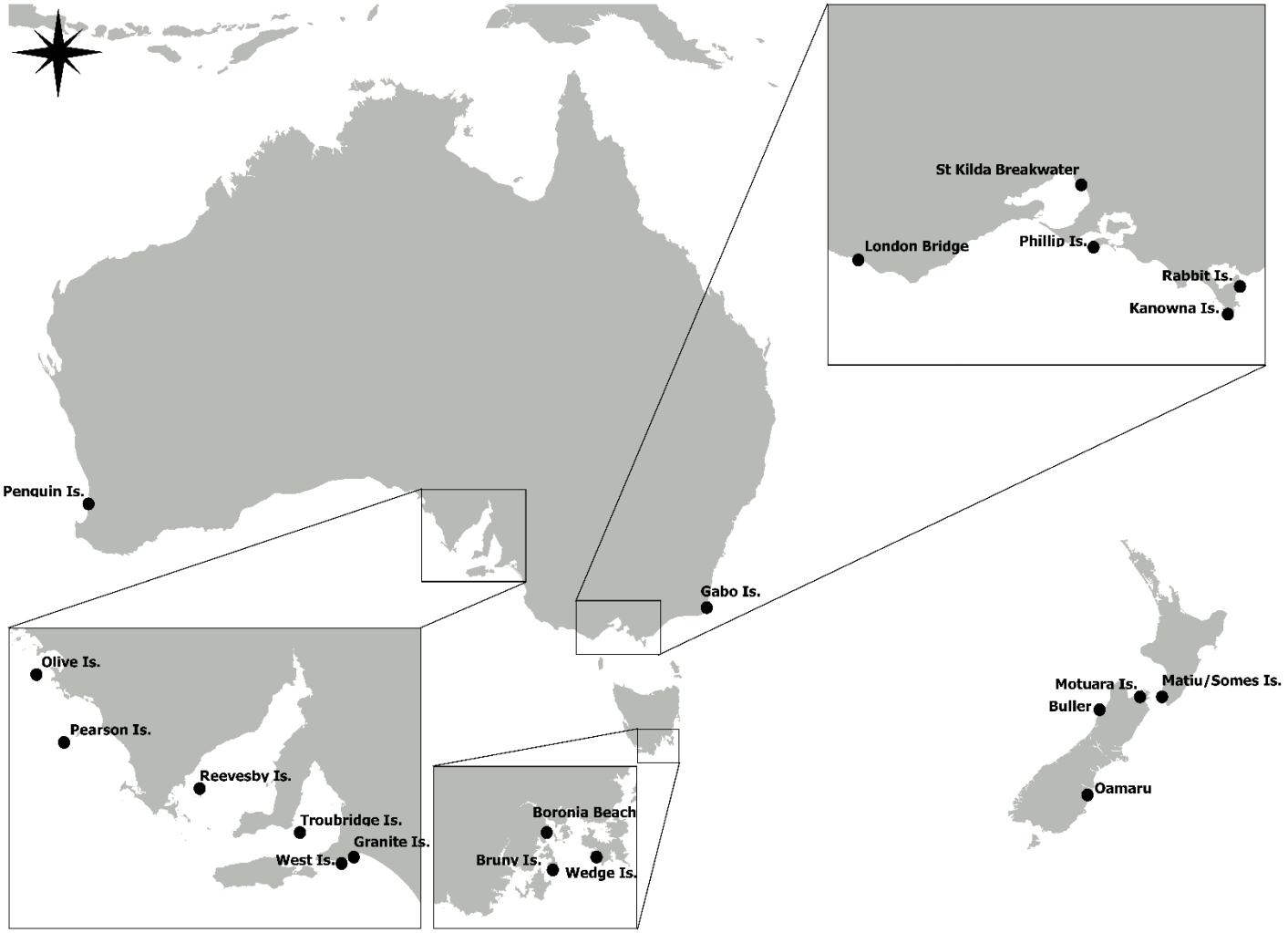

Fig. 1.3. Locations where GPS tracking data are available for little penguins.

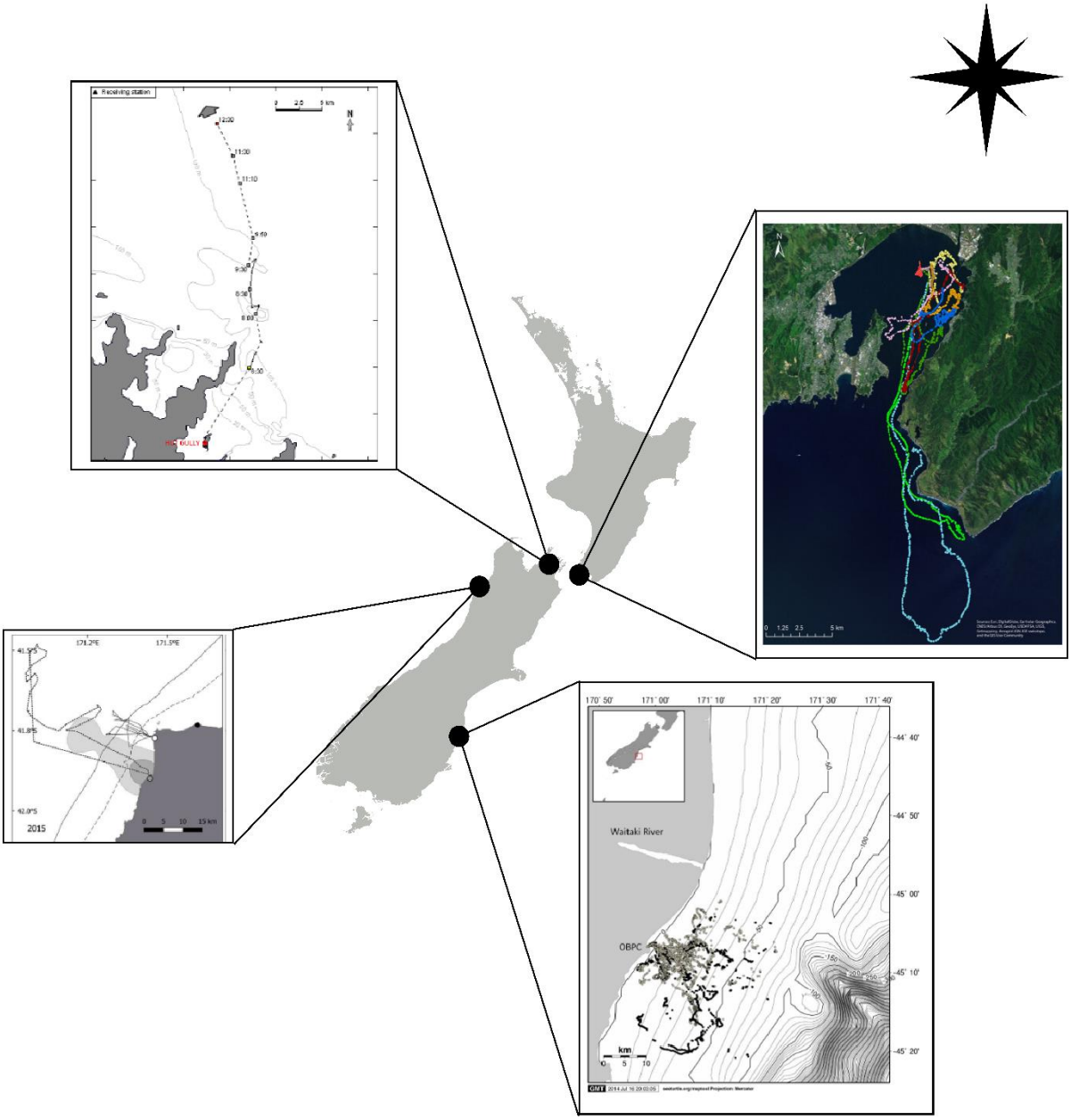

Fig. 1.4. Little penguin colonies in New Zealand where published tracking studies have been conducted. The colonies were at Motuara Island (Mattern, 2001), Cape Foulwind and Nile River in Buller (Poupart *et al.*, 2017), Matiu/Somes Island (Zhang *et al.*, 2015) and Oamaru (Agnew, 2014). Some results are shown from each of the previous studies. These results do not provide comprehensive data about foraging of penguins from each colony.

1.4.4 Breeding season foraging

1.4.4.1 Incubation

Little penguins can make short or long trips during incubation, with mean trip durations reported from 2 to 10.3 days (Collins *et al.*, 1999; Poupart *et al.*, 2017). However, most studies report mean durations of 3 to 5 days (Table 1.2). Short trips are not uncommon, with the proportion of short trips during incubation reported as between 14 and 53% (Collins *et al.*, 1999; Numata *et al.*, 2000). Trip duration is highly correlated with total distance travelled (Collins *et al.*, 1999). While it is generally presumed that birds undergoing long trips swim further from the colony than birds that make short trips, there are limited data on travel distances during incubation (Table 1.2). Results from studies of foraging behaviour that did not distinguish between guard and post-guard stages of breeding are summarised in Table 1.3. In 2015 birds from Motuara Island in the Marlborough Sounds had very long foraging trips during early incubation (mean maximum distance from colony of 102 km), then short day trips during chick rearing (mean distance 11 km). In contrast, maximum distance from colony or total travel distance did not differ between incubation and chick rearing at Matiu/Somes Island (Poupart *et al.*, 2017). This appears to be the result of very few long- trips during incubation. Penguins at Oamaru often undertake single day trips during incubation, staying within 20 km of the colony (Agnew, 2014). Presumably, prey is abundant near the colony, eliminating the need for trips to distant prey patches.

Foraging trip duration during incubation is constrained by the need to replace partners on the nest. Prolonged foraging trips can lead to nest desertion by the incubating partner. For example, at Motuara Island and Oamaru, birds that abandoned the nest before their partner returned had been incubating eggs for approximately 9 days. This was significantly longer than the mean foraging duration during incubation (Numata *et al.*, 2000). Incubation trip

duration compromises between restoring body condition, and ensuring individuals return to the colony soon enough to prevent nest desertion by their partner. Long trips are thought to be more beneficial for replenishing body reserves because penguins can reach distant and profitable prey patches. The total trip duration may increase when body condition is low. Body condition index (body mass / flipper length) was in both sexes negatively correlated with trip duration during incubation at both Oamaru and Motuara Island (Numata *et al.*, 2000). This relationship was also observed at Phillip Island, with birds in poorer condition foraging for longer during incubation (Kato *et al.*, 2008). However, foraging trip durations may also change during the approximately five-week incubation period. Trips may be longest during the middle of the incubation period, before decreasing in length before hatching. Near the end of incubation, birds are more likely to undertake single-day trips and mean trip duration decreases (Chiaradia and Kerry, 1999; Numata *et al.*, 2004; Kato *et al.*, 2008). Short foraging trips near the end of incubation ensure a parent is available to feed chicks when they hatch.

1.4.4.2 Guard stage

Chick-rearing begins with the guard stage when one parent remains at the nest brooding the chicks to help regulate their body temperature, while the other parent forages. The guard stage typically lasts from two to three weeks, although guard periods from 8 to 38 days long have been reported (Chiaradia and Kerry, 1999; Numata *et al.*, 2004; Heber *et al.*, 2008). The maximum 38-day period may be overestimated by up to 6 days due to infrequent monitoring (Heber *et al.*, 2008)). It has been suggested that the length of the guard period may relate to foraging conditions and food availability. At Phillip Island, the guard stage was longer during a more successful breeding year, compared to a poor year (20.9 and 15.3 days; Chiaradia, 1999). During the 1998 breeding season Oamaru penguins guarded chicks for a

mean 20.0 days, while at Motuara Island guard lasted 15.1 days on average. There was greater breeding success, chick growth rates and fledge weights at Oamaru. Parents brooding one chick had longer guard phases at each colony than parents brooding two chicks (Numata *et al.*, 2004). It is possible that parents can sustain a longer guard period when they are in better body condition, which could occur in years of greater food availability near the colony. However, this has not been investigated.

Foraging trips during guard stage are mostly day trips, although long- trips do occur occasionally (Chiaradia and Kerry, 1999; Collins *et al.*, 1999; Numata *et al.*, 2004). Consequently, mean foraging distance is relatively low during this period and birds typically remain within 25 km of the colony (Table 1.2). Little penguins can travel further than this in a single day, and maximum distances up to 36 km from a colony have been recorded (Hoskins *et al.*, 2008). However, trips this far are rare during the guard stage. Some trips are very short, with maximum distance from the colony as low as 3.5 km (Zhang *et al.*, 2015).

At Phillip Island, there was a positive correlation between chick age and foraging effort during the guard stage. More time was spent underwater as chicks grew. Although this may reflect parental efforts to increase the provision of food for larger chicks, there was no correlation between prey encounter rates and chick age. Moreover, prey encounter rate and median dive depth were negatively correlated with foraging date, while the number of dives was positively correlated with date. More dives to shallower depths later in the season is in agreement with the behaviour of Oamaru penguins in the 2010 season (Agnew, 2014), although in this instance the change in strategy did not alter foraging effort (Zimmer *et al.*, 2011b). Similarly Amélineau *et al.* (2021) reported the frequency of short and shallow dives increased throughout the season. In addition, foraging effort increased between the breeding

stages, and increased linearly with chick age and foraging date. This change in behaviour seems to be most related to changes in prey abundance or accessibility throughout the season, rather than through abrupt changes as individuals shift through breeding stages. However, it cannot be discounted that increasing chick demands may influence changes in foraging behaviour throughout the breeding season.

1.4.4.3 Post-guard stage

The post-guard stage begins two to three weeks after hatching when chicks are left unattended while both parents forage. Parents can be more flexible in their foraging during post-guard in comparison with guard. Most trips are one day long, although as the chicks grow, they can fast for a longer period and may be left alone for longer than younger chicks. Mean trip durations during post-guard of 1 to 4.6 days have been reported (Collins *et al.*, 1999; Berlincourt and Arnould, 2015), with proportions of one day trips during the post-guard stage from 44 to 85% (Collins *et al.*, 1999; Chiaradia and Nisbet, 2006). Data on post-guard trip duration are lacking for New Zealand colonies, as data is often reported for the chick-rearing period, rather than for guard and post-guard separately. A higher proportion of trips longer than 1 day may be more common in years of reduced resource availability. The proportion of long trips was 21% in a year of high breeding success and 66% in a year of low breeding success at Phillip Island (Chiaradia and Nisbet, 2006). Longer trips may allow penguins to reach distant prey patches, and these trips could be more prevalent when prey is scarce near the colony. Trips longer than 2 days are rare. The proportion of trips longer than 2 days did not exceed 20% and was typically below 10% each season between 2001 and 2011 at Phillip Island (Saraux *et al.*, 2016). Between 2003 and 2008, the mean duration of trips longer than 2 days was 4.3 days long (Saraux *et al.*, 2011). Short trips are thought to be more beneficial for chicks, as they will be fed more frequently. Furthermore, parents returning

from short trips have been shown to feed their chicks a larger meal than birds returning from long trips. Parents embarking on long- trips also had significantly lower body mass than their counterparts undertaking short trips. In addition, mass gains were higher among birds that undertook long trips, once chick meal mass was accounted for (Saraux *et al.*, 2011).

Little penguins face high energetic demand during this time, field metabolic rate increases throughout the breeding period, and reaches an annual peak during the late chick rearing phase. Up to 31% of annual energy expenditure is accounted for during breeding, with most of this used in the post-guard period (Gales and Green, 1990). Saraux *et al.* (2011) also reported that birds typically begin the post-guard stage with a long trip. This was recorded in 416 out 459 first post-guard trips over 8 years. Possibly, penguins are attempting to restore body mass after being bound to conduct one-day trips during the guard stage. During post-guard, an alternating pattern of 2 consecutive long- trips, followed by many single day trips was then observed (Saraux *et al.*, 2011). This plasticity may allow little penguins to balance the nutritional requirements of chicks and themselves, conducting short trips to provision for chicks, and then switching to longer trips if their own body condition is depleted.

Table 1.2. Summary of studies that report foraging distances and duration. Results are sorted by breeding stage. Further sub-setting of results is indicated in the notes column. Sample size (number of tracks), and standard deviation reported when available.

Breeding stage	Mean trip duration (days)	Mean trip duration (hours)	Mean maximum distance (km)	Mean total distance (km)	Mean number of tracks	Location	Year	Notes	Reference
Incubation	2		25	108	1	Buller (Nile River)	2016		Poupart *et al.* (2017)
Incubation	5		57	170	1	Buller (Nile River)	2015		Poupart *et al.* (2017)
Incubation	7 ± 4		102 ± 69	253 ± 189	24	Motuara Is.	2015		Poupart *et al.* (2017)
Incubation	16		155	482	1	Motuara Is.	2014		Poupart *et al.* (2017)
Incubation	6.6 ± 2.6				18	Motuara Is.	1998	Males	Numata *et al.* (2000)
Incubation	6.3 ± 2.6				19	Motuara Is.	1998	Females	Numata *et al.* (2000)
Incubation		12.8	33.6			Oamaru	2012	1-day trips only	Agnew (2014)
Incubation		19.4	46.5			Oamaru	2012	1-day trips only, 2nd brood	Agnew (2014)
Incubation		18.4	47			Oamaru	2011	1-day trips only	Agnew (2014)
Incubation		14.2	39.5			Oamaru	2010	1-day trips only	Agnew (2014)
Incubation		16.4	43			Oamaru	2010	1-day trips only, 2nd brood	Agnew (2014)
Incubation	2.8 ± 0.9				20	Oamaru	1998	Males	Numata *et al.* (2000)

Breeding stage	Mean trip duration (days)	Mean trip duration (hours)	Mean maximum distance (km)	Mean total distance (km)	Mean number of tracks	Location	Year	Notes	Reference
Incubation	3.6 ± 2.2				20	Oamaru	1998	Females	Numata *et al.* (2000)
Incubation			42.0 ± 18.2		9	Phillip Is.	2016	Sub-colony 1	Gómez (2019)
Incubation			39.0 ± 18.1		10	Phillip Is.	2016	Sub-colony 2	Gómez (2019)
Incubation	1 ± 0				5	Phillip Is.	2015	Males, sub-colony 1	Sánchez *et al.* (2018)
Incubation	2.6 ± 2.2				5	Phillip Is.	2015	Females, sub-colony 1	Sánchez *et al.* (2018)
Incubation	3.5 ± 2.3				4	Phillip Is.	2015	Males, sub-colony 2	Sánchez *et al.* (2018)
Incubation	1.2 ± 0.4				5	Phillip Is.	2015	Females, sub-colony 2	Sánchez *et al.* (2018)
Incubation			20.1 ± 12.1		10	Phillip Is.	2015	Sub-colony 1	Gómez (2019)
Incubation			29.0 ± 35.3		9	Phillip Is.	2015	Sub-colony 2	Gómez (2019)
Incubation	3.06					Phillip Is.	2011	*	Saraux *et al.* (2016)
Incubation	3.51					Phillip Is.	2010	*	Saraux *et al.* (2016)
Incubation	3.82					Phillip Is.	2009	*	Saraux *et al.* (2016)
Incubation	4.43					Phillip Is.	2008	*	Saraux *et al.* (2016)
Incubation	3.15					Phillip Is.	2007	*	Saraux *et al.* (2016)
Incubation	4.45					Phillip Is.	2006	*	Saraux *et al.* (2016)
Incubation	4.54					Phillip Is.	2005	*	Saraux *et al.* (2016)
Incubation	3.0 ± 0.7				10	Phillip Is.	2004	Males	Kato *et al.* (2008)

Breeding stage	Mean trip duration (days)	Mean trip duration (hours)	Mean maximum distance (km)	Mean total distance (km)	Mean number of tracks	Location	Year	Notes	Reference
Incubation	4.1 ± 1.2				10	Phillip Is.	2004	Females	Kato *et al.* (2008)
Incubation	3.33					Phillip Is.	2004	*	Saraux *et al.* (2016)
Incubation	3					Phillip Is.	2003	*	Saraux *et al.* (2016)
Incubation	3.13					Phillip Is.	2002	*	Saraux *et al.* (2016)
Incubation	3.66					Phillip Is.	2001	*	Saraux *et al.* (2016)
Incubation	3.4 ± 2.5				49	Phillip Is.	1995	Males	Chiaradia and Kerry (1999)
Incubation	3.5 ± 1.6				54	Phillip Is.	1995	Females	Chiaradia and Kerry (1999)
Incubation	3.9 ± 2.4				16	Phillip Is.	1993		Collins *et al.* (1999)
Incubation	4.8 ± 4.9				17	Phillip Is.	1992		Collins *et al.* (1999)
Incubation	10.3 ± 0.5				3	Phillip Is.	1991		Collins *et al.* (1999)
Incubation	4.5 ± 3.5				10	St Kilda breakwater	2006		Preston *et al.* (2008)
Incubation	2 ± 1		11 ± 4	69 ± 24	18	Wellington	2014		Poupart *et al.* (2017)
Guard		16.3 ± 8.7	20.9 ± 9.8	51.5 ± 24.0	32	Gabo Is.	2013		Berlincourt and Arnould (2015)
Guard		13.5 ± 1.2	19.9 ± 4.4	47.6 ± 8.1	27	Gabo Is.	2012		Berlincourt and Arnould (2015)
Guard		15.7 ± 0.3	14.2 ± 5.3	49.3 ± 11.0	17	Gabo Is.	2011		Berlincourt and Arnould (2015)
Guard			16.9 ± 5.8	41.8 ± 11.2	20	Kanowna Is.	2005		Hoskins *et al.* (2008)
Guard		15.3 ± 2.4	16.9 ± 4.3	43.3 ± 7.8	26	London Bridge	2013		Berlincourt and Arnould (2015)
Guard		15.0 ± 5.8	15.3 ± 12.1	42.5 ± 25.2	25	London Bridge	2012		Berlincourt and Arnould (2015)

Breeding stage	Mean trip duration (days)	Mean trip duration (hours)	Mean maximum distance (km)	Mean total distance (km)	Mean number of tracks	Location	Year	Notes	Reference
Guard		14.9 ± 0.8	13.4 ± 6.0	49.1 ± 15.9	17	London Bridge	2011		Berlincourt and Arnould (2015)
Guard		12.01 ± 1.1	9.5 ± 8.5	26.9 ± 8.8	8	Matiu/Somes Is.	2012		Zhang *et al.* (2015)
Guard		15.8 ± 0.4			8	Motuara Is.	2000		Mattern (2001)
Guard	1.1				14	Motuara Is.	1998		Numata *et al.* (2004)
Guard	1.11				28	Oamaru	1998		Numata *et al.* (2004)
Guard		16.3 ±9.7	47.5 ± 24.0	13.3 ± 5.	11	Olive Is.	2006		Wiebkin (2012)
Guard		32.8 ± 35.1	38.2 ± 18.3	137.2 ± 130.6	7	Pearson Is	2005		Wiebkin (2012)
Guard		89.1 ± 105.1	39.9 ± 33.1	196.8 ± 215.4	9	Pearson Is	2004		Wiebkin (2012)
Guard			22.7 ± 4.1		12	Phillip Is.	2016	Sub colony 1	Gómez (2019)
Guard			22.9 ± 3.1		13	Phillip Is.	2016	Sub colony 2	Gómez (2019)
Guard			21.4 ± 4.6		13	Phillip Is.	2015	Sub colony 1	Gómez (2019)
Guard			19.0 ± 4.9		14	Phillip Is.	2015	Sub colony 2	Gómez (2019)
Guard			21 ± 5.3	54 ± 7.9	7	Phillip Is.	2010	Females, middle-aged	Pelletier *et al.* (2014)
Guard			20 ± 4.9	51 ± 4.9	6	Phillip Is.	2010	Females, old	Pelletier *et al.* (2014)
Guard			20 ± 4	54 ± 8	4	Phillip Is.	2010	Males, middle-aged	Pelletier *et al.* (2014)
Guard			19 ± 3	52 ± 9	9	Phillip Is.	2010	Males, old	Pelletier *et al.* (2014)

Breeding stage	Mean trip duration (days)	Mean trip duration (hours)	Mean maximum distance (km)	Mean total distance (km)	Mean number of tracks	Location	Year	Notes	Reference
Guard			19.3 ± 8.2	45.2 ± 17.4	20	Phillip Is.	2005		Hoskins *et al.* (2008)
Guard			18.3 ± 6.3	48 ± 12.1	20	Rabbit Is	2005		Hoskins *et al.* (2008)
Guard		13.1 ± 1.3	21.3 ± 5.2	64.4 ± 15.6	5	Reevesby Is.	2004		Wiebkin (2012)
Guard			10.5 ± 4.1	34.6 ± 7.4	17	St Kilda Breakwater	2008		Preston *et al.* (2010)
Guard	1.1 ± 0.3		17.2		11	St Kilda Breakwater			Preston *et al.* (2008)
Guard			13.8 ± 4.1		10	St Kilda Breakwater		1 -day trips only	Preston *et al.* (2008)
Guard			16		10	St Kilda breakwater		Median, *, low river depth, low salinity	Kowalczyk *et al.* (2015a)
Guard			12		11	St Kilda breakwater		Median, *, low river depth, high salinity	Kowalczyk *et al.* (2015a)
Guard			20.7		23	St Kilda breakwater		Median, *, high river depth	Kowalczyk *et al.* (2015a)
Guard				56.5	27	St Kilda breakwater		Median, *, low salinity	Kowalczyk *et al.* (2015a)
Guard				41.5	17	St Kilda breakwater		Median, *, high salinity	Kowalczyk *et al.* (2015a)
Guard		14.5 ± 0	11.5 ± 2.8	52.1 ± 13.3	4	Troubridge Is.	2006		Wiebkin (2012)

Breeding stage	Mean trip duration (days)	Mean trip duration (hours)	Mean maximum distance (km)	Mean total distance (km)	Mean number of tracks	Location	Year	Notes	Reference
Guard		18.4 ± 12.4	15.8 ± 5.4	54.9 ± 21.5	15	Troubridge Is.	2005		Wiebkin (2012)
Guard		14.5 ± 0.62	11.5 ± 3.2	45.5 ± 13.9	24	Troubridge Is.	2004		Wiebkin (2012)
Post-guard		20.1 ± 13.1	16.4 ± 11.7	50.9 ± 30.5	16	Gabo Is.	2013		Berlincourt and Arnould (2015)
Post-guard		19.1 ± 9.1	19.9 ± 13.0	52.9 ± 28.5	12	Gabo Is.	2012		Berlincourt and Arnould (2015)
Post-guard		17.4 ± 1.3	14.7 ± 8.3	49.0 ± 14.4	10	Gabo Is.	2011		Berlincourt and Arnould (2015)
Post-guard		15.7 ± 0.5	12.5 ± 6.1	38.8 ± 11.8	7	London Bridge	2013		Berlincourt and Arnould (2015)
Post-guard		16.0 ± 6.4	25.9 ± 6.5	60.6 ± 18.8	17	London Bridge	2012		Berlincourt and Arnould (2015)
Post-guard		15.2 ± 0.5	12.2 ± 4.6	39.1 ± 11.8	4	London Bridge	2011		Berlincourt and Arnould (2015)
Post-guard			22.3 ± 2.3		10	Phillip Is.	2016	Sub colony 2	Gómez (2019)
Post-guard			33.0 ± 13.2		8	Phillip Is.	2016	Sub colony 1	Gómez (2019)
Post-guard	2.7 ± 1.6				3	Phillip Is.	2015	Females, sub colony 2	Sánchez *et al.* (2018)
Post-guard	3 ± 2.6				4	Phillip Is.	2015	Males, sub colony 2	Sánchez *et al.* (2018)
Post-guard	1.2 ± 0.4				5	Phillip Is.	2015	Females, sub colony 1	Sánchez *et al.* (2018)

Breeding stage	Mean trip duration (days)	Mean trip duration (hours)	Mean maximum distance (km)	Mean total distance (km)	Mean number of tracks	Location	Year	Notes	Reference
Post-guard	1 ± 0				5	Phillip Is.	2015	Males, sub colony 1	Sánchez *et al.* (2018)
Post-guard			17.5 ± 3.6		10	Phillip Is.	2015	Sub colony 1	Gómez (2019)
Post-guard			49.4 ± 42.1		7	Phillip Is.	2015	Sub colony 2	Gómez (2019)
Post-guard	1.4					Phillip Is.	2011	*	Saraux *et al.* (2016)
Post-guard	1.3					Phillip Is.	2010	*	Saraux *et al.* (2016)
Post-guard	1.3					Phillip Is.	2009	*	Saraux *et al.* (2016)
Post-guard	1.5					Phillip Is.	2008	*	Saraux *et al.* (2016)
Post-guard	1.3					Phillip Is.	2007	*	Saraux *et al.* (2016)
Post-guard	1.2					Phillip Is.	2006	*	Saraux *et al.* (2016)
Post-guard	1.2					Phillip Is.	2005	*	Saraux *et al.* (2016)
Post-guard	1.7					Phillip Is.	2004	*	Saraux *et al.* (2016)
Post-guard	1.3					Phillip Is.	2003	*	Saraux *et al.* (2016)
Post-guard	1.3					Phillip Is.	2002	*	Saraux *et al.* (2016)
Post-guard	1.5					Phillip Is.	2001	*	Saraux *et al.* (2016)
Post-guard	1.4 ± 0.0				14116	Phillip Is.	2001-2008	All trips	Saraux *et al.* (2011)
Post-guard	4.3					Phillip Is.	2001-2008	Trips >3 days only	Saraux *et al.* (2011)
Post-guard	1.2					Phillip Is.	2001-2008	Trips < 3 days only	Saraux *et al.* (2011)
Post-guard	4.6 ± 8.3				85	Phillip Is.	1993		Collins *et al.* (1999)
Post-guard	1.2 ± 0.7				52	Phillip Is.	1992		Collins *et al.* (1999)
Post-guard	2.6 ± 1.4				22	Phillip Is.	1991		Collins *et al.* (1999)

Table 1.3. Summary of results from studies that do not differentiate between guard and post-guard, and rather present data for the whole chick-rearing phase. Further sub-setting of results is indicated in the notes column. Sample size (number of tracks), and standard deviation reported when available.

Mean trip duration (days)	Mean trip duration (hours)	Mean maximum distance (km)	Mean total distance (km)	Number of tracks	Location	Year	Notes	Reference
	19.2 ± 1	18.1	45.6	8	Boronia beach	2015		Phillips *et al.* (2019)
	18.3	22.7 ± 4.4	58.3 ± 6.4	9	Bruny Is.	2015		Phillips *et al.* (2019)
1 ±0		22 ± 2	34 ± 23	4	Buller (Cape Foulwind and Nile river)	2016		Poupart *et al.* (2017)
1 ±1		15 ± 6	34 ± 15	7	Buller (Cape Foulwind and Nile river)	2015		Poupart *et al.* (2017)
		16 ± 3			Gabo Island			Soanes *et al.* (2016)
	14.8 ± 4.1		41.2 ± 18.7		London Bridge			Berlincourt and Arnould (2014)
1 ± 1		11 ± 9	28 ± 18	28	Motuara Is.	2015		Poupart *et al.* (2017)
7 ±5		49 ± 32	213 ± 182	5	Motuara Is.	2014		Poupart *et al.* (2017)
		16.5	40.8	4	Oamaru	2012		Agnew (2014)
		18.3	43.9	8	Oamaru	2012	2nd brood	Agnew (2014)
		17.8	46.4	10	Oamaru	2011		Agnew (2014)
		11.7	38.9	8	Oamaru	2010		Agnew (2014)
		22.6	57.6	4	Oamaru	2010	2nd brood	Agnew (2014)
	17.0 ± 0.77			10	Oamaru	2000		Mattern (2001)
1.8					Phillip Is.	2002		Nisbet and Dann (2009)
3.3					Phillip Is.	2001		Nisbet and Dann (2009)

Mean trip duration (days)	Mean trip duration (hours)	Mean maximum distance (km)	Mean total distance (km)	Number of tracks	Location	Year	Notes	Reference
2.6					Phillip Is.	2000		Nisbet and Dann (2009)
1.4					Phillip Is.	1996		Nisbet and Dann (2009)
2.8					Phillip Is.	1995		Nisbet and Dann (2009)
1.4 ± 1.0					Phillip Is.	1993		Nisbet and Dann (2009)
1.3 ± 1.0					Phillip Is.	1992		Collins *et al.* (1999)
	17.5 ± 0.4	15.8	47.7	12	Wedge Is.	2015		Phillips *et al.* (2019)
2 ± 1 d		12 ± 11	54 ± 22	7	Wellington	2014		Poupart *et al.* (2017)
		9 ± 8		13	Wellington	2012		Poupart *et al.* (2017)
		7 ± 7		4	Wellington	2011		Poupart *et al.* (2017)

1.4.5 Foraging behaviour outside the breeding season

During autumn and winter little penguins are free to forage without being constrained to the colony. They can cover much greater distances and travel for longer periods than during the breeding season. In Oamaru, the number of penguins returning each night is lower throughout autumn and winter, compared to spring and summer. At Phillip Island, penguins return to the colony less often and are less likely to be present on the nest outside of the breeding season, compared to when breeding (Chiaradia and Kerry, 1999; Salton *et al.*, 2015).

However, continued absence from the nest may not indicate that birds are taking long foraging trips. Penguins may conduct short trips, return in the evening, and depart the next morning. Short trips are similar to those in the breeding season, with individuals typically remaining within 25 km of the colony. However, tracking studies have shown that winter-foraging individuals can travel hundreds of kilometres. Weavers (1992) reported that most birds undertook long trips during the winter, travelling up to 710 km from the nest. The mean duration of these trips was 16 days. The likelihood of a bird undertaking a long or short trip was dependent on body condition. Birds undertaking long trips had a mean mass of 1027 g compared with 1145 g for birds taking short trips**.** In contrast, McCutcheon *et al.* (2011) found that 72% of foraging trips during winter were short. The mean duration of trips longer than one day was 22.7 days, much longer than long trips during the breeding season. Body condition did not influence whether a trip was to be long or short.

When penguins are away for long periods and swim long distances from a colony outside of the breeding season, this enables them to find and use food sources not available locally. For example, little penguins at Phillip Island often forage in the waters of Port Phillip Bay when

undertaking long winter trips. The bay is an anchovy spawning ground during mid-winter (Weavers, 1992; McCutcheon *et al.*, 2011). Despite the longer total distances travelled, little penguins still probably forage inshore. Birds from Phillip Island had a mean distance of 14.9 km from the coast, and 74% of tracked locations were within 20 km of the coast during long winter foraging trips (Weavers, 1992). Data on non-breeding foraging is scarce for New Zealand colonies. However, recoveries of banded birds indicate little penguins may travel long distances. More than 150 recoveries have been > 200 km from the banding location, and one was over 900 km from the banding site (Department of Conservation Banding Office pers. comm. to Dr Cockrem). However, short pre-breeding foraging trips have been recorded in Oamaru. Pre egg laying trips were often only a single day in duration between 2010 and 2012 (Agnew, 2014). In May 2018, before breeding, single day trips were recorded with a maximum distance from the colony of only 17 km (Agnew, 2019). Generalisations about movements of New Zealand little penguins in autumn, winter and approaching egg-laying cannot be made from the limited available data.

Up to 81% of total annual adult mortalities of Phillip Island occurred during the non-breeding period (Dann *et al.*, 1992). In winter there are fewer daylight hours available to forage in comparison with summer. Therefore, it may take greater foraging effort to meet nutritional demands, so foraging behaviour may change. Little penguins have a relatively high metabolic rate during the winter, therefore would need to increase food intake to maintain body reserves over the winter. Gales and Green (1990) studied little penguin annual feeding behaviour and found winter food consumption may be as low as 74 g/kg/d, whereas during other stages of the annual cycle it varied from 183 to 664 g/kg/d (Gales and Green, 1990). The high metabolic rate and low food consumption indicates that little penguins are experiencing high energetic costs with little reward compared to other seasons. Dann *et al.*

(1992) observed higher levels of mortality during the non-breeding period, particularly from post-moult through mid-winter. Given the negative energy balance and body mass decline associated with this period, decreased survival is often attributed to starvation (Dann *et al.*, 1992; Harrigan, 1992). Beach recoveries throughout the New Zealand coastline between 1960 and 1982 showed peak mortality occurred from January to March (Powlesland, 1984). Johannesen *et al.* (2002b) also reported lower survival probability between moult and mid-winter, compared to breeding months at Taiaroa Head, Otago. The cause of mortality was not clear, although starvation was suggested by the authors, based on reports from Australian studies which indicate this is the most common cause of death. With limited information on foraging success or prey abundance around New Zealand little penguin colonies generalisations on seasonal reductions in survival cannot be made.

1.4.6 Diet

Little penguins are generalist predators; however, they typically target small inshore, schooling fish species. Clupeoid species, a family comprising small forage fish such as sardines or sprat, often form a large portion of the diet, with crustaceans and squid often eaten as well. Most reported prey items range from 15 to 170 mm in length (Cullen *et al.*, 1991; Fraser and Lalas, 2004; Flemming *et al.*, 2013). Due to the limited foraging range of little penguins, they are particularly susceptible to fluctuations in local food supply. However, as generalist predators, little penguins are able to exploit a range of prey sources, which may help to buffer against reductions in specific prey items (Phillips *et al.*, 2017). Opportunist feeding strategy allows little penguins to continue to feed effectively when typical prey items are scarce.

Klomp and Wooller (1988) showed that key prey species for little penguins varied seasonally at Penguin Island between 1986 and 1987. During the non-breeding period *Hyporhamphus* and *Sardinop* species formed a large component of the diet. *Hyporhamphus* species accounted for 90% of food samples recorded in the month following moult. During the breeding season these species contributed to a significantly smaller proportion of the diet, while the proportion of *Spratelloides* species increased. These changes in prey choice match seasonal changes in abundance observed by fisherman and from beach seine-net catch data (Klomp and Wooller, 1988). This indicates that little penguins may target species in response to seasonal changes in prey availability.

Likewise, little penguins in New Zealand exhibit seasonal changes in diet composition. During non-breeding in Oamaru, 72 to 99% of the total mass of the diet was slender sprat (*Sprattus antipodum*), whereas during the spring and summer there was a range of prey species (Fraser and Lalas, 2004). During years of pilchard and anchovy decline other species were eaten more frequently by Phillip Island penguins (Cullen *et al.*, 1991). During years of high abundance, pilchards and anchovy appeared in 51% and 61% of stomach samples respectively, while only two other species appeared in >10% of stomach samples. In years where pilchard and anchovy were less prevalent, barracouta (*Thyrsites atun*), gurnard (*Trilidae spp.*) and leatherjacket (*Monocanthidae spp*.) appeared at higher frequencies in the diet. Prey species present and their relative biomass in the diet vary between colonies. During the 2010 breeding season in Oamaru, Graham's gudgeon (*Grahamichthys radiata*) contributed >90% of prey items and diet biomass; at Stewart Island Arrow squid (*Nototodarus sloanii*) formed almost 75% of the diet, while in Bank's Peninsula squid and multiple fish species contributed to the diet in more equal proportions (Flemming *et al.*, 2013). Similarly, during the 2003 and 2004 breeding seasons, Phillip Island penguins

consumed a variety of prey items, while the diet of penguins from the St Kilda colony was dominated by anchovy. Diet composition from these two colonies differed during the pre-lay and incubation periods when their foraging ranges overlapped. Despite the differences in prey items, nutritional composition of the diet was similar at each colony (Chiaradia *et al.*, 2012). It appears that little penguins can meet nutritional demands while altering the prey composition their diet.

When penguins can forage across a wider range, prey diversity may also increase. Poupart *et al.* (2017) compared stable isotope ratios between incubation and chick-rearing at Motuara Island, and found a wider isotopic niche during incubation, indicating a wider variety of prey taxa were consumed when penguins were foraging throughout a wider range. Similarly, a wide isotopic niche was reported for pre-breeding penguins at Phillip Island in 2011. Without the constraints of breeding limiting the foraging range, little penguins may encounter a broader range of prey species. However, this pattern may not be consistent between years. A narrow isotopic width was observed during the 2010 pre-breeding period at Phillip Island. This coincided with low fish diversity within Port Phillip Bay during that period (Kowalczyk *et al.,* 2014).

Ultimately, diet composition is influenced by the abundance and diversity of prey species around the colony. As generalist predators, little penguins will consume whichever prey species are abundant within their foraging range. However, they appear to prefer Clupeoid species and feed on anchovy and pilchard in Australia, and sprat in New Zealand. These species are fatty and provide high energy content. Although squid are commonly caught, they do not usually form a large portion of total prey biomass. Little penguins show dietary plasticity and will switch prey in response to changes in prey availability between years or

seasons. The penguins require a diversity of prey items with high nutritional value to buffer against any reduction in key prey species.

1.4.7 Environmental effects on foraging behaviour

Although the maximum foraging distance and duration are highly influenced by physiological and central place foraging constraints, foraging locations are related to prey distribution. Penguins are most likely to forage where prey are present. The marine environment is spatially heterogeneous, with productive zones patchily distributed. Within the foraging area available to little penguins, zones of high primary production and prey aggregations are unlikely to be distributed uniformly. Prey are dispersed in a spatially hierarchical manner, with high density aggregations clustered within larger zones of lower prey density. Lower-density zones are further nested within areas where prey is scarce. Little penguins may employ specific foraging tactics to help locate prey patches and increase foraging success. As prey aggregations are hierarchically nested there will be zones within the foraging range with low prey abundance. In response, penguins may concentrate their foraging efforts in certain areas, rather than dispersing throughout their entire accessible range. For example, Carroll *et al.* (2016) showed 82% of 1 km^2 grid cells that formed the available foraging habitat were not visited by little penguins across 112 single day trips. That only 18% of accessible foraging habitat was used suggests that penguins were selective in their foraging locations. Furthermore, the distribution of prey capture events from little penguins at Montague Island matched the distribution of prey aggregations in the top 20 m of the water column. This suggests little penguins can effectively detect prey and can distribute themselves within the foraging range in an efficient manner.

Movements within their foraging area may also occur at multiple scales which reflect the spatial scale hierarchy at which prey aggregate. Depending on whether seabirds are searching for prey at coarse or fine scales, their foraging behaviour may vary. For example, area restricted search (ARS) behaviour is common among seabirds once prey patches have been located. This behaviour typically involves slower travelling speeds and higher turning rates and is indicative of more intensive searching behaviour (Weimerskirch, 2007). Little penguins do engage in ARS behaviour, which occurs over relatively small areas and is interspersed with more directed travelling behaviour (Zhang *et al.*, 2015). In addition, Carroll *et al.* (2017) showed travel distances between prey capture events for little penguins were bi-modal, indicating small distances for within-prey patch foraging, and larger movements for between-patch movements. This indicates a foraging strategy where little penguins search for prey patches across a larger scale and then hunt prey within these aggregations. The characteristics of an aggregation may also affect foraging success. Prey patches that were densely concentrated, shallow, and compact within the water column were associated with greater prey capture success by penguins (Carroll *et al.*, 2017).

Prey distribution is influenced by many oceanographic and environmental variables. For example, coastal upwellings or frontal zones are associated with high nutrient levels that promote phytoplankton growth, which then attracts fish to these areas. Certain environmental factors are proxies for primary production. For example, high chlorophyll alpha (chl-α) concentration indicates an abundance of phytoplankton, which in turn indicates an area of high primary productivity. Areas where seabirds are most likely to forage may correlate with specific environmental variables which are related to prey distribution. For little penguins, lay dates may be correlated with mean chlorophyll concentration within the foraging range. At Oamaru, mean chlorophyll concentration between January and April correlated with

median lay dates between 1998 and 2010. Median lay dates were earlier when average chlorophyll concentration within the foraging range was higher before breeding (Agnew et al., 2015). At Phillip Island, trends in chlorophyll concentrations were calculated from weekly data, within a range approximately 500 km around the colony (deemed the 'area of influence'). The area of influence was dynamic and influenced by ocean currents. Mean lay dates between 1998 and 2009 typically fell within three weeks of the yearly peak in chlorophyll concentration within this area of influence (Afan *et al.*, 2015). Furthermore, high chlorophyll concentration either during or prior to the breeding season may positively correlate with adult survival (Agnew *et al.*, 2015; Ganendran, 2017). If variation in ocean productivity (represented by chlorophyll concentrations) is correlated with survival or reproductive parameters, changes in foraging behaviour may also occur in response to variation in productivity. For example, the home range of little penguins foraging within Port Phillip Bay had higher chl- α content compared to the area that penguins did not frequent but could have reached during a 1-day trip. Despite changes in the absolute values of chl-α concentration between seasons, this relationship was apparent in two breeding seasons (Kowalczyk *et al.*, 2015b). It is possible that penguins are more likely to encounter prey aggregations in these zones of higher productivity. During the 2005 breeding season, chl- α data were extracted from 8-day averages at Phillip and Rabbit Island, for the accessible foraging range (areas penguins could reach in a single day). Both sites had a wide range of chl-α concentrations throughout the foraging area accessible for single day trips (0 -8.0 mg ml). However, penguins did not distribute randomly throughout this area with respect to chl-α. Rabbit Island individuals appeared to select areas with chl-α concentrations between 0.0 - 4.8 mg m^{-3}, while Phillip Island penguins foraged in areas between 0.4 – 0.8 mg m^{-3}. Not only were these areas relatively low in chl-α, particularly at Phillip Island, but each site varied in the chl-α concentration selected (Hoskins *et al.*, 2008). Local conditions which

affect prey distribution may have greater influence on foraging behaviour than changes in chl- α concentrations. In addition, results from Pearson and Troubridge Island showed that little penguins spent a higher proportion of their foraging time in areas with high and low chl-α concentration, respectively. However, this relationship was weak, those models which included chl-α as an explanatory variable had only marginally lower deviance than the null models (Wiebkin, 2012). Chl- α does not seem to be a strong predictor of foraging locations among little penguins. Local conditions are likely to be more important for foraging distribution than changes in productivity throughout the range.

Sea surface temperature (SST) may be related to foraging zone preferences in little penguins. Low SST is often associated with greater primary productivity. Low temperatures themselves do not increase phytoplankton production, but rather they often indicate areas where deeper cooler waters have upwelled, carrying nutrients to the surface which promote phytoplankton growth**.** SST has been studied in relation to breeding success in little penguins. However, results have been contradictory, with both positive and negative correlations with breeding success reported (Cullen *et al.*, 2009; Cannell *et al.*, 2012). If any relationship does exist with breeding success, it may be mediated by variation in foraging success. Hoskins *et al.* (2008) showed penguins from three colonies selected foraging areas with the same SST. Variability in SST was estimated for the available foraging zone (a radius 36 km around the colony), from 8-day averaged data across the tracking period at each site. Areas where SST was approximately 16°C formed a larger proportion of the selected foraging area, compared to the total area that penguins could forage in on a single day trip. It was suggested that this temperature association was mediated by prey distribution. If prey species exhibit a preference for areas with this temperature, it is reasonable that little penguins will also be present in these zones. However, prey preferences are variable between

seasons and colonies. This relationship between SST and preferable foraging areas is representative only of these colonies, during the 2005 breeding season.

SSTs were estimated for 1 km grid cells, within a 25 km radius around Montague Island between September and December, during the 2012, 2013 and 2014 breeding seasons. Little penguins were GPS tracked and spent more time in grid cells that were colder than the mean SST of all grid cells, compared to cells that were warmer than the mean. (Carroll *et al.*, 2016) In contrast, little penguins at Port Phillip Bay foraged in areas with higher SST compared to the non-foraging area. This was observed over 2 years, despite both foraging locations and absolute SST values changing (Kowalczyk *et al.*, 2015b).

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Carroll *et al.* (2016) also assessed prey capture success in relation to SST. SST was measured at an offshore location and averaged at monthly intervals. An SST anomaly was inversely correlated with prey capture success. When SST decreased relative to the mean for that month across the 3-year study period, prey capture success increased. However, this relationship was reversed during September, where only data from 2013 and 2014 was available. In addition, SST data was integrated with single day foraging tracks to calculate the mean SST encountered by penguins at 10% increments of a trip. The highest prey capture success occurred when penguins encountered the lowest SST throughout a foraging trip.

Sharp changes in SST driven by physical processes such as currents may shape preferred foraging areas. Warmer waters driven by the Eastern Australian current appear to limit little penguin foraging movements and prey captures to inshore areas (Carroll *et al.*, 2017). The East Australian Current (EAC) is thought to influence foraging behaviours by altering marine

productivity. SST is one of many environmental variables that change in response to the EAC. Increasing SST is correlated with reduced chl-α in this system (Carroll *et al.*, 2016). This compounding effect of environmental variables makes it difficult to isolate the influence of SST. In addition, at other colonies, other variables may drive prey distribution or foraging behaviour more. However, it appears that areas of relatively low SST provide suitable foraging habitat for little penguins, and they may exhibit a preference for these areas, or have greater foraging success in years SST is low.

It has been suggested that the presence of rivers may also influence foraging behaviours. Rivers may provide an influx of nutrients which sustain planktonic species, which in turn provide a food source for fish which could be prey for penguins. Little penguins in Oamaru tend to travel towards the Waitaki River when foraging for greater than 1 day (Agnew, 2014). At Phillip Island in 1993, parents undertaking long trips during chick rearing were recorded foraging near river outlets (Collins *et al.*, 1999). Poupart *et al.* (2017) noted a positive correlation between mean maximum foraging range and colony distance to a river among incubating little penguins. The authors suggested that penguins could forage close to the colony when a river outlet is nearby, due to the nutrient rich freshwater enhancing productivity and attracting prey to the area. However, penguins did not appear to travel towards the rivers. Little penguins breeding at Matiu/Somes Island appeared to engage in prey searching behaviour most often near river mouths, either within Wellington Harbour at the Hutt River mouth, or when travelling beyond the harbour, at the Orongorongo River (Zhang *et al.*, 2015). Changes in the outflow of the Yarra River in Port Phillip Bay can influence the foraging behaviour of little penguins breeding adjacent to the river mouth. During periods of low water levels in the river, the distance to core foraging areas, maximum distance travelled, and home and core range size is reduced compared to when water levels

are high. This is possibly a result of nutrients being more widely dispersed during periods of greater river outflow. This dispersion may influence the distribution of forage fish, thus altering little penguin foraging patterns (Kowalczyk *et al.*, 2015b).

In addition, increased river outflow could result in greater sediment runoff which can alter ocean visibility. Little penguins are visual predators that rely on light to capture prey (Cannell and Cullen, 1998). It is possible that increased sedimentation can reduce water clarity around the river outflow, resulting in penguins foraging further away. In addition, little penguins within Port Phillip Bay appeared to forage in waters of high chl-α concentration and low turbidity in two years of study. During the 2008 and 2011 breeding seasons, the home-range had high chl-α concentration, SST, and turbidity relative to the total accessible foraging area. However, the core-range had lower levels of chl-α, and turbidity compared to the home-range (Kowalczyk *et al.*, 2015a). Lower chl-α concentrations suggest this is an area of lower productivity relative to the home-range. However, this zone still had high chl-α concentration compared to the non-foraging area. It is hypothesised that little penguins forage in these zones due to the lower turbidity, and therefore greater prey visibility. This suggests little penguins are foraging within areas of high productivity but are using visual cues to then select areas where prey capture may be enhanced, due to greater visibility. It is not fully understood how river outflow can influence little penguin foraging success, but it may have both positive and negative effects on foraging behaviour. This could be dependent on nutrient output, dispersal, and increased sedimentation.

Little penguins must forage within a limited distance of the colony during chick rearing, can go away for long trips during incubation and can make very long trips at other times of year. Water depth in foraging areas during chick rearing differ between little penguin colonies. For

example, the Oamaru seafloor slopes gently for 40 km from the coast to a depth of 100 m, before dropping steeply to 1,000 m**.** Most of the accessible foraging range during chick-rearing falls within the shallower zone. In contrast, Phillip Island and Motuara Island have a much smaller area of shallow water within the accessible foraging range, with < 35 % of water within 20 km < 30 m deep at both sites (Chiaradia *et al.*, 2007b). Shallow water is often cited as a favourable condition for little penguin foraging. Colonies with shallow water nearby typically have reduced diving effort, and often have greater reproductive success than colonies without shallow water (Chiaradia *et al.*, 2007b). In Oamaru, penguins foraged in water < 50 m deep and remained within 20 km of the coastline. This occurred even during the pre-egg and incubation period when birds can travel further from the colony and reach areas of deeper water. On long foraging trips penguins travelled north and were usually in water <40 m deep, rather than swimming east into deeper water (Agnew, 2014). Similarly, little penguins foraging in winter from Phillip Island either entered the shallow waters of Port Phillip Bay or remained near the coastline (Weavers, 1992; McCutcheon *et al.*, 2011). However, the ocean depths in areas where Phillip Island penguins foraged during the breeding season are notably greater than those depths where Oamaru penguins foraged. The median depth within the home range varied from 58 to 74 m during the 2015 breeding season at Phillip Island (Sánchez *et al.*, 2018).

At sites such as Phillip Island, individuals must forage in deeper water during chick-rearing. The mean depth within 30 km of Motuara Island is 108.4 m (Meyer *et al.*, 2017). Water within Queen Charlotte Sound is <50 m deep, while water beyond the heads reaches depths over 200 m. During the breeding season, when undertaking single-day trips, penguins remained within the sound, foraging in relatively shallow water. Mattern (2001) suggested that the bathymetric features of the sound restrict the foraging range of penguins, as the steep

gradient forms a boundary that penguins do not cross on single-day trips. When penguins leave the Marlborough Sounds during long trips there is evidence to suggest they do not forage in the deep waters of Cook Strait, with core range areas towards the South Taranaki coast or in the shallow waters of Cloudy Bay (Poupart *et al.*, 2017). Colonies that are surrounded by a high proportion of shallow water tend to have lower diving effort (daily sum diving duration), than colonies with deep water. For example, relatively low diving effort is reported for Oamaru and Penguin Island colonies. A high proportion of water within 25 km of each is less than 30 m deep. In contrast Phillip and Motuara Island penguins forage in water predominantly deeper than 30 m and exhibit greater effort than Oamaru or Penguin Island penguins. Greater foraging effort in this instance was associated with deeper dives. Those sites with shallower water also had greater breeding success, than colonies with deep water in the foraging range (Chiaradia *et al.*, 2007b).

Little penguins are known to undertake both benthic dives, when prey are pursued at the seafloor, and pelagic dives, when prey are captured in the water column, above the seafloor. Sites with shallow water could allow a higher proportion of benthic dives to occur, compared to colonies with deeper surrounding water. Benthic diving in little penguins has been reported at the St Kilda Breakwater colony and at Penguin Island where penguins frequently foraged in water < 20 m deep (Ropert-Coudert *et al.*, 2006b; Chiaradia *et al.*, 2007b; Preston *et al.*, 2008). At Rabbit Island, mean dive depth was 8.1 m and the mean seafloor depth in the foraging area was 10.2 m (Hoskins *et al.*, 2008). It is possible that a high proportion of dives were to the demersal zone. Benthic dives may enhance prey capture as the seafloor could act as a physical barrier, reducing the field of escape for prey. Although benthic dives do occur, it seems that, even in shallow environments, mid-water diving is the predominant strategy. Shallow depths may concentrate prey more than in deeper waters, as fish are

restricted in the depths they can descend to. This could improve foraging success. Carroll *et al.* (2017) showed little penguins had a greater rate of prey capture when feeding on prey aggregations that were shallower and more densely grouped.

Weather conditions can influence foraging success and foraging behaviour. For example, high winds in the Bass strait were associated with long trips during the post-guard stage. When wind speeds were >14 m/s, trips were on average 28% longer, and there was a greater proportion of trips >3 days long, compared to calm wind conditions. In addition, body mass gain was lower following foraging trips with high winds, during incubation and guard, compared to trips conducted under calm conditions. These results indicate that penguin foraging success was related to wind speed. However, this relationship was not apparent during post-guard (Saraux *et al.*, 2016). When maximum wind gust speeds were strong, little penguins at Wedge Island were more likely to adopt a foraging strategy in which they travelled far from the colony, often travelled very quickly and conducted prey searching movements for relatively short periods, compared to when winds gusts were weak (Phillips *et al.*, 2019). These results may suggest that searches for prey patches increased, and time spent in each patch decreased when winds were relatively strong in comparison with calmer conditions. At Oamaru, when stormy conditions were prevalent and modelled wave heights were consistently over 2.32 m, the number of penguins arriving ashore dropped significantly in comparison with calm conditions. While stormy conditions typically lasted for hours, they were associated with a reduction in numbers of arriving penguins that lasted for many days (Agnew *et al.*, 2015). Berlincourt and Arnould (2015) reported an inverse relationship between diving time and wave heights. Penguins may need to remain at sea longer to meet nutritional requirements in stormy conditions in comparison with calm conditions. This is supported by the reduced survival probability for both adults and first-year individuals under

stormy conditions (Agnew *et al.*, 2015). High winds and large waves could increase the effort required to commute from the colony or travel between prey patches, compared with calmer seas. Alternatively, stormy conditions may increase the amount of suspended sediment in the water, thus reducing visual clarity. Little penguins are visual predators, so do not feed at night (Cannell and Cullen, 1998) and are less able to feed when turbidity of water is increased in comparison with conditions of low turbidity.

High winds and storms could also disrupt thermal stratification by mixing water masses. A thermocline is a point in the water column where the mixed surface layer meets stratified deep water. Thermoclines can influence prey distribution by affecting their vertical movements in the water column. Fish may aggregate around the thermocline or remain above it in the mixed surface layer (Hansen *et al.*, 2001). A reduction in the thermocline around Phillip Island was associated with storms in the 2006 breeding season. Little penguins had greater foraging success when the thermocline was present during the 2005 season, exhibiting higher prey encounter rates in the highly stratified water compared to the 2006 season. Individuals also spent less time pursuing prey when the thermocline was absent (Ropert-Coudert *et al.*, 2009). In addition, hunting efficiency (proportion of dives that prey was encountered) was highest when a thermocline was present during the guard stage (Pelletier *et al.*, 2012). However, prey encounter rates were only estimated for depths >10 m. It is likely that most prey encounters were shallower than this, so this may have influenced results. Prey may aggregate around the thermocline, making their vertical distribution more predictable and easier to exploit (Ropert-Coudert *et al.*, 2009). However, mean dive depths and prey encounter depths are typically shallower than where the thermocline is likely to begin. For example, during the 2005 guard stage at Phillip Island thermoclines began at 44, 24 and 38 m deep on successive weeks, while mean dive depth was consistently less than 11

m. However, if the thermocline limits fish dispersal, prey may be more concentrated in the upper parts of the water column when stratification is present. In addition, the thermocline may act as a barrier, reducing the field of escape for prey or the sudden drop in temperature may reduce fish metabolism and escape speeds, thus increasing their chance of being captured.

1.4.8 Sex differences in foraging behaviour

Male birds are generally larger than female birds. In diving species males have a greater aerobic capacity than females. Males often dive deeper than females and hence may feed on different prey species. Sex specific foraging behaviours have been reported for penguin species including African, rockhopper and Adelie penguins (Clarke *et al.*, 1998; Ludynia *et al.*, 2013; Pichegru *et al.*, 2013). Sexual dimorphism is minor in little penguins, although males are generally larger with larger beaks (Hocken and Russell, 2002). Minor dietary differences between the sexes were observed by Shaw (2009). Males ate a higher proportion of fish than females, particularly barracouta. Most prey items were larger for males than females, but not significantly so. However, differences between sexes in diet occurred in some years and breeding stages but not others, so there was no clear sex difference in diet. Chiaradia *et al.* (2012) noted no differences between sexes in stable isotope values of prey, indicating that males and females foraged at the same trophic level. Most foraging studies found no differences between sexes in foraging behaviour. Foraging distance and duration did not differ in three studies (Mattern, 2001; Hoskins *et al.*, 2008; Preston *et al.*, 2008). In another study, males and females foraged in locations with similar SST, chl-α and seabed depths (Hoskins *et al.*, 2008). At Phillip Island, males made shorter foraging trips during incubation compared to females between 2001-2011, foraging on average for 3.18 and 4.08 days, respectively (Saraux *et al.*, 2016). During long trips in winter, males foraged over a

considerably smaller range than females, 841 and 1983 km^2, respectively. These ranges overlapped by only 34%, suggesting spatial segregation between sexes (McCutcheon *et al.*, 2011). Pelletier *et al.* (2014) observed a similar pattern during the guard stage. Females of both middle and older age classes foraged over a greater core and focal area compared to their male counterparts. In addition, these foraging areas were spatially segregated.

Differences between sexes in diving parameters have been observed in some studies. Hoskins *et al.* (2008) found that males had a greater mean dive duration, maximum dive duration was longer, and they achieved deeper mean dive depths than females. Ropert-Coudert *et al.* (2003) found that all females were shallow divers, with over 90% of dives less than 5 m deep, whereas males were either shallow or deep divers. The small sample size precludes conclusions being drawn from the study of Ropert-Coudert *et al.* (2003) and differences between sexes in diving behaviour were not found in other studies (Berlincourt and Arnould, 2015). Overall, there do not appear to be clear differences between male and female little penguins in their foraging and diving behaviour.

1.4.9 Age and foraging behaviour

Age specific foraging behaviour has also been observed among little penguins. Foraging behaviour may change as individuals gain experience and become more efficient foragers. Older birds may have greater foraging skill and knowledge of more profitable foraging sites (Lescroël *et al.*, 2019). In contrast, physical capability leading to a reduction in ability to foraging efficiently may decrease with age. Reduced reproductive and physiological ability has been observed in many seabirds. Little penguins may exhibit reproductive senescence, with breeding success lower in older birds compared to middle aged birds at Phillip Island (Nisbet and Dann, 2009; Saraux and Chiaradia, 2021). Reduction in survival probability as

penguins aged beyond 9 years was also reported at Phillip Island (Sidhu *et al.*, 2007). However, no such relationship existed at Oamaru (Agnew *et al.*, 2016). Differences in foraging location has been reported for little penguins of different ages during the guard stage. Birds from 'middle aged' and 'old' age classes showed significant spatial segregation. Foraging ranges estimated from prey capture locations had 0% and 3% overlap in core and focal range, respectively. The foraging area was also over 40% larger for middle aged birds. In addition, birds from each age class appeared to depart from the colony in different directions, with significant differences in bearing. These distinct foraging ranges were in areas of different water depths. Old birds foraged inshore, in shallower water, while younger birds were further offshore (Pelletier *et al.*, 2014). This spatial segregation was not related to breeding success, nor did diving behaviour differ between the groups. This contrasts with Zimmer *et al.* (2011a) who found that middle aged birds dived for a shorter duration than both old and young birds. In addition, dive effort was lower for middle aged birds. The dive effort index was calculated as: dive duration/ (dive duration + post-dive duration). Prey pursuit also occurred at different depths within a dive. Older birds were more likely to pursue prey after reaching maximum depth compared to other age classes. The authors propose a more efficient hunting tactic, whereby older birds use up-thrust momentum from expanding respiratory air while ascending to aid in prey pursuit. However, it may be expected that older birds would pursue prey from below more often and age had no effect on whether a prey pursuit occurred in an upward or downward orientation. Further analysis by Zimmer *et al.* (2011b) revealed a correlation between adult age and both mean bottom duration and total diving time. Older birds tended to have a greater mean bottom duration and longer total diving time. Greater total diving time suggests higher foraging effort from older individuals. The effects of age on foraging ability may only be apparent in years of low resource availability. Any negative consequences of inexperience or senescence may only be

felt when prey is more difficult to acquire. Therefore, it is important for future studies to ensure a range of ages in samples.

1.4.10 Individual variation in foraging

The repeatability of certain behaviours may be related to intrinsic traits at an individual level. Alternatively, some species exhibit little behavioural consistency and are highly plastic in their foraging behaviours. Plasticity can occur at the population level where a range of behaviours are observed between individuals; however, individuals themselves may be somewhat specialised and repeatable. Alternatively, individuals may show high variability in their own behaviours (Phillips *et al.*, 2017). Furthermore, a population could consist of individuals that are flexible and vary their behaviours and individuals that are more rigid (Potier *et al.*, 2015).

Mean or median values of foraging parameters for individuals often show striking variation within a population. For example, median dive depths among 38 penguins recorded at Phillip Island ranged between 1.9 – 20.8 m (Ropert-Coudert *et al.*, 2006a). The broad range of dive depths represent very different strategies between the deepest and shallowest diving birds. Mattern (2001) reported significant differences between individuals at both Motuara Island and Oamaru, with some individuals diving deeper and longer than others. For example, median dive duration ranged from 15 to 30 seconds in Oamaru birds. Whether this population level variation represents many individuals conducting different foraging strategies based on their intrinsic traits, or flexibility within individuals is unclear. Studies of individuals over longer timescales would be beneficial and would also provide more accurate interpretations of colony level behaviours. For example, diving behaviour in the guard stage at Phillip Island showed significant variation across different weeks. In weeks one and two

of sampling, mean dive depth was 10.9 m with 600 dives per day. In contrast, penguins dived 6.1 m deep and over 1400 times per day in week five (Pelletier *et al.*, 2012). A study conducted in a single week would have led to a different interpretation of foraging behaviour at this colony for that season.

Little penguins at Penguin Island appeared to adopt either a shallow or deep diving strategy throughout a foraging trip. Shallow divers reached mean depths of 1.9 m while deep divers swum down 8.1 m on average. Furthermore, deep divers showed either a unimodal style where most dives were 8-11 m, or a bimodal distribution of dive depths with most dives either to 4 m or from 10 to 15 m (Ropert-Coudert *et al.*, 2003). Shallow divers conducted over 1400 dives per trip on average, while deep divers typically conducted fewer than 700. Whether this variation in diving behaviour relates to an intrinsic individual trait is unclear. The small sample size (n = 6) and limited number of consecutive trips from the same individuals preclude statements about repeatability of short or deep dives. However, it does illustrate the difference in behaviours that can occur between individuals foraging on the same day in the same environment. While a higher foraging effort may relate to demands of breeding, these behaviours were not related to chick or individual body weight. It is possible that differences were partially explained by sex, as all females were shallow divers, whilst males were either shallow or deep divers.

Further analysis of individual differences was conducted by Amélineau *et al.* (2021). Diving data were recorded from individuals throughout all stages of the breeding season. Diving parameters were grouped by principal component analysis (PCA). PC1 primarily related to the depth and frequency of dives, while PC2 conveyed information on the proportion of time spent at the bottom of dives, and the proportion of U-shaped dives. There appeared to be

high variation in diving behaviour within individuals and individuals were not consistently shallow or deep divers. Furthermore, the degree of variability was greater within some individuals. Some shifted from a pattern of few deep dives at the beginning of the season to many shallow dives by post-guard, while others were highly variable within a breeding stage. It appears that individual little penguins have a high degree of behavioural plasticity, rather than specialisation of behaviour. Similarly, low behavioural consistency was observed among penguins at London Bridge and Gabo Island, especially with regard to diving depth (Camprasse *et al.*, 2017). Penguins were tracked through multiple seasons, to assess behavioural consistency at different timescales. There appeared to be no individual consistency between breeding stages, clutches, and years. Between consecutive trips there was low to moderate consistency in the maximum distance from the colony and total distance travelled per hour, but not in other foraging parameters. Lower consistency over longer timescales could be expected if little penguins are responding to shifts in prey distribution. Over longer time periods there is likely to be greater variation in environmental conditions and therefore changes in prey distribution, compared to between consecutive trips. The degree of consistency did not relate to body mass or morphology, but rather it varied between years and sites. Individual little penguins appear to have high plasticity and can respond to changes in prey distribution by varying their behaviour.

Optimal foraging theory suggests that individuals adopt a strategy that maximises energy intake. However, a range of foraging behaviours are observed among little penguins, at even short temporal scales. The benefits of a particular foraging strategy could vary between different sexes or ages. However, differences in behaviour are only occasionally related to sex or age. While individual differences could arise through personality, the few studies on individual consistency show that repeatability is low. The inter-individual differences in

foraging behaviour over short timescales suggests that individuals may have different responses to day-to-day environmental variability. Ultimately, diving behaviour or foraging strategy may be related to intrinsic traits which affect an individual's ability, such as sex, age, or body condition; as well as extrinsic factors such as the varying demands of breeding and chick-rearing, and the fluctuations in prey distribution or abundance. The interaction of these factors likely contributes to the variety of diving behaviours observed within a population on any given day.

High plasticity may be beneficial for little penguins to cope with changing environments and allow populations to persist at many locations with differing environmental conditions. However, the variability within and among individuals highlights that many foraging trips will not conform to the general trends of the population. Certainly, this should be considered when making generalisations about little penguins' behaviour and their interaction with the environment. Furthermore, the wide variety of behaviours should be considered when conservation management decisions are made.

1.4.11 Conspecific interactions

1.4.11.1 Group foraging

At sea interactions with conspecifics can influence foraging success positively and foraging associations between seabirds are not uncommon. Both co-operative foraging and local enhancement can improve foraging success. Local enhancement occurs when individuals use cues from conspecifics or other marine predators to detect food (Veit *et al.*, 2017). African penguins benefit from foraging in groups when feeding on schooling species (McInnes *et al.*, 2017). Little penguins may associate in groups when departing or arriving at the colony and group association may also occur at sea. Berlincourt and Arnould (2014) showed that little

penguins associated at sea, both while travelling and diving. In addition, diving associations could be further grouped as synchronous or non-synchronous. Synchronous diving occurred when individuals initiated a dive within 4 seconds of each other. Most individuals did associate at some point during a foraging trip. However, time spent in association as a proportion of total foraging time was low and highly variable. Median degree of association ranged from no association up to 20.9% of total daily foraging time. However, due to the small number of individuals being tracked concurrently, it is possible that the degree of association is much higher, as tracked penguins may have associated with non-tracked penguins.

Asynchronous diving associations may indicate local enhancement or could occur if penguins independently located prey patches using the same environmental cues. However, the presence of synchronous diving indicates a social element to their foraging behaviour. Cooperative hunting may increase foraging success by helping to aggregate prey schools, which may improve prey capture success. Greater prey capture success is correlated with dense prey aggregations for little penguins (Carroll *et al.*, 2017). The probability of little penguins associating with conspecifics may also depend on prey type. Group association was more likely when little penguins encountered schooling, rather than solitary prey. However, this foraging strategy may not improve foraging success. Neither prey capture rate nor energy gain per dive was higher when schooling prey was targeted by grouped penguins compared to when hunting alone. Important schooling prey species anchovy and sprat provided greater energy gain per dive when hunted alone (Sutton *et al.*, 2015). In addition, visual observation of video footage did not reveal cooperative hunting behaviour. Little penguins are possibly grouping together due to local enhancement, using conspecifics' foraging locations to identify prey patches or grouping to increase prey patch detection.

Optimal foraging suggests that individuals should trade-off benefits of using conspecifics to inform foraging decisions and the negative consequence of higher competition while foraging in groups.

Foraging association may vary between colonies. Breeding season tracking from London Bridge revealed >90% of instrumented individuals associated during a forging trip, whereas only 18 and 34% of birds from Gabo Island associated during guard and post-guard, respectively. However, Gabo Island is a much larger colony and tracked birds form a small proportion of the total population. As a result, many associations of tracked birds would not have been recorded if they were with non-tracked individuals. Such limitations make it difficult to compare colonies of different size. Furthermore, little penguins may re-associate with the same individuals between trips. Over 50% of tracked birds re-associated with the same individual between trips at London Bridge (Sutton *et al.*, 2017). Whether re-associating with familiar individuals has any benefit to foraging success is unclear. It seems that little penguins do associate at sea, but these associations may be transient, with little penguins foraging both in groups and solitarily. However, previous studies may have underestimated the incidence of foraging associations, as only GPS tracked individuals were considered. Video loggers could more accurately reveal how common group foraging is.

1.4.11.2 Competition

Throughout the breeding season, larger colonies may experience density-dependent food shortages near the colony. A zone of food depletion is known as “Ashmole’s halo” and can occur as central-place foragers deplete food around their colony (Ashmole, 1963). If food is depleted near the colony, this may drive individuals to forage further from the colony where prey patches may be more profitable (Lewis *et al.*, 2001; Corman *et al.*, 2016). Little

penguins, however, are limited in how far they can travel when feeding chicks. Adults can be more flexible in post-guard than guard in how long they may forage and may make a higher proportion of long trips in post-guard than guard. Larger populations might have a larger foraging range than small populations, as they might deplete prey more rapidly as the season progresses. Few studies have recorded foraging distances exclusively in post-guard, and most studies examining duration have been conducted at Phillip Island. The limited data available indicate that larger colonies do not have a wider foraging range. For example, both Phillip and Gabo Island (c. 28 000 and 35 000 breeding pairs) had foraging durations and maximum distances comparable to much smaller colonies. Wiebkin (2012) reported a positive correlation between colony size and foraging distance during guard, but this relationship did not hold when Pearson Island, a single large colony, was removed from the dataset**.**

It is likely that foraging distances are more influenced by yearly fluctuations in prey availability and distribution, caused by environmental variability, rather than density-dependent depletion. During years of poor resource availability trips may be longer and the proportion of long trips may be greater (Chiaradia and Nisbet, 2006). Given the positive correlation between trip duration and distance, penguins may travel further during years of reduced resource availability. However, further research is needed on this relationship at New Zealand colonies. Penguins at Golden Bay have undertaken trips longer than 10 days but remained within 30 km of the colony (Dr J. Cockrem, personal communication). However, any effects of density-dependent prey depletion could be exacerbated during years of reduced prey availability.

Middle-aged and older individuals at Phillip Island foraged in different areas during guard. Older birds foraged in-shore while middle aged foraged in deeper waters further from the coast. The degree of spatial segregation increased throughout the study as chicks aged. McCutcheon *et al.* (2011) also reported a low level of spatial overlap between males and females conducting long- trips during the winter. Their respective foraging areas only overlapped by 34%. Most studies report no significant difference in foraging behaviour between cohorts of a single colony; however, spatial use by different cohorts remains a relatively under researched area.

In addition to spatial segregation between cohorts at a single colony, foraging segregation may exist between distinct neighbouring colonies. An extension to Ashmole's halo is the hinterland model proposed by Cairns (1989). This model suggests that the foraging range of adjacent colonies will be spatially segregated and that individuals forage closer to their own colony than to their neighbours. This behaviour has been reported for many seabirds. A recent review of inter-colony segregation reported that over 24 different seabird species, including 5 penguin species, engaged in this behaviour (Bolton *et al.*, 2019). Little attention has been given to foraging zones of adjacent little penguin colonies. Certainly, many sites throughout Australia and some in New Zealand are close enough that their foraging ranges can overlap (Dann and Norman, 2006). Sánchez *et al.* (2018) investigated spatial segregation of sub-colonies at Phillip Island. As a 'mega-colony' Phillip Island has many breeding sites within the larger colony that are separated by rocky outcrops. The distinction between separate colonies or sub-colonies is challenging to define, however, in this instance individuals are visually separate and return to breed at the same site. For the comparison of foraging ranges, there was little difference between these sub-colonies and 2 neighbouring colonies in proximity. Spatial segregation was observed throughout the breeding season,

with non-overlapping core ranges present during incubation, guard, and post-guard. The degree of segregation increased throughout the season, with the home ranges during post-guard exhibiting almost complete segregation. Energetic demands will increase throughout the season as chicks require more food. In conjunction with the reduced foraging range relative to incubation, intra-specific competition will be highest during chick rearing. The authors suggest that individuals may reduce inter-colony competition by increasing the degree of segregation.

Inter-colony segregation has also been observed between the West and Granite Island populations in South Australia. The islands are approximately 5.5 km apart. During chick-rearing the foraging range overlapped by only 9%. West Island individuals focused their foraging south-west of the colony, while the Granite Island population appeared to distribute the foraging range more evenly around the colony (Bool *et al.*, 2007). The degree of segregation has not been quantified for other adjacent colonies. Kanowna Island and Rabbit Island have overlapping potential habitat, in that individuals from one colony could reach the foraging zone of the other within a single day trip. Hoskins *et al.* (2008) tracked individuals from each site and foraging tracks did not overlap. Penguins from Boronia beach, Bruny and Wedge Island all foraged in distinct areas during chick-rearing, despite the fact that their foraging ranges could broadly overlap if the available habitat was used in a uniform fashion (Phillips *et al.*, 2019). In contrast, when little penguins from Phillip Island can forage further, during the non-breeding and incubation periods, they often forage within Port Phillip Bay and overlap with individuals from the St Kilda breakwater colony. However, rather than spatial segregation, dietary segregation has been observed between these 2 colonies. During pre-lay, anchovy formed a major part of the St Kilda diet but was absent from the diet of Phillip Island individuals, which consumed a wider range of prey. St Kilda penguins also had higher

stable isotope measurements of nitrogen, even when ranges overlapped. The lower trophic level of Phillip Island individuals may reflect the greater consumption of krill and squid, compared to the anchovy dominated diet of St Kilda individuals (Chiaradia *et al.*, 2012). Whether little penguins engage in niche partitioning, both within and between colonies, and either through dietary or spatial segregation, could be dependent on the availability of resources.

1.5 Thesis outline

The present study was conducted to investigate foraging behaviour of little penguins at two Oamaru colonies. Foraging trips were analysed to determine foraging locations, to examine foraging variables such as trip duration and trip distance, and to examine diving behaviour of penguins at the two colonies. Foraging ranges were calculated and compared to determine the extent to which penguins from the two colonies foraged in the same areas. The last chapter of the thesis provides a discussion of the results of the study and offers recommendations for future studies.

2. Methods

2.1 Study site

The study was conducted at the Oamaru Blue Penguin Colony (referred to as the OBPC colony; 45°6.63'S, 170°58.842’E) and the Oamaru Creek Penguin Refuge (referred to as the Creek; 45°6.22'S, 170°58.326’E). The location of these colonies is shown in Fig 2.1. The OBPC is on the south-eastern side of the Oamaru harbour, adjacent to the harbour breakwater. It is managed as a tourist site by Tourism Waitaki. Visitors can walk within the colony during the day, view nesting penguins in a dark room, and see penguins as they return ashore in the evening. Visitors are confined to grandstands and boardwalks to reduce disturbance to penguins. Lighting so that visitors can see the penguins at night is provided by low intensity sodium vapour bulbs. Furthermore, visitor behaviour is managed by staff to ensure that noise, movement, use of electronics, or any other behaviour that could be a disturbance is minimised. Tourists are not present around dawn when penguins leave the colony. The Creek colony is located 1 km from the OBPC, next to a beach between Holmes Wharf and the Oamaru Creek. It is closer to the township than the OBPC but is closed to the public and does not have artificial lighting or other tourist infrastructure.

There were 350 nest boxes at the OBPC and 250 nest boxes at the Creek colony at the time of the study. Penguins at the Creek colony also nest in cavities in the rock armouring along the shoreline. Predator trapping and habitat maintenance is conducted at both colonies. All nest boxes at each colony are checked weekly. All adults are individually marked with flipper bands or PIT tags. Chicks are marked in their sixth week after hatching, and adults that arrive in a nest box from outside of Oamaru are microchipped if they begin to breed. All birds in the current study had been sexed from bill measurements as a part of the long-term monitoring program (Agnew *et al.*, 2014). The two little penguin colonies at Oamaru

together form the largest monitored population of individual marked little penguins in New Zealand. There were 144 and 103 breeding pairs present at the OBPC and Creek colonies respectively during the 2016 season.

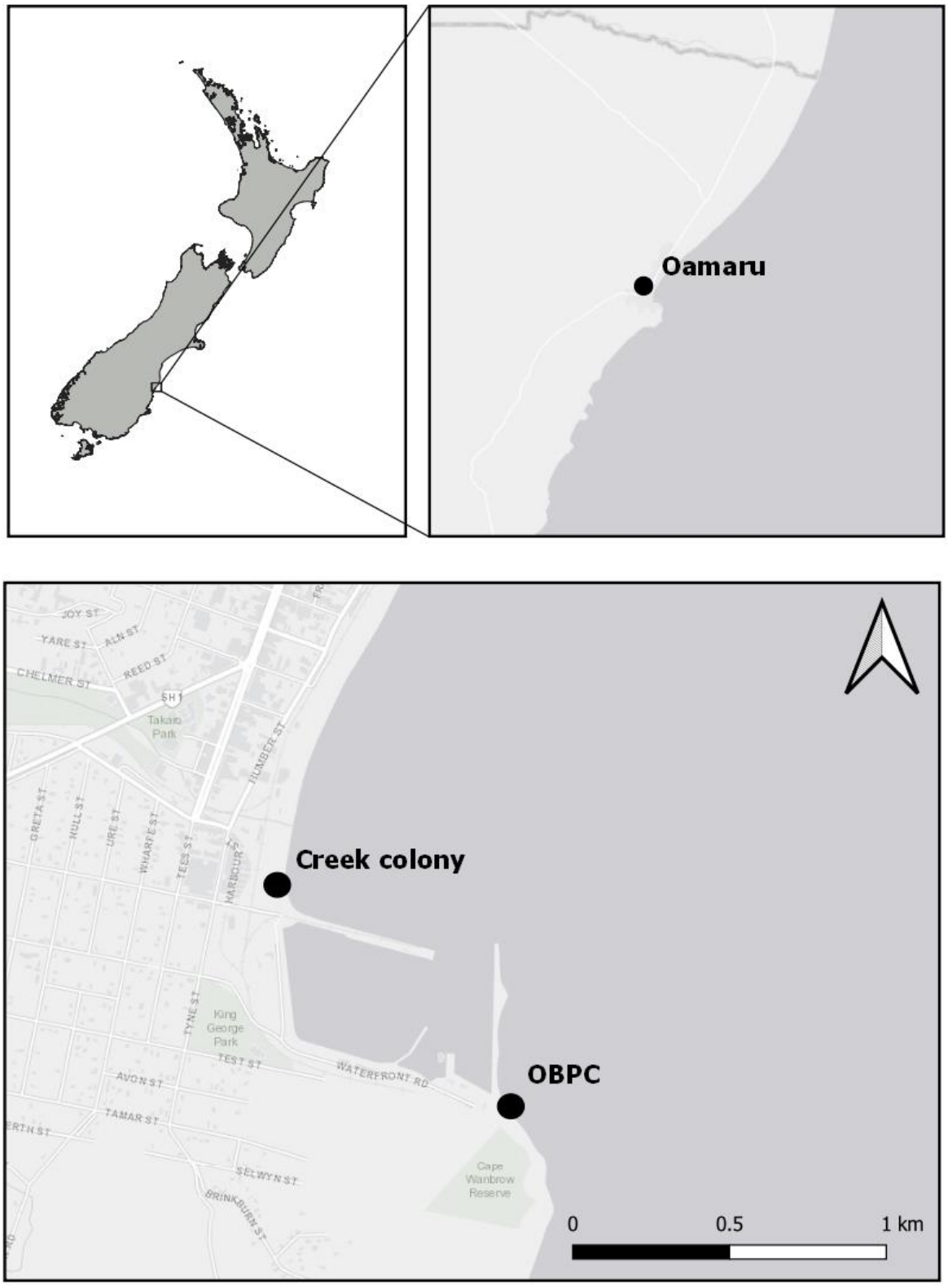

Fig 2.1. Locations of the OBPC and Creek little penguin colonies on the east coast the South Island, New Zealand. The colonies are approximately 1 km apart.

2.2 Data collection

2.2.1 Device deployment

Tracking devices were deployed on little penguins at the OBPC and Creek colonies from 21 October to 22 November 2016. Foraging behaviour was recorded in three dimensions, with GPS tracking data and dive depth data collected by the tracking devices. Tracking was conducted during the guard stage when parents made single day foraging trips. This stage lasts two to three weeks following hatching. Birds in guard stage with chicks at least one week old were randomly selected at each colony. Removing adults from nests with younger chicks was considered too great a disturbance, as young chicks have poor thermoregulatory ability and should be always guarded by a parent. Parents during guard stage go to sea every second day, so we expected birds to begin foraging the day after device attachment. A total of 25 birds were tracked, 12 from the OBPC (6 male, 6 female) and 13 from the Creek (8 male, 5 female).

We used Axy-Trek data loggers which record GPS location, pressure (which can be converted to water depth) and accelerometery data. To attach devices, birds were removed from the nesting box and placed in a bag. Adults were blocked off from their chicks while being removed to ensure they did not harm them. Individuals were weighed with a Pesola balance prior to device attachment. Loggers were attached to the central dorsal area with waterproof Tesa ® tape. Feathers were lifted and tape was placed underneath them. Feathers were kept straight when stuck to the tape, this ensured a clean attachment which would hold the device on firmly and reduce feather loss when removing the device. The device was then placed on the feathers and the tape was firmly wrapped around it (Fig 2.2). Tape was further bound to the devices with glue to minimise the chance of detachment during deployment. The dimensions of each device were 36x23x12 mm and weighed 25 g (2 -2.8% of body

weight when attached). Device size and weight is considered small enough to not influence foraging success or survival (Agnew, 2014). Following the first few attachments it was noted that devices were being knocked on the nest box entrance as birds moved in and out. This may have weakened the attachment and increased the chance of device loss. An extra rubber triangular piece was added to the front to streamline the device which reduced disruption to the device on the box entrance (Fig 2.2). Device attachment was completed in less than 5 minutes; during this time birds were also weighed. All devices were attached the day before a foraging trip; this could be predicted as parents swap daily between guarding and foraging. Loggers were intended to be attached for 6 days, to record 3 foraging trips, however in practice logger deployment times varied. Loggers remained attached for 4-8 days and 1-4 foraging trips were recorded per individual. Birds were re-weighed when devices were removed. When detaching devices, tape was peeled carefully to minimise feather damage and maintain plumage integrity. Device detachment was complete in less than 5 minutes. All handling was conducted in accordance with permits from the Massey University Animal Ethics Committee and the Department of Conservation.

Data loggers recorded GPS data at 1 fix per minute. This fix rate conserved battery power while providing enough location fixes to accurately calculate foraging parameters (Preston *et al.*, 2010). GPS on-time was set at 300 seconds, while off-time was set to 30, 150 or 300 seconds. On-time represents the time the logger will search for a GPS fix before going into a power saving mode if the location cannot be found. While in the power saving mode the device will not try to obtain a GPS fix. Off-time is the duration the device will remain in the power saving mode. Multiple off-times were tested to find a compromise between low battery consumption and minimal number of gaps in the GPS data, which can occur if the device remains off for too long. In addition, to reduce battery consumption, a movement

threshold was set to prevent GPS fixes occurring when individuals were resting on land. As devices were attached for multiple days, half of the deployment period was spent within the nesting box, and this setting significantly reduced the number of unusable land fixes. Depth was recorded once per second by the pressure sensor (resolution = 20mbar, accuracy ± 10mbar).

Fig. 2.2. An Axy-Trek device attached to a penguin. Tape was wrapped around the device and the underside of the feathers. An additional triangular piece was attached at the front to further streamline the device and reduce the chance of device loss when moving in and out of the nestbox.

2.2.2 Data processing

Raw data files were extracted from Axy-Trek devices and edited to remove data not needed for analyses of location and depth. Each deployment of a tracking device recorded data from multiple foraging trips. The GPS data from each deployment were edited, with separate files created for each foraging trip, these files did not contain fixes from when the bird was on land between foraging trips. The beginning of a foraging trip was defined as the time when a bird departed from the colony. The GPS point representing this time was the last pre-trip fix on land. The end of a trip was when a bird arrived ashore and was the first post-trip GPS fix on land. The first and last GPS fixes for a foraging trip were determined from visual inspection of the fixes. Incomplete trips, where GPS fixes stopped before arrival on land or only began recording after trip departure, were excluded from trip duration analysis as departure and arrival times were unknown.

All points where travel speed was greater than 2 m/s were removed with the 'speedfilter' function (Sumner, 2009) using the 'trip' package in the R statistical environment. A speed greater than 2 m/s was considered faster than the little penguin travelling speed (Hoskins *et al.*, 2008). This removed less than 1% of GPS points.

For home and core range analysis, all GPS fixes that occurred before the first dive of the day and after the final dive were removed. This removed many fix locations surrounding the colonies at the start and end of a trip, which likely represent commuting or rafting behaviour, rather than time spent foraging. Retention of points near the colony could bias home and core range estimates towards the colonies and over-represent these non-foraging areas (Hoskins *et al.*, 2008; McCutcheon *et al.*, 2011). Although devices were set to record location at 1 fix/minute, there were gaps in the data as the penguins spend much of the day

diving and GPS fixes cannot be recorded when a penguin is underwater. GPS gaps occurred both during diving bouts and within periods of no diving. Data gaps during non-diving periods were probably times when penguins were swimming quickly, undertaking shallow horizontal dives with only brief periods at the surface. To ensure all tracks had consistent temporal resolution and to estimate locations during gaps, data were interpolated at 1-minute intervals using the 'move' package in R (Kranstauber *et al.*, 2018). Some tracks had large gaps and interpolating between these points may have been inaccurate and excluded areas where penguins foraged for much of the day. Tracks with a single gap longer than 50% of the foraging duration were removed from spatial distribution analysis.

Raw depth data were also split into individual foraging trips. The start and end times of each trip were the same as for the GPS data. Trips with errors that could not be rectified were removed from the dataset. For example, a trip with all depths recorded as 19 m was removed.

2.3 Foraging trip variables

Several foraging parameters were calculated using the 'trip' package in R. These included trip duration (h; the total time between trip departure and return), total distance travelled (km, the sum of distances between all recorded GPS fixes during a trip), and maximum distance from colony (km; the distance from the colony to the furthest GPS point). Trip departure time (h, relative to sunrise) and return time (h, relative to sunset). Foraging duration, defined as the time between the first dive of the day and the final dive, was recorded for each trip. The foraging duration represented the period when penguins were foraging and did not include time spent in the morning swimming from the colony to a foraging area or time spent rafting near the colony in the evening before arriving on shore.

2.4 Foraging ranges

The home range and core range were calculated for each trip, and for all trips together for each colony. Home range has classically been defined as "that area traversed by an individual in its normal activities of food gathering, mating and caring for young" (Burt, 1943), while the core range is an area within the home range, used at higher intensity, typically thought of as a foraging hotspot. In quantifiable terms a home range has been referred to as 'a minimum area in which an animal has some specified probability of being located' (Worton, 1989). Probability densities are derived from the utilisation distribution which is the distribution of individual locations on a plane. This distribution is obtained from the GPS locations where the individual was present. A 95% probability is commonly used to define the home range of an individual or population. This represents a 95% chance of an individual being found within the defined area. A 50% area is commonly considered to be the core range (Fig 2.3).

Spatial analysis was conducted using the kernel density estimation (KDE) method in the 'adehabitatHR' package. The KDE method calculates the utilisation distribution by applying a kernel function to each location point. The kernels and their associated bandwidth estimate a distribution based on the GPS locations and the density of the locations. A low kernel bandwidth results in a probability distribution which matches the GPS relocations tightly, while a higher kernel bandwidth results in a smoother and wider distribution. A value too small will create a non-contiguous range, matching the sample GPS fixes but unlikely to represent a true range, while a value too high can over-estimate home range area (Schuler *et al.*, 2014). Using the 'kernelUD' function, kernel estimation was calculated with a grid value of 1, while the default 'href' function was used to calculate the smoothing parameter (bandwidth). The 'href' function calculates the smoothing parameter using the reference

bandwidth method. This method is commonly used and assumes bivariate normal distribution of the utilisation distribution (Calenge, 2006). Smoothing parameter values ranged from 0.44 – 2.5 km for individual trips. Population ranges had smoothing parameters of 0.96 and 1.3 km for the OBPC and Creek colony, respectively. The home range was calculated as the 95% kernel utilisation distribution (KUD), while the core range was the 50% KUD.

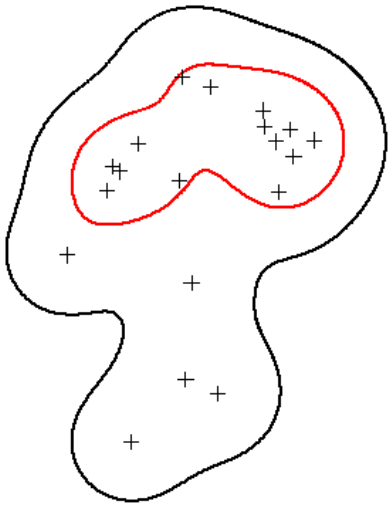

Fig. 2.3. Example of a home and core range area estimated using the utilisation distribution and adehabitatHR. The black line represents the home range (95% KUD), and the red line represents the core range (50% KUD). + symbols indicate recorded GPS relocations of an individual.

The size of the home and core range areas in km^2 were calculated using the 'kernel.area' function. To estimate the population ranges, GPS locations were pooled, and points were categorized by the trip, individual, sex and colony they were associated with.

The extent of overlap between foraging ranges of penguins from the two colonies was calculated using the 'kernel.overlap' function. The utilisation distribution overlap index

(UDOI) was used as the overlap metric. This method calculates the overlap between two utilisation distributions, assuming they use space independently of each other. A value of 0 indicates no overlap (full segregation), and 1 indicates complete overlap. Values can be >1 if utilisation distributions are not uniformly distributed and there is a high degree of overlap. UDOI values are informative but do not reveal if the degree of overlap (or segregation) is statistically significant. A randomisation process was used to determine whether an observed spatial segregation was significant. Trips were randomly assigned to colonies, then colony ranges were calculated, and an overlap analysis performed on the randomised samples. The randomisation procedure was repeated 1,000 times using an R script adapted from Sánchez *et al.* (2018). The proportion of results with an overlap value lower than the observed UDOI was used to test for statistical significance. A high proportion of randomised UDOI's that are lower than the observed UDOI value would indicate the observed spatial segregation could occur by chance. A proportion of <0.05 was considered to indicate less overlap than expected by chance i.e., foraging ranges were spatially segregated.

Estimated water depths within the foraging ranges of birds from each colony were calculated. Bathymetry data were obtained from GEBCO (https://download.gebco.net/) and had a resolution of 15 arc-seconds (~ 450 m). Using QGIS, home and core ranges were plotted over bathymetric data, and the estimated depth values within a given range were averaged to calculate the mean depth within the range. Furthermore, bathymetric data were used to illustrate depth contours for all maps that are presented.

2.5 Diving analysis

Diving analysis was conducted using the 'diveMove' package (Luque, 2007). The 'calibrateDepth' function was used to sort dives into phases (ascent, bottom, and descent) and

calculate diving parameters for each trip. Diving parameters included dive depth, duration, bottom time, and post-dive duration. Pressure sensors often incur surface drift, a calibration error where the surface depths are recorded as higher or lower than 0 m, so zero offset corrections were applied. Sensor drift was identified when no 0 m values were recorded for a period longer than little penguins can dive. The 'offset' method was used when calibration drift was consistent through an entire foraging trip. The extent of the drift was entered, and dive depths were corrected by that value. The 'visual' method was used when drift occurred throughout a trip, with different drift values entered during the course of a trip.

A 1 m dive threshold was set, with all dives less than 1 m excluded from analysis. Dives with depths less than 1 m likely represent short travelling dives (Agnew, 2014). To calibrate dive phases, the smoothing spline model was selected, with a smoothing parameter of 0.5. A critical quantile of 0.25 was set as the ascent and descent rate threshold. That is, when descent or ascent rates fell below this threshold, those phases were deemed to have ended. Estimation of dive phases is sensitive to the smoothing parameter value. Rate threshold and smoothing parameter values were selected after repeated trials of different values. The chosen values estimated dive phases that best matched the descent, bottom, and ascent phases apparent from visual observation of the dive profiles. A wiggle tolerance threshold of 0.8 was set, so any dive wiggles during descent that occurred above 80% of the maximum depth did not terminate the descent phase. Furthermore, any wiggles below this threshold did not indicate the end of the bottom phase. Dives less than 5 seconds in duration were excluded from analysis as these were likely associated with surface travelling (Agnew, 2014).

Descriptive statistics were calculated for dive duration, maximum depth, bottom time, and post-dive duration. In addition, bottom time proportion (bottom/dive time) and dive

efficiency (bottom time / (dive time + post-dive) were calculated. Other variables that were calculated included number of dives per trip, dives per hour, total daily diving time, and total vertical distance travelled. The number of dives per hour was calculated as the number of dives divided by foraging duration, rather than total trip duration. Total vertical distance was the sum of vertical distances during descent, bottom phase (including any undulations), and ascent within a dive.

2.6 Statistical analysis

All statistical tests were conducted using Prism (GraphPad Software, LA Jolla, CA). Because multiple trips were recorded for some individuals, observations were not independent. To account for this, nested t-tests were used to test for significant differences between groups. The nested t-test accounts for repeated measures by including the individual as a random effect. For all tests, residuals were assessed for normality (Shapiro-Wilk test), and data were transformed when appropriate. Total trip distance, log maximum distance from the colony, trip duration, foraging duration, and departure and arrival times were compared between colonies using nested t-tests. Trip departure and arrival times are correlated with sunrise and sunset, respectively (Rodriguez *et al.*, 2016). These times were compared between colonies, with time of departure from the colony converted to hours before sunrise and arrival time converted to hours after sunset. Furthermore, colony arrival times were log transformed. Dive depth, duration, bottom time, proportion of time at bottom, dive efficiency and post-dive interval were averaged across individual trips to obtain single parameter values per trip. Mean values were compared between colonies. Number of dives per trip, total diving duration, total vertical distance (squared) and diving rate were also compared between colonies using nested t-tests. In addition, mean number of dives, mean dive depth and mean diving duration per trip was calculated for each day that tracking occurred. Linear regression

was conducted to determine if these variables changed during the sampling period. Non-parametric Kruskal-Wallis H tests were used to test for differences in the diving rate and mean dive depth throughout the day within each colony. Diving rate and mean dive depth were calculated for 1-hour time periods. Dunn's multiple comparison tests were used to compare pairs of time periods.

3. Results

3.1 Foraging tracks

Tracks were recorded for 54 foraging trips made by 12 penguins at the OBPC and 13 penguins at the Creek during the guard stage of breeding, with one to four trips recorded from each penguin. Tracks of penguins from each colony are shown in Fig. 3.1 and tracks of male and female penguins are shown in Fig. 3.2. Most penguins left their colony on an easterly bearing, perpendicular to the coastline, before travelling north, while some birds foraged to the east of the colonies and others foraged to the south. All trips were a single day in duration, and penguins typically remained within 20 km of their colony. For most trips, penguins remained in water less than 25 m deep, and frequently foraged where the water was approximately 20 m deep.

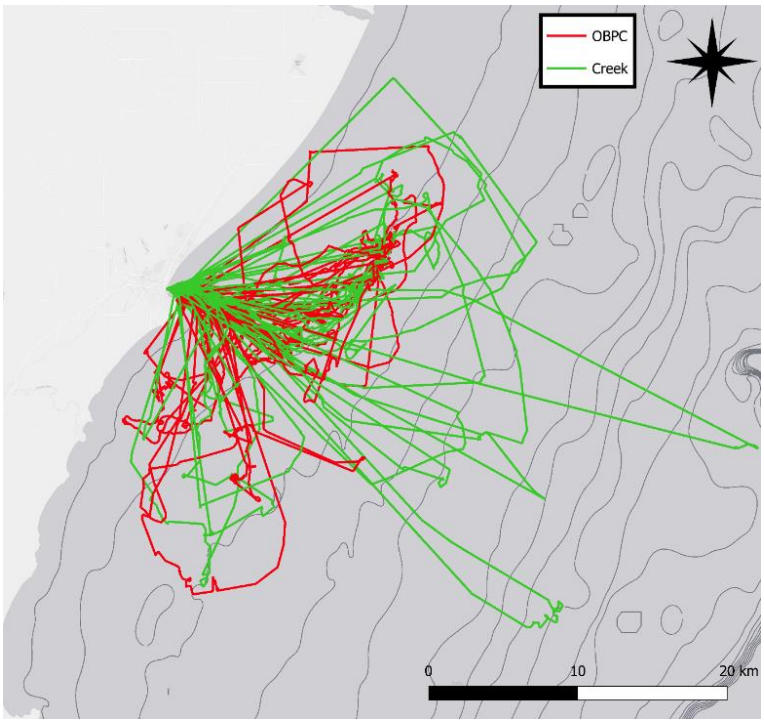

Fig. 3.1. All foraging tracks from the OPBC (red) and the Creek (green) colonies. The contour lines show the water depth at intervals of 10 m.

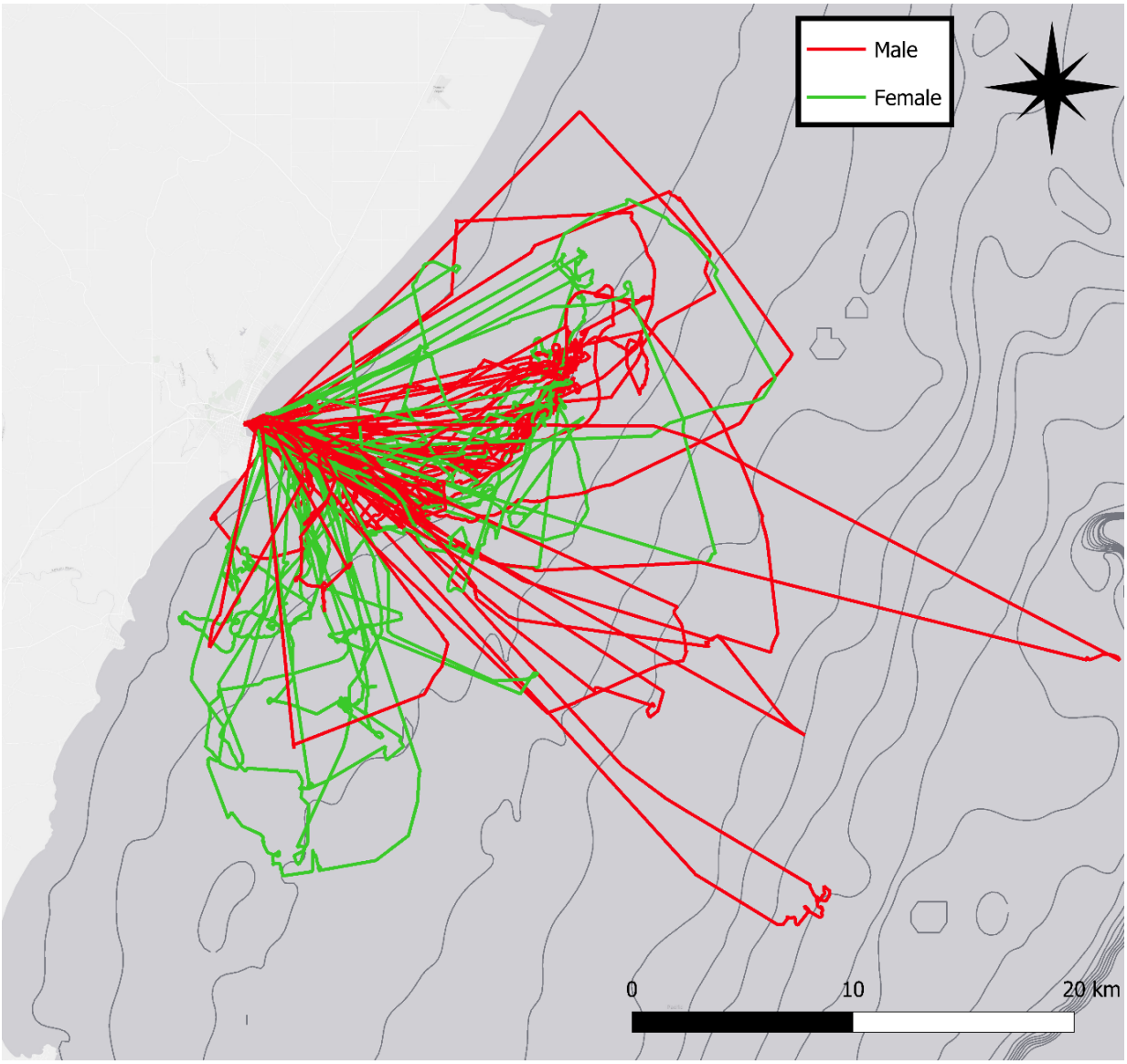

Fig. 3.2. All 54 foraging tracks from the OBPC and Creek colonies. Tracks of male penguins are shown in red and tracks of female penguins in green. The contour lines show the water depth at intervals of 10 m.

Trips could be broadly categorised as wide ranging, when birds followed a large looping path and travelled a large maximum distance from the colony, or short range, when birds remained closer to the colony and foraged within a smaller area (Fig. 3.3). Individuals conducting wide-ranging trips often swam further from the shore into deeper water than penguins that made short range trips that were usually in water less than 25 m deep. 10 trips were wide-ranging, 35 were short range, and nine trips had characteristics of both categories with looping tracks close to the coast or long tracks that were not circular. Circular travelling patterns may be underestimated in these trips due to gaps in the GPS fixes. Gaps in GPS data are seen as straight lines that do not indicate the actual locations of the birds. Six of the 10 wide-ranging trips (five from the Creek colony and one from the OBPC) were recorded on days 13 to 15 of the study.

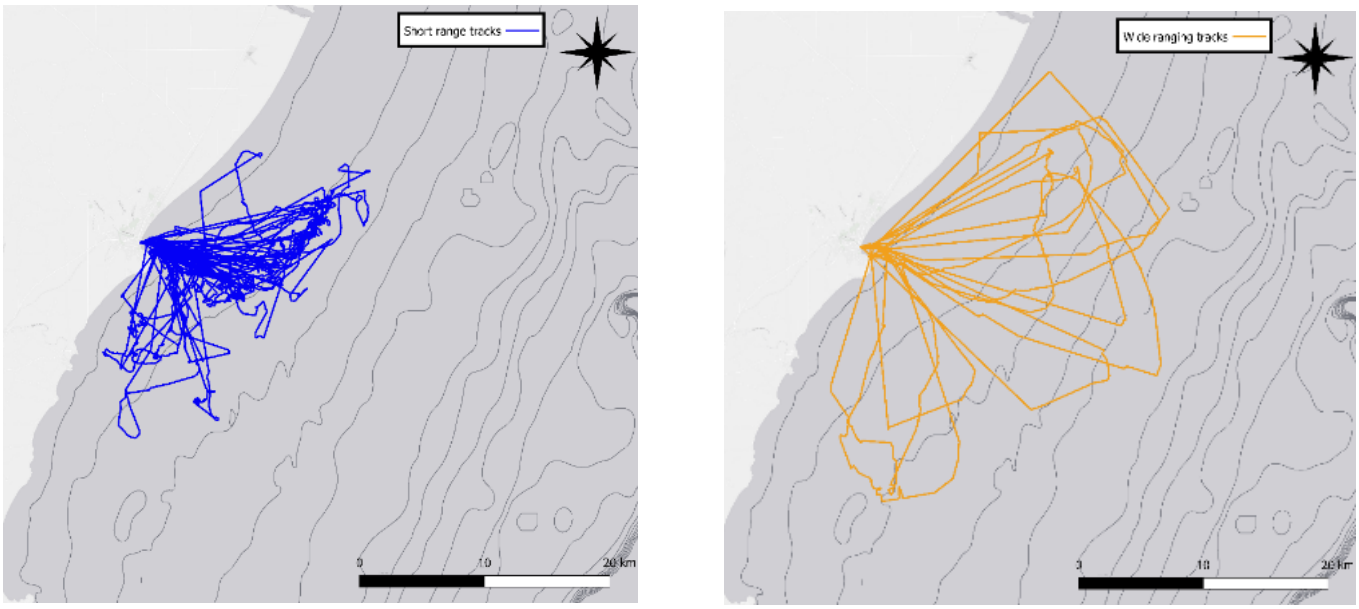

Fig. 3.3. Short range tracks (blue) and wide-ranging trips (orange) from both the OBPC and Creek colony. Wide ranging trips following a looping path and usually reached a greater maximum distance from the colony than short range tracks. The contour lines show the water depth at intervals of 10 m.

Tracks and dive profiles for individual penguins are shown in Figs. 3.4 to 3.29.

The repeatability of foraging tracks varied between birds. Some individuals had foraging tracks that were remarkably similar between consecutive trips, whilst other individuals foraged in different locations on consecutive trips. For example, bird 10 (Fig. 3.13) had three similar tracks, while the distances and directions travelled differed between three trips made by bird 13 (Fig. 3.16). Foraging trips were similar on consecutive trips for 17 of 19 birds for which multiple trips were recorded. Some consecutive trips were repeatable in distances travelled but were variable in direction.

Variation in foraging trips can be seen through visual inspection of consecutive tracks. Bird 10 had consistent foraging locations (Fig. 3.13). The bird departed at 4.30 am, before 4.00 am (exact time unknown) and at 3.04 am. It swam east on all three trips then, when the water was about 20 m deep, swam north-east and continued to swim where the water was about 20 m deep for six to 11 hours. The bird frequently turned and made loops whilst swimming north-east, indicating that it was likely to have been foraging. The mean dive depths during this period on each trip were 15.7, 17.4 and 17.8 m, with 56 – 71% of dives to a depth greater than 18 m. Dive depths on the three trips increased as the bird swam away from the colony, were relatively consistent where the water was about 20 m deep, then decreased as the bird swam back to the colony. The dive profiles suggest that the bird was diving close to the seafloor and hence that benthic diving was common during these trips.

Bird 7 was also very consistent between trips (Fig. 3.10). It departed in a south-east direction at 4.49 am and 4.03 am on the two trips. Diving began at 5.45 and at 5.33 am, while the bird was swimming away from the shore., then approximately 2.5 hours after departure the bird stopped swimming away from the shore and begun looping and turning frequently in water 15 to 20 m deep. Maximum dive depths increased as the bird swam into deeper water. The penguin remained in water 15 to 20 m deep for much of each trip, then swam back to the shore and arrived at 8.42 pm and then at 8.44 after the two trips.

Bird 18 swam north on one trip and south on the next two trips (Fig. 3.21). The penguin departed at 4:00 am on the first trip and headed in a south-west direction until 5:30 am when diving commenced for the day. It then travelled north-east until 7:09 am, travelled north-west back towards the coastline, and eventually foraged approximately 1 km from the shore. Foraging occurred in water approximately 10 m deep, with most dives being benthic. It then

travelled further from the coastline back into water between the 10 and 20 m contour, before returning to the colony at 9:05 pm. Bird 18 travelled south on its second trip. It left the colony at 4:50 am and swam south-west and then south. This trip was all in water <20 m deep. The maximum distance from the colony was 9.7 km, with a maximum distance from the coast of 5 km. The track came close to coastline, as for the first trip, with foraging occurring approximately 2 km from the shore. The penguin also travelled south on the third trip and remained in water less than 20 m deep for most of the time. A period of sharp turns and loops occurred from 8:00 am until 2:45 pm in an area less than 3 km from the coastline.

Bird 14 undertook three trips that were not consistent in their foraging patterns (Fig. 3.17). Two trips had circular patterns, but quite different distances travelled, while the third trip was more direct with much of the trip spent around the 20 m depth contour. Departure times were 4:20 am, 3:38 am and 3:11 am respectively. Each trip begun in a south-east direction, perpendicular to the coastline. On the first trip, this path continued for 4.5 h until the penguin was >20 km from the colony and near the 50 m depth contour. Most time beyond the 50 m contour was spent on the surface, without diving. After 9:20 am, the penguin begun travelling north-west, back towards the coastline. There was a period of deeper dives approaching the 20 m depth contour, then the bird returned to the colony. Diving ceased at 8:11 pm, and the penguin arrived on shore at 9:25 pm. The second trip was in a south-east direction, as for the first trip. However, on this trip the penguin travelled only 10 km over 5 h, to the 20 m depth contour, before turning north-west. Furthermore, fewer dives and a smaller total vertical distance was swum before the turning point compared to the first trip. The bird was travelling slower and spending less time diving compared to the day before. The penguin continued north-west until it neared the 10 m contour line. The dive profile appears to match that of the bathymetry along the path travelled. That is, dive depths

gradually reduced from >20 to 10 m at the same rate as the sea depth changed, so it is likely that most dives were benthic during this stage of the trip. Diving ended at 7:42 pm and the trip ended at 9:15 pm. The third trip did not have a wide-ranging pattern, and foraging was focused around the 20 m depth contour. After initial departure in a south-east direction, the penguin shifted to a north-east bearing and continued along this path until it reached the 20 m depth contour, approximately 13 km from the colony. While heading away from the coast there was a gap in GPS fixes. However, during this gap, dive depths slowly increased from 10 to 20 m. The change in dive depth matches the ocean depth encountered if the path between fixes was linear. This same pattern was observed when the penguin left the 20 m deep area and returned towards the shore. Over 8 h was spent near the 20 m depth contour, and many loops and turns were observed. There was a long break in diving (26 min) before the bird approached the 20 m depth area. Dives were deep during the 8 h spent in the 20 m depth area, with a mean dive depth of 19.4 m. At 3:44 pm the penguin began swimming towards the shore, then it reached the colony at 9:15 pm.

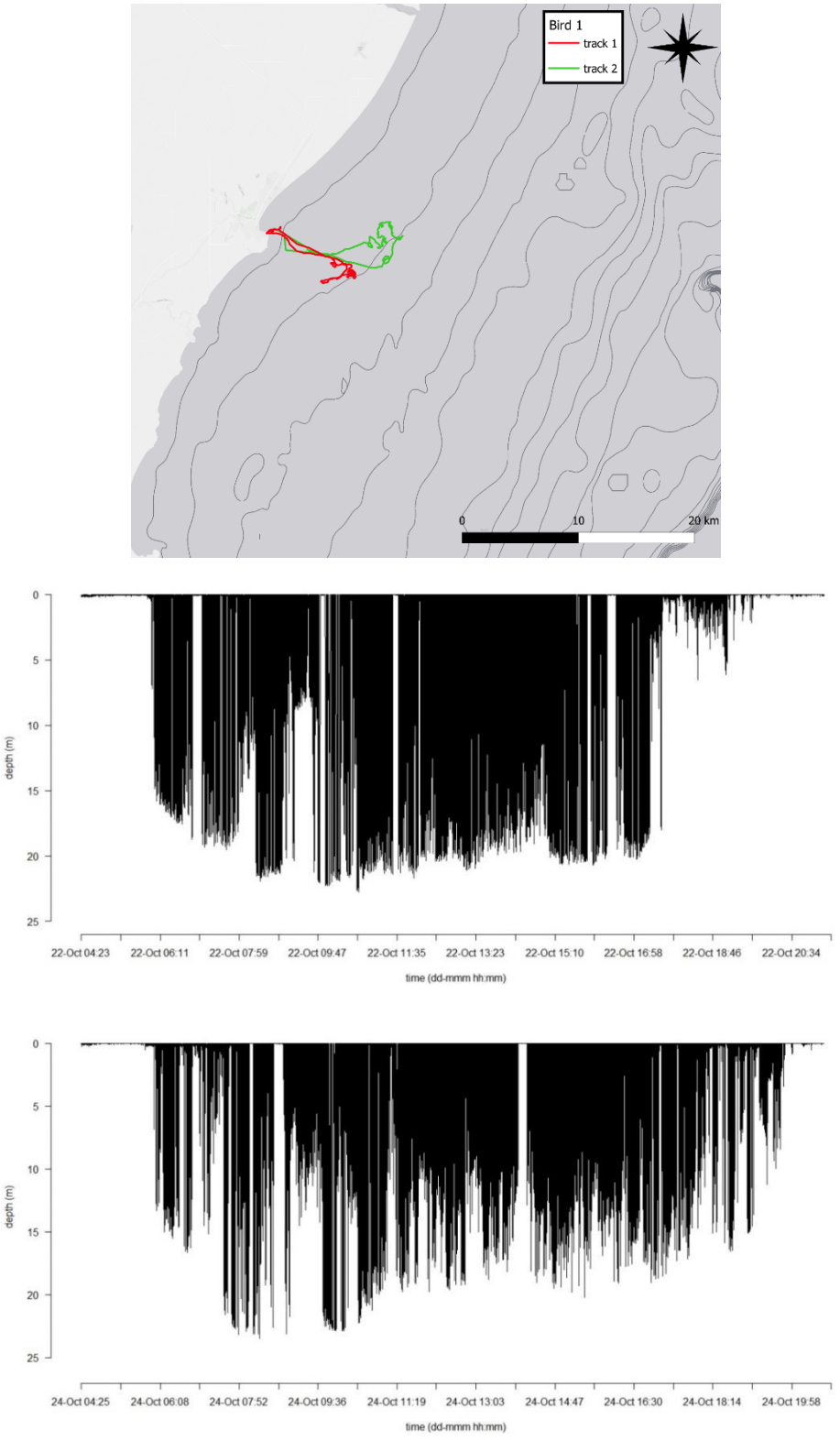

Fig. 3.4. Tracks and dive profiles for two consecutive foraging trips by bird 1. The contour lines show the water depth at intervals of 10 m. The top dive profile represents trip 1, the lower profile is for trip 2. This bird foraged relatively close to the colony for both trips.

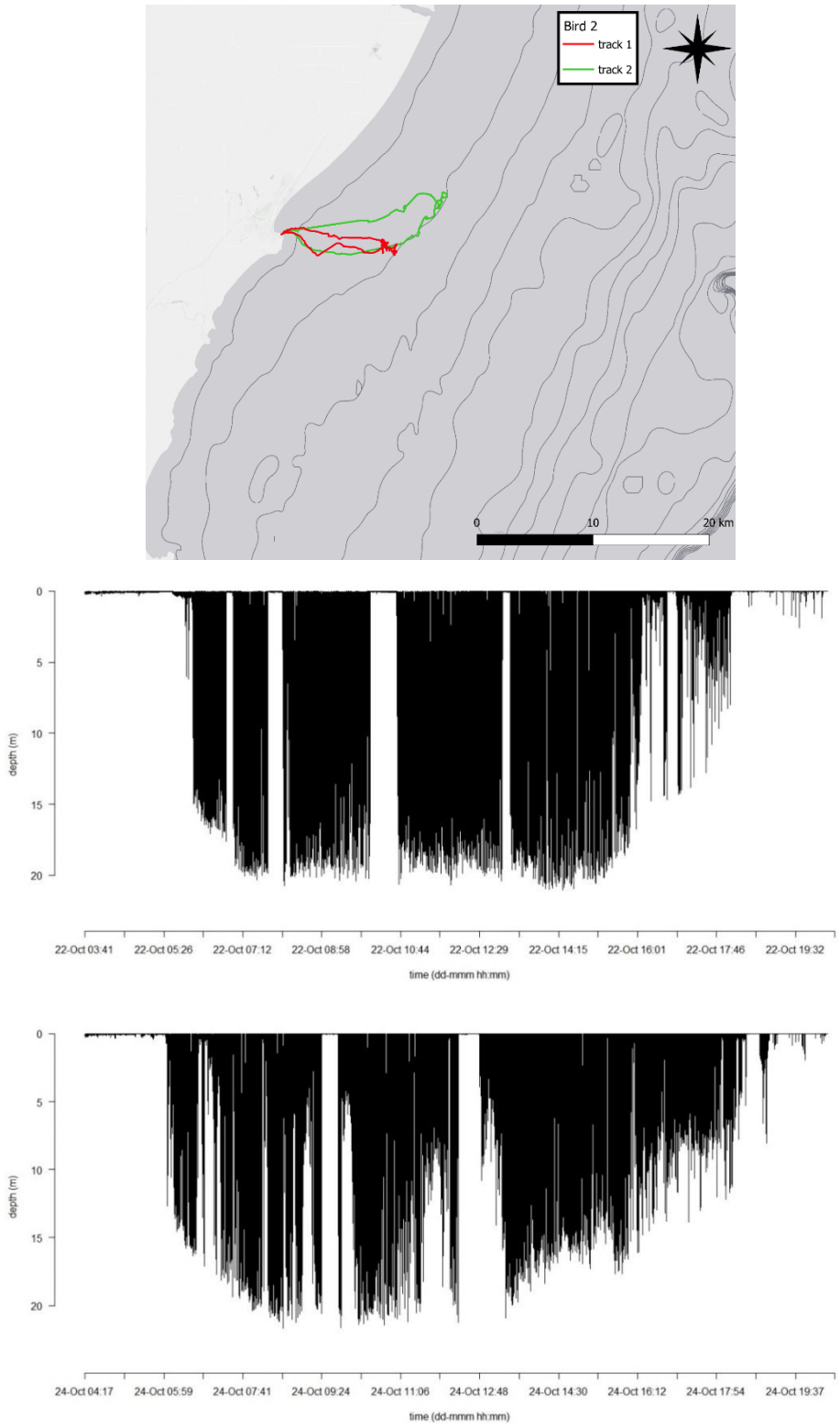

Fig. 3.5. Tracks and dive profiles for two consecutive foraging trips by bird 2. The contour lines show the water depth at intervals of 10 m. The top dive profile represents trip 1, the lower profile is for trip 2. This bird foraged relatively close to the colony for both trips.

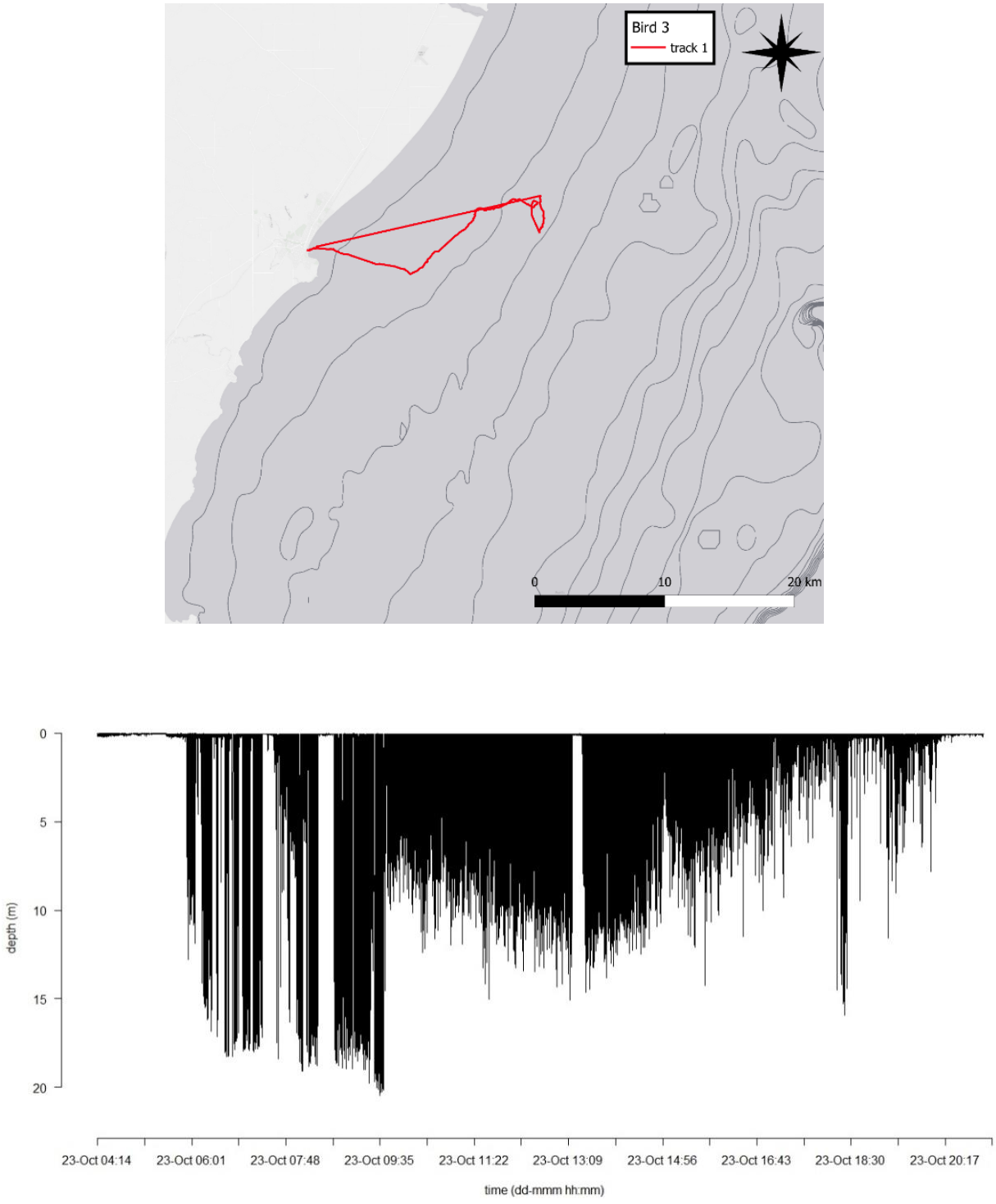

Fig. 3.6. Track and dive profile for a foraging trip by bird 3. The contour lines show the water depth at intervals of 10 m.

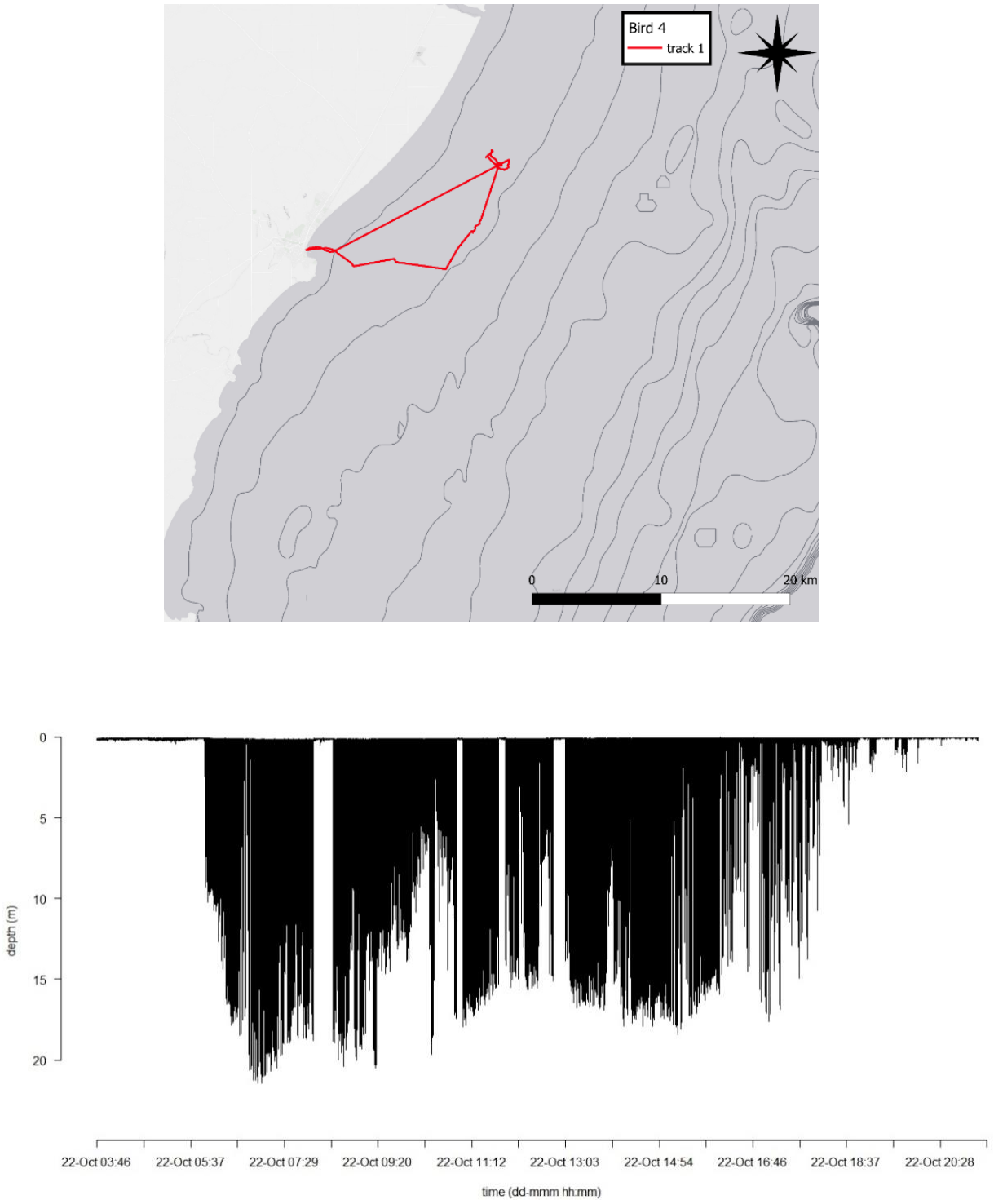

Fig. 3.7. Track and dive profile for a foraging trip by bird 4. The contour lines show the water depth at intervals of 10 m.

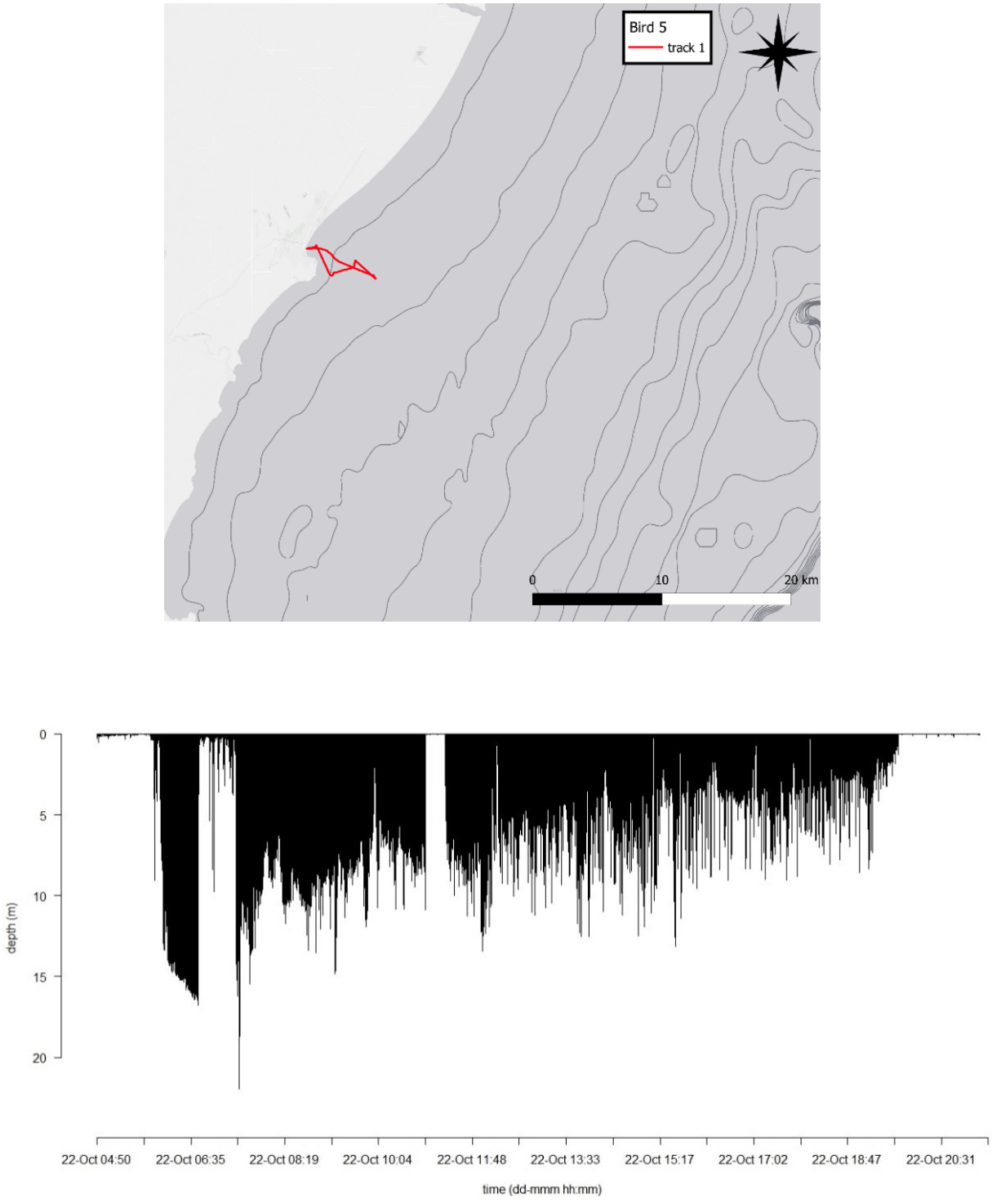

Fig. 3.8. Tracks and dive profiles for a foraging trip by bird 5. The contour lines show the water depth at intervals of 10 m.

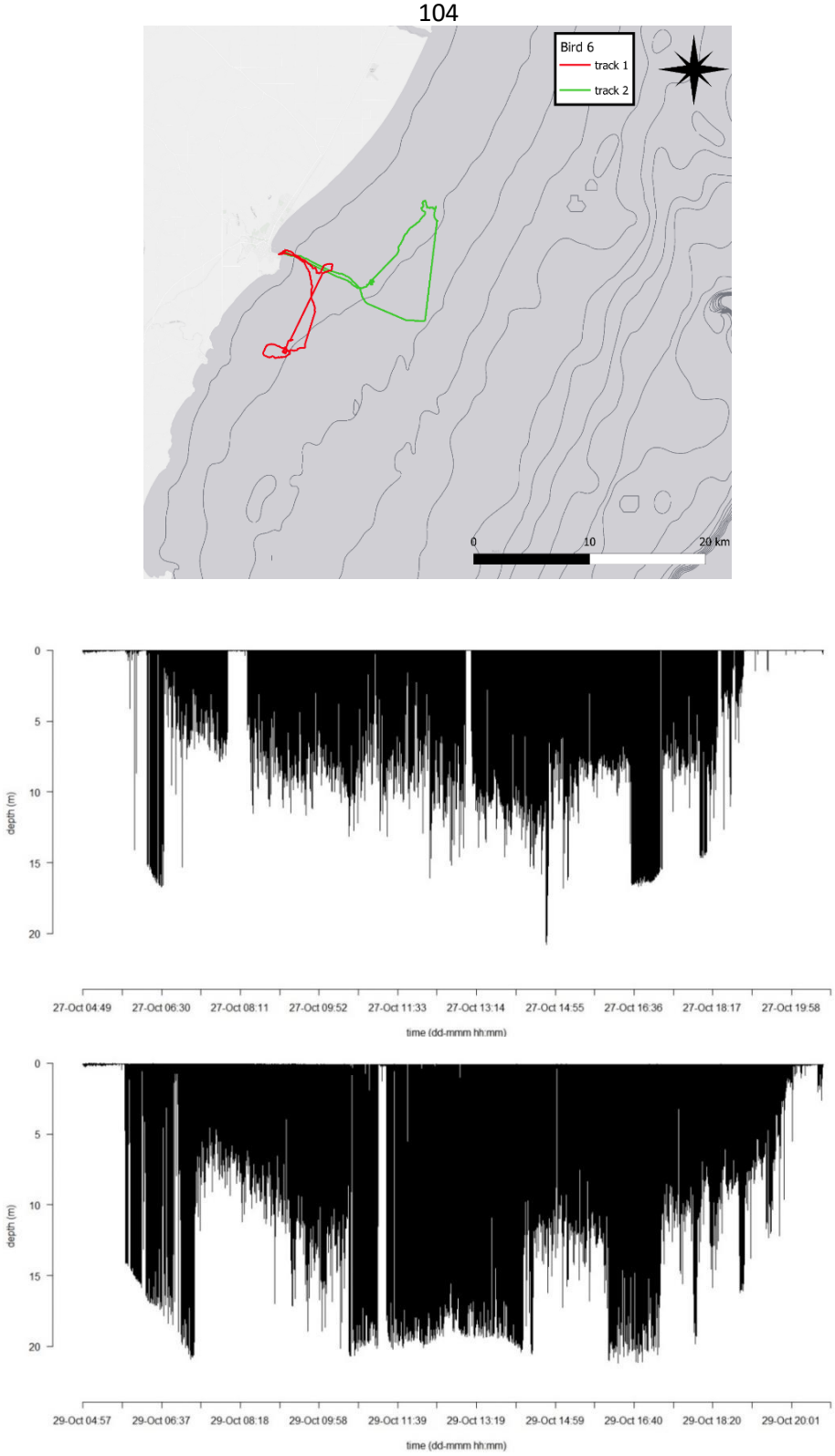

Fig. 3.9. Tracks and dive profiles for two consecutive foraging trips by bird 6. The contour lines show the water depth at intervals of 10 m. The top dive profile represents trip one and the lower profile is for trip two. This bird travelled in opposite directions on each trip.

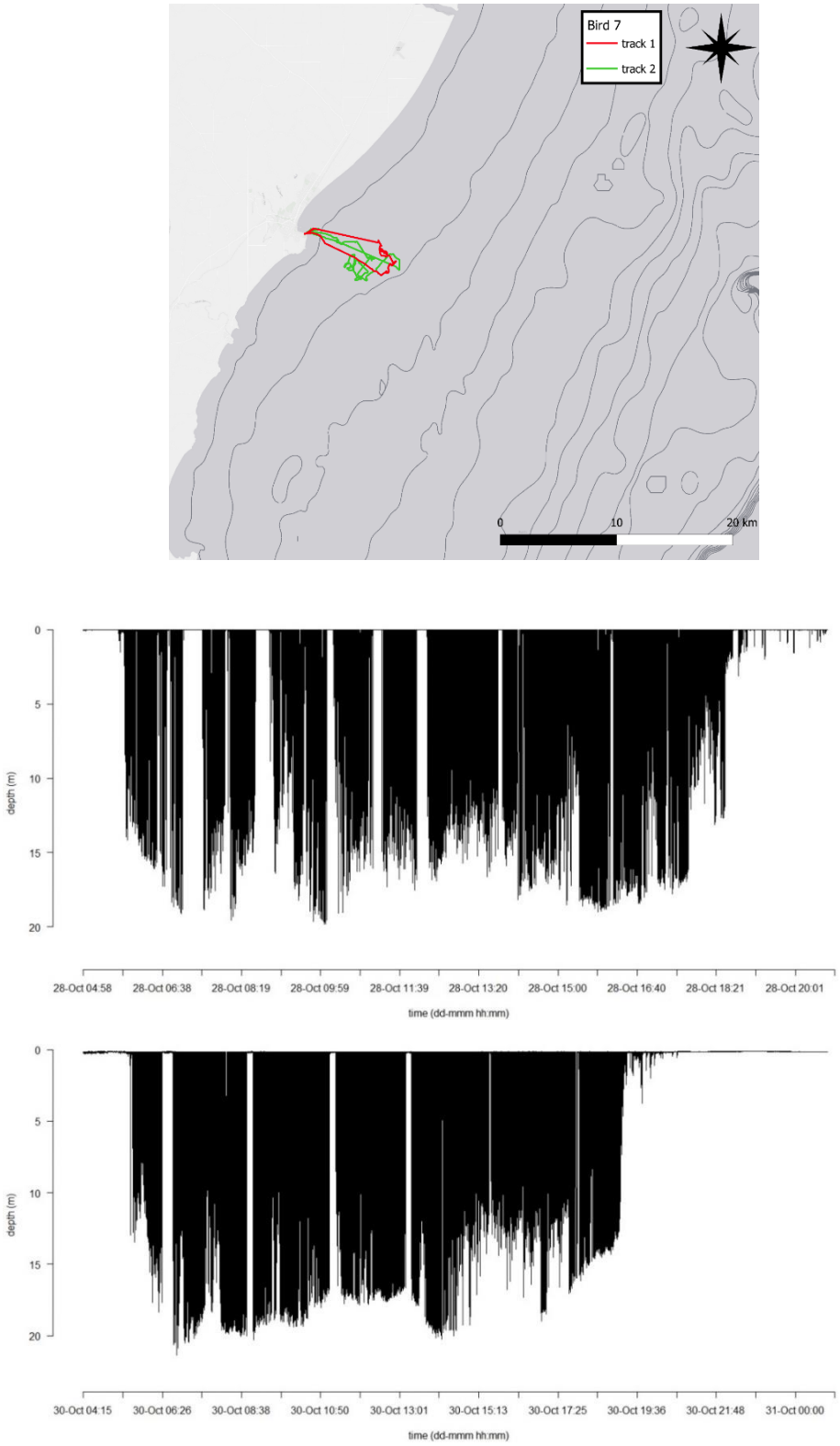

Fig. 3.10. Tracks and dive profiles for two consecutive foraging trips by bird 7. The contour lines show the water depth at intervals of 10 m. The top dive profile represents trip one and the lower profile is for trip two. This bird had highly overlapping tracks and remained close to the colony during each trip.

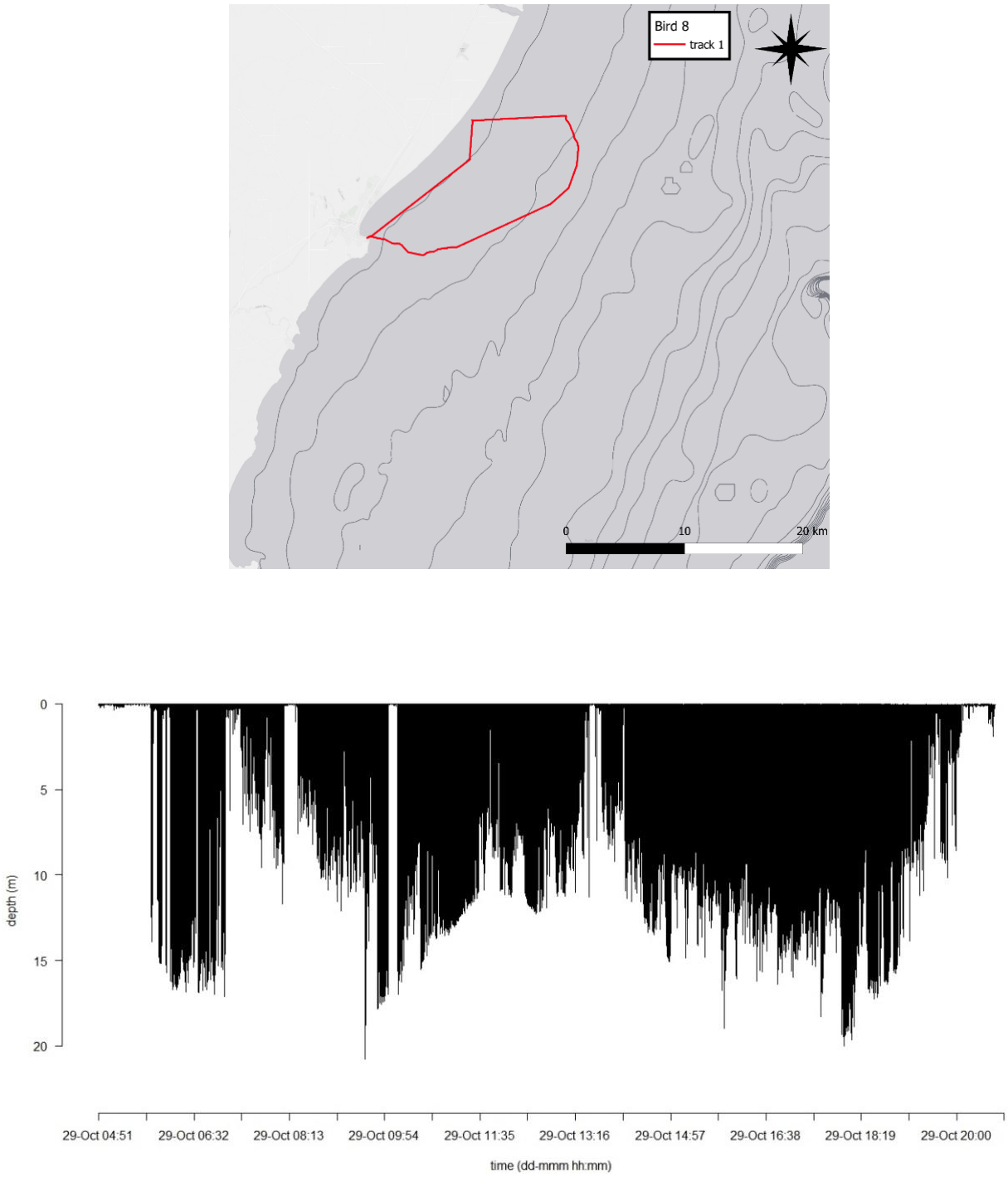

Fig. 3.11. Track and dive profile for a foraging trip by bird 8. The contour lines show the water depth at intervals of 10 m.

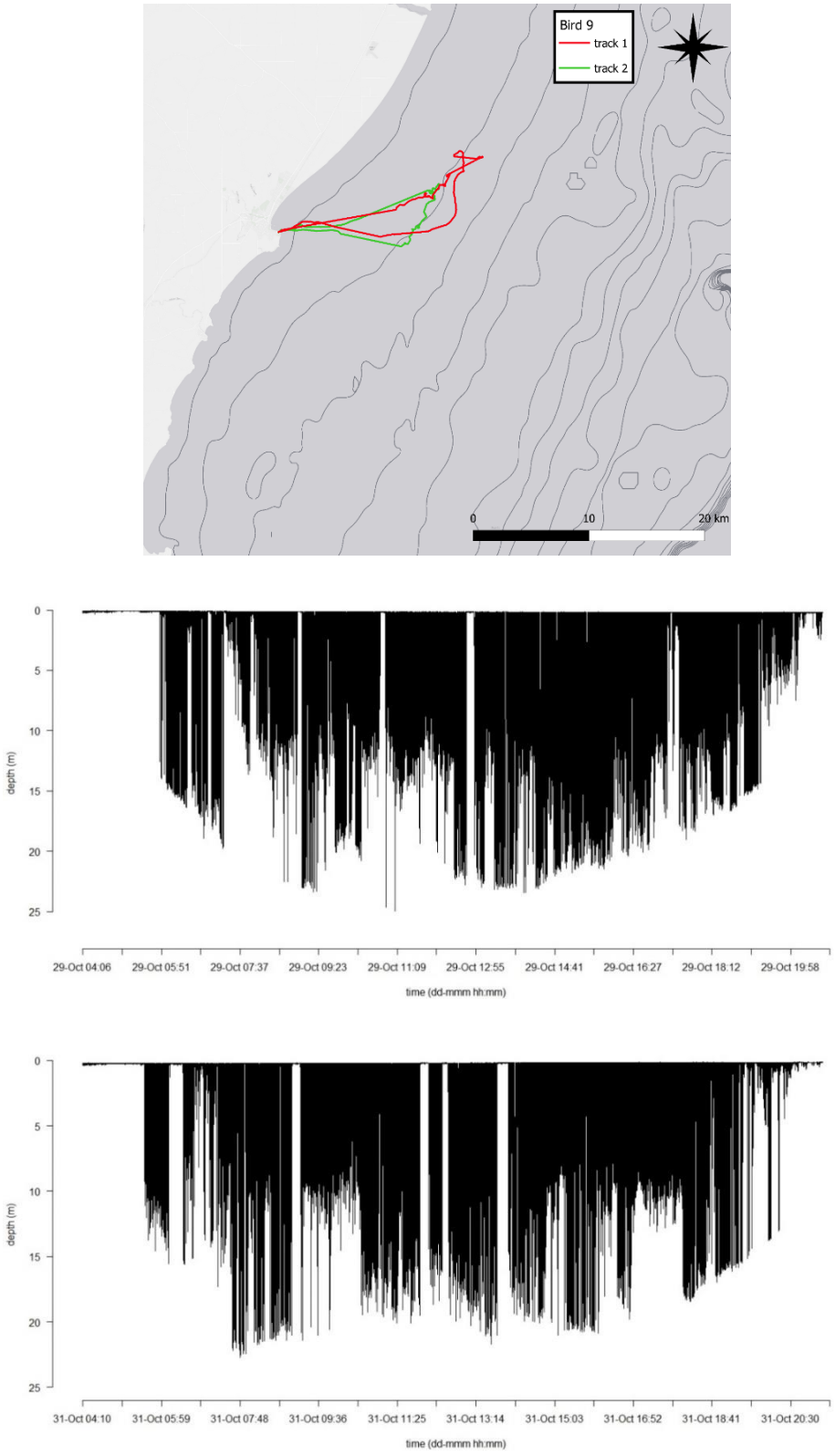

Fig. 3.12. Tracks and dive profiles for two consecutive foraging trips by bird 9. The contour lines show the water depth at intervals of 10 m. The top dive profile represents trip one and the lower profile is for trip two.

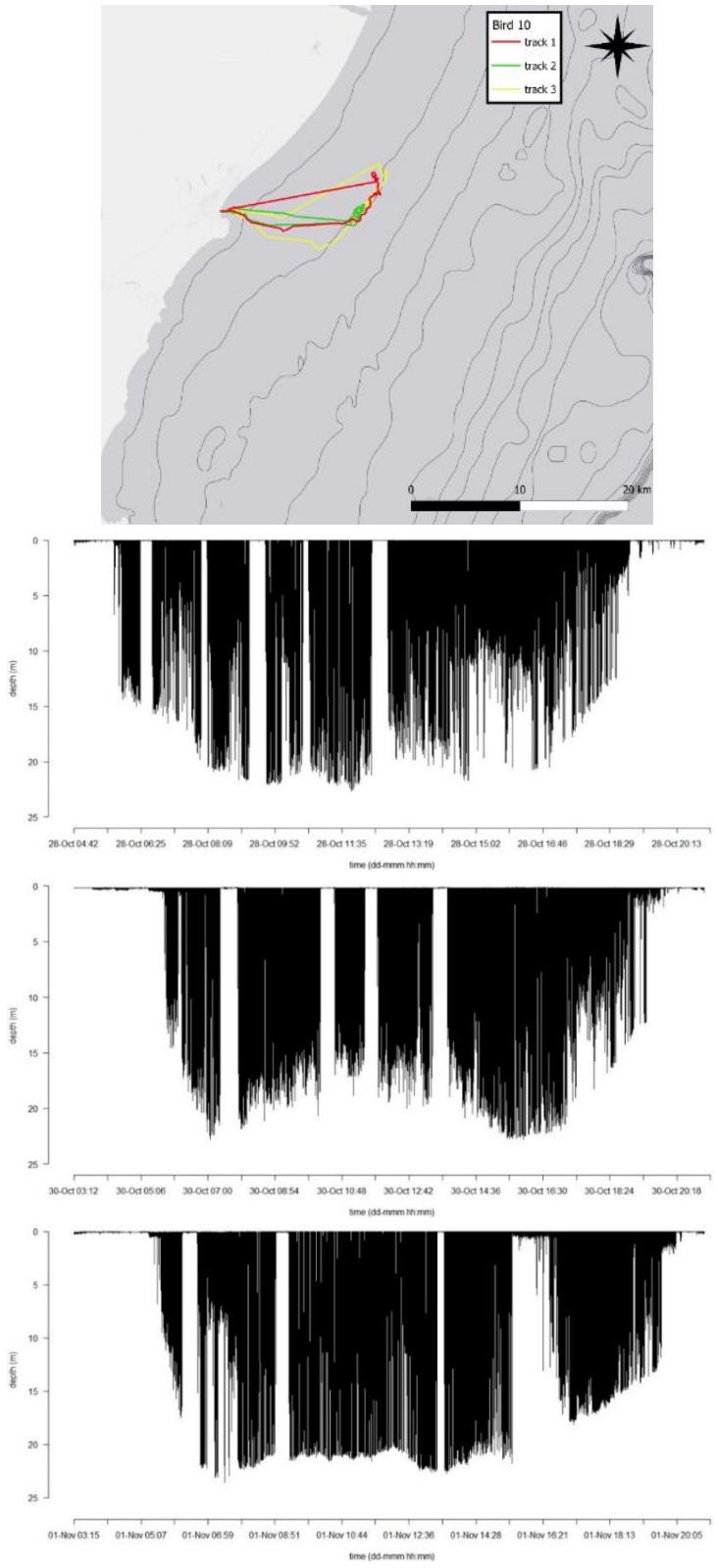

Fig. 3.13. Tracks and dive profiles for three consecutive foraging trips by bird 10. The contour lines show the water depth at intervals of 10 m. The top dive profile represents trip one, the centre profile trip two and the lower profile trip three.

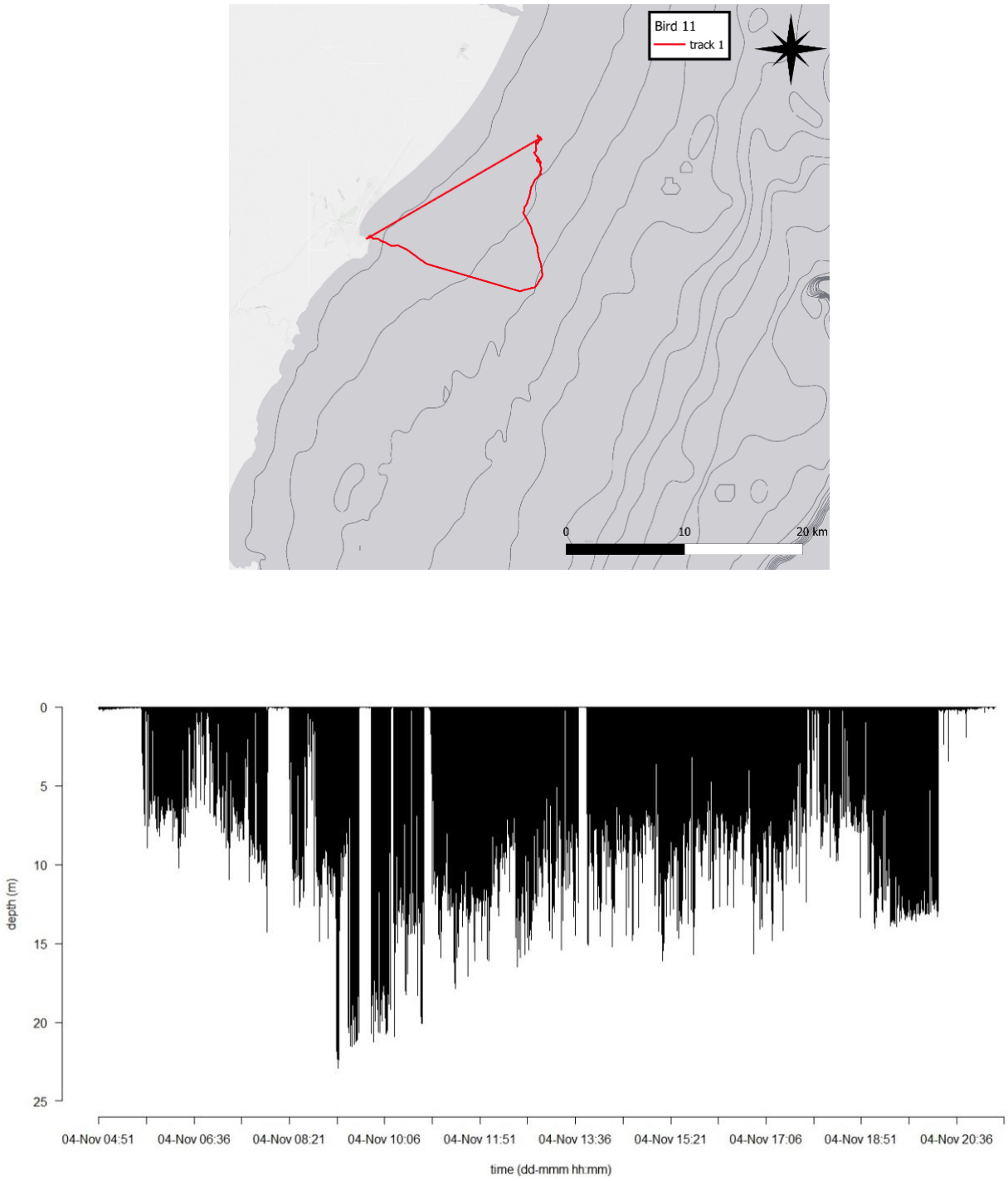

Fig. 3.14. Track and dive profile for a foraging trip by bird 11. The contour lines show the water depth at intervals of 10 m.

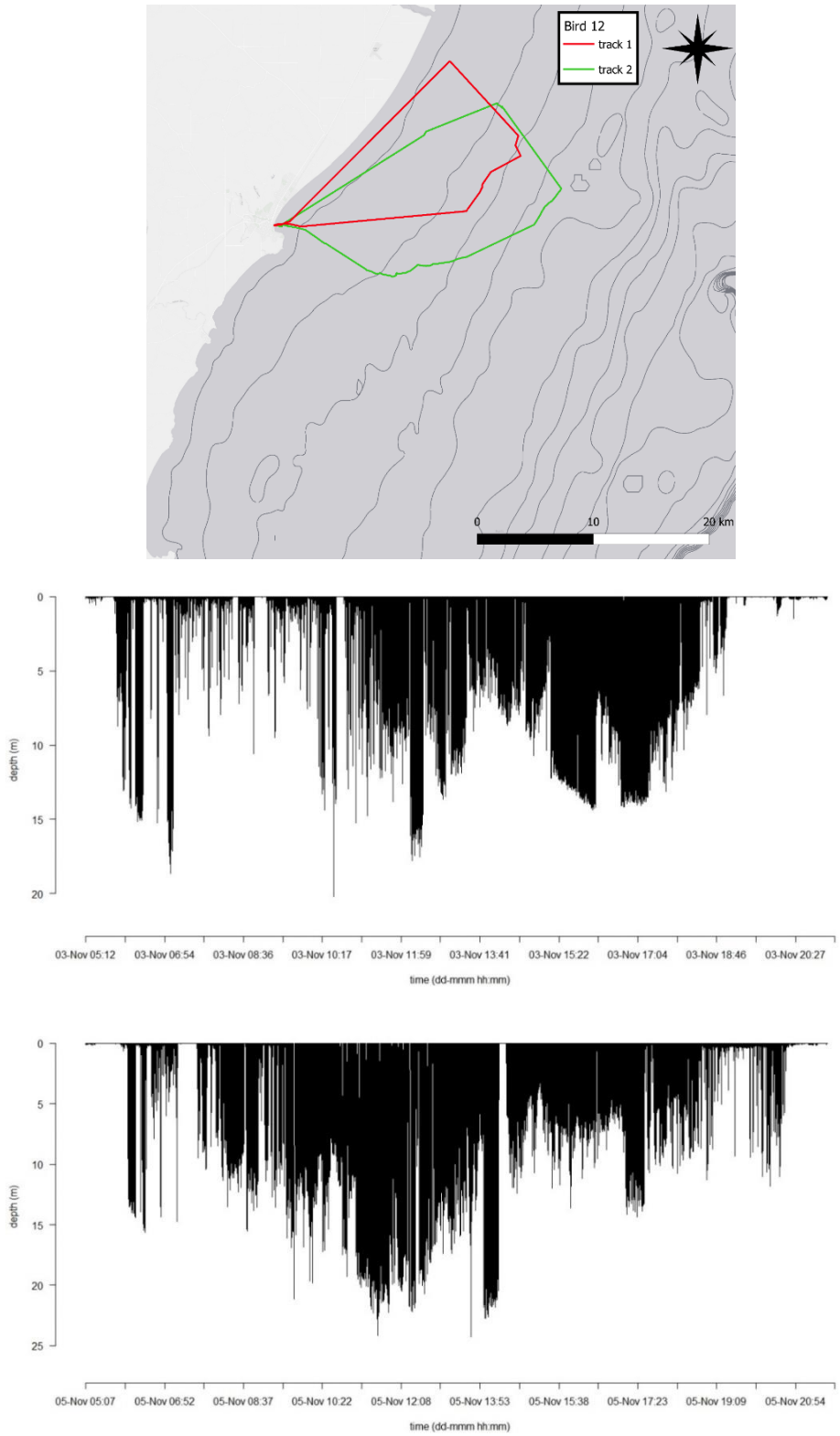

Fig. 3.15. Tracks and dive profiles for two consecutive foraging trips by bird 12. The contour lines show the water depth at intervals of 10 m. The top dive profile represents trip one and the lower profile is for trip two.

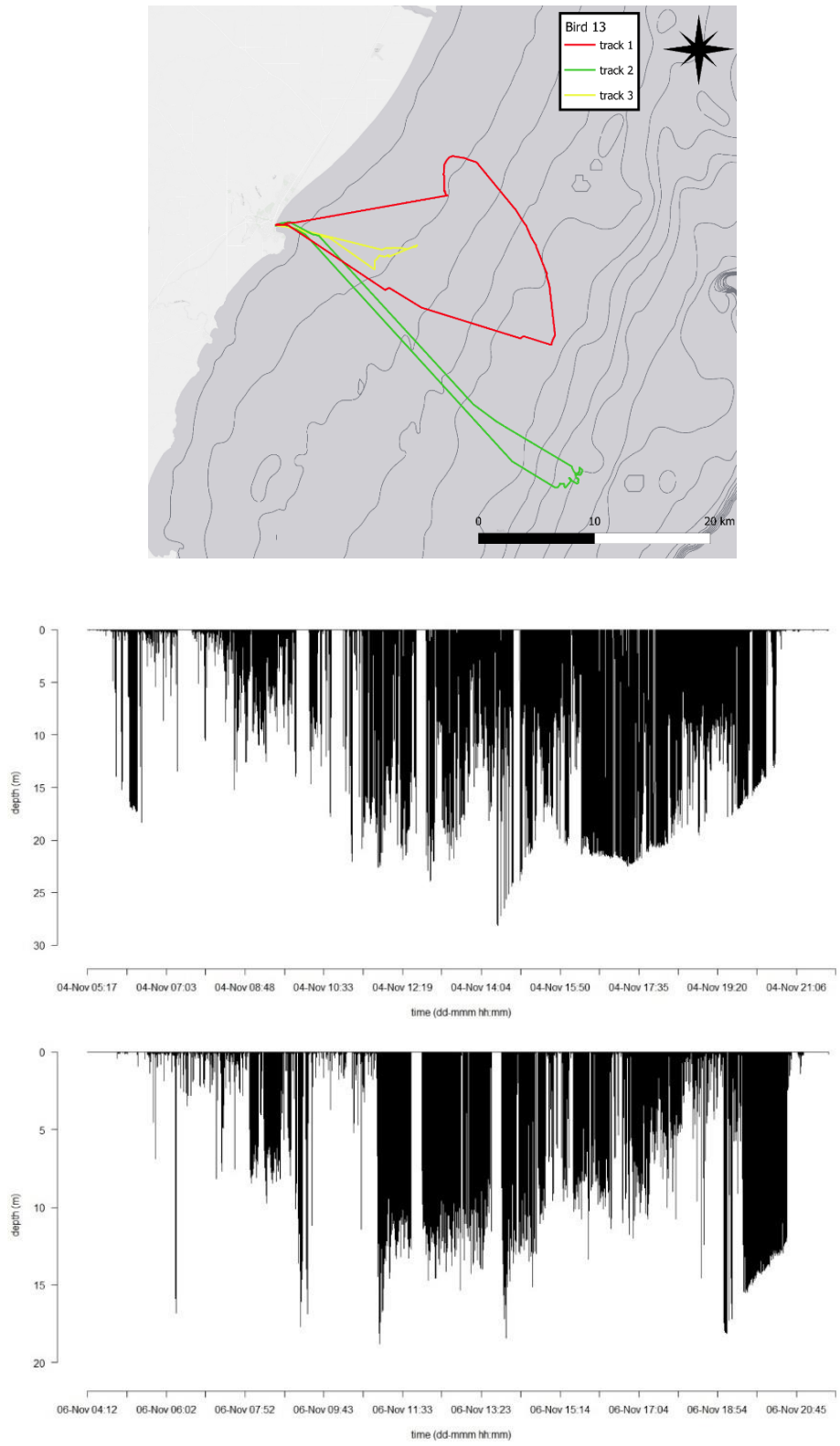

Fig. 3.16. Tracks for three consecutive foraging trips by bird 13. The contour lines show the water depth at intervals of 10 m. The top dive profile represents trip one and the lower profile is for trip two. There was no dive data for trip three due to a device error.

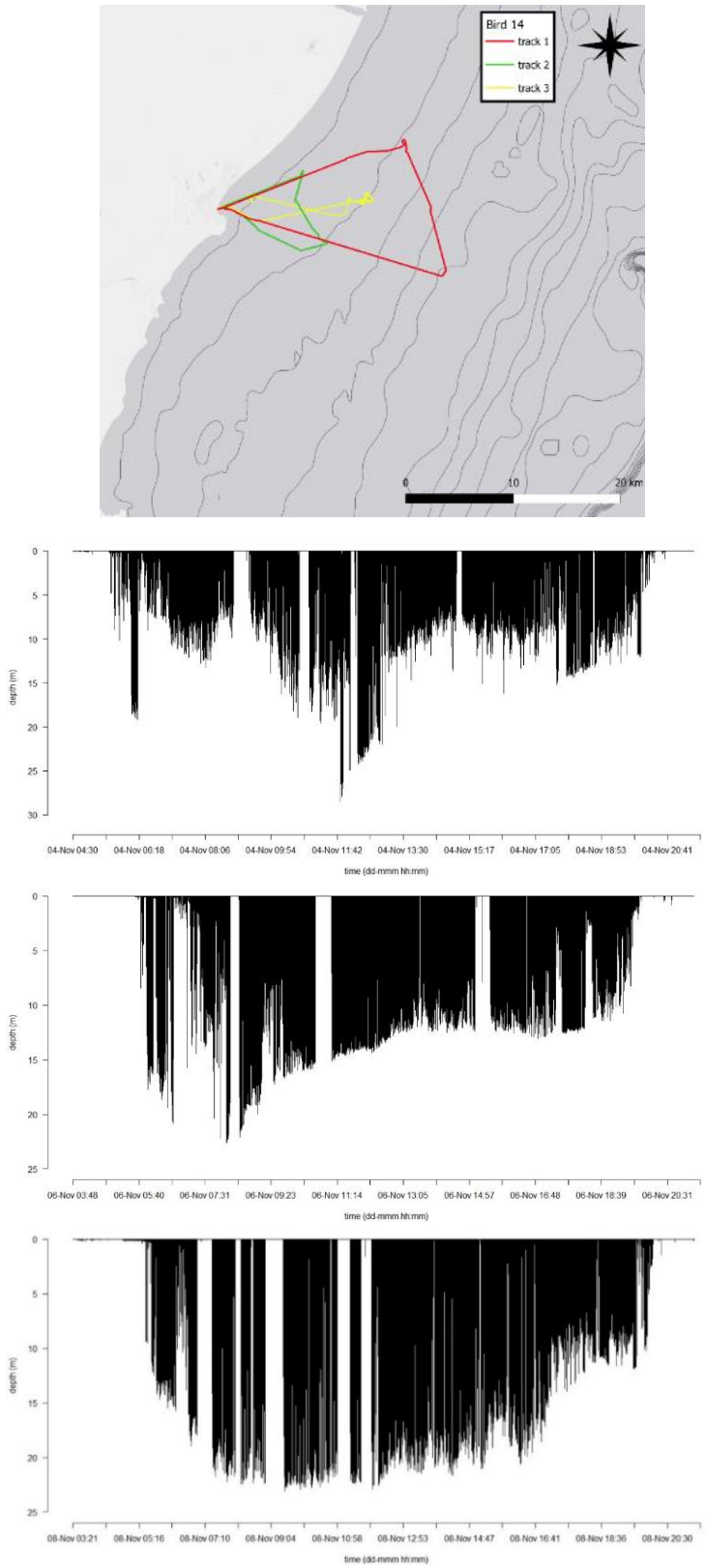

Fig. 3.17. Tracks and dive profiles for three consecutive foraging trips by bird 14. The contour lines show the water depth at intervals of 10 m. The top dive profile represents trip one, the centre profile trip two and the lower profile trip three.

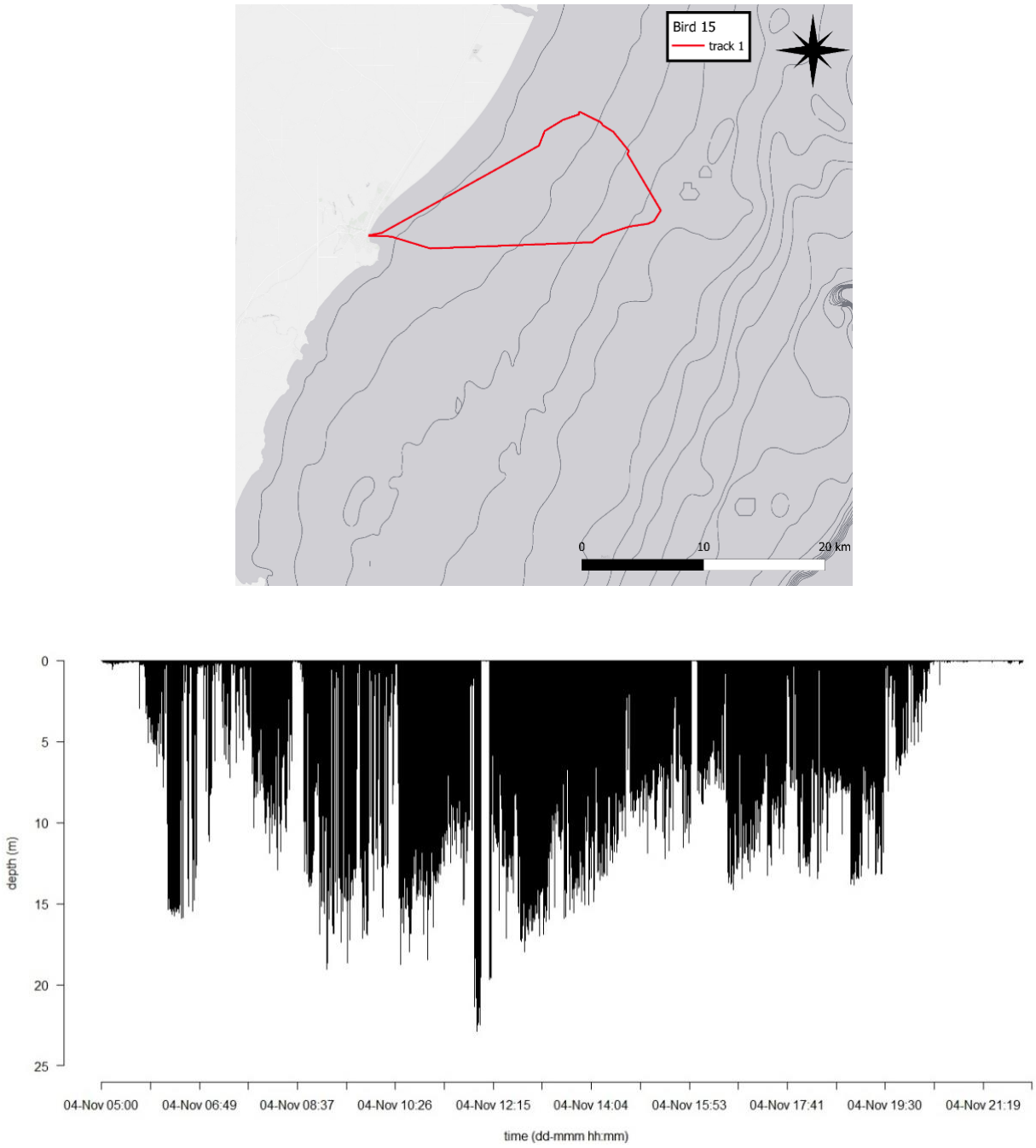

Fig. 3.18. Track and dive profile for a foraging trip by bird 15. The contour lines show the water depth at intervals of 10 m.

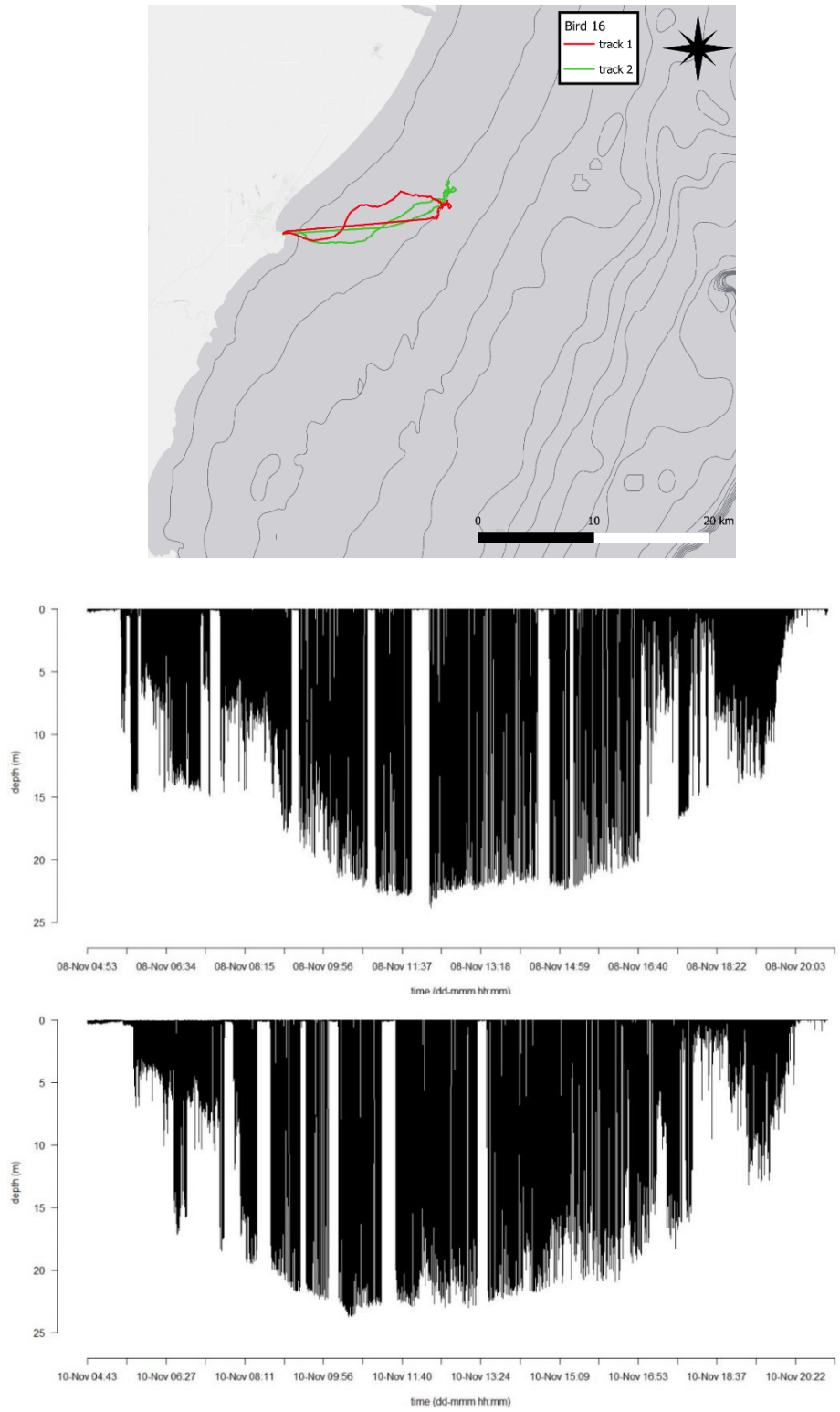

Fig. 3.19. Tracks and dive profiles for two consecutive foraging trips by bird 16. The contour lines show the water depth at intervals of 10 m. The top dive profile represents trip one and the lower profile is for trip two.

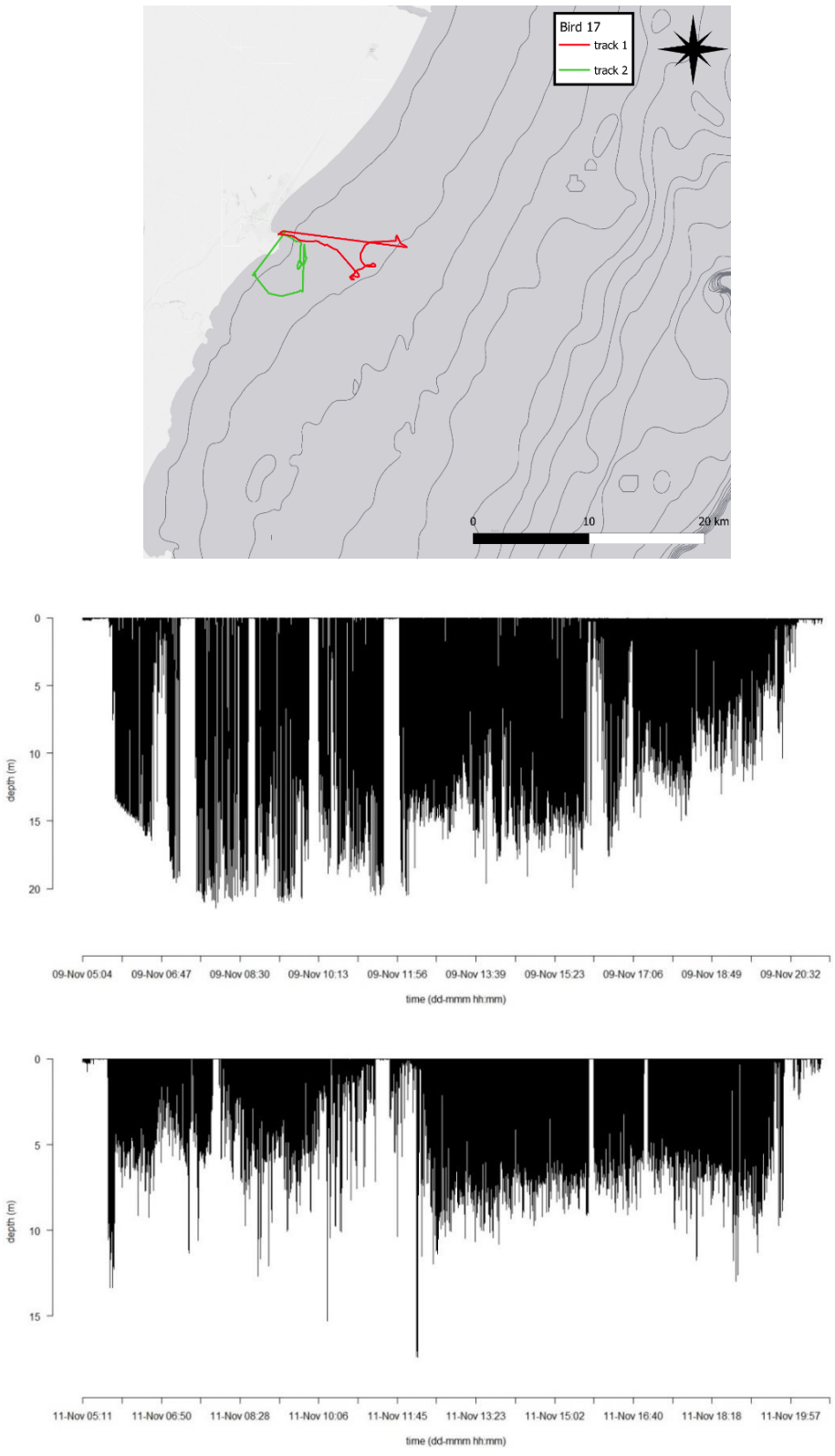

Fig. 3.20. Tracks and dive profiles for two consecutive foraging trips by bird 17. The contour lines show the water depth at intervals of 10 m. The top dive profile represents trip one and the lower profile is for trip two.

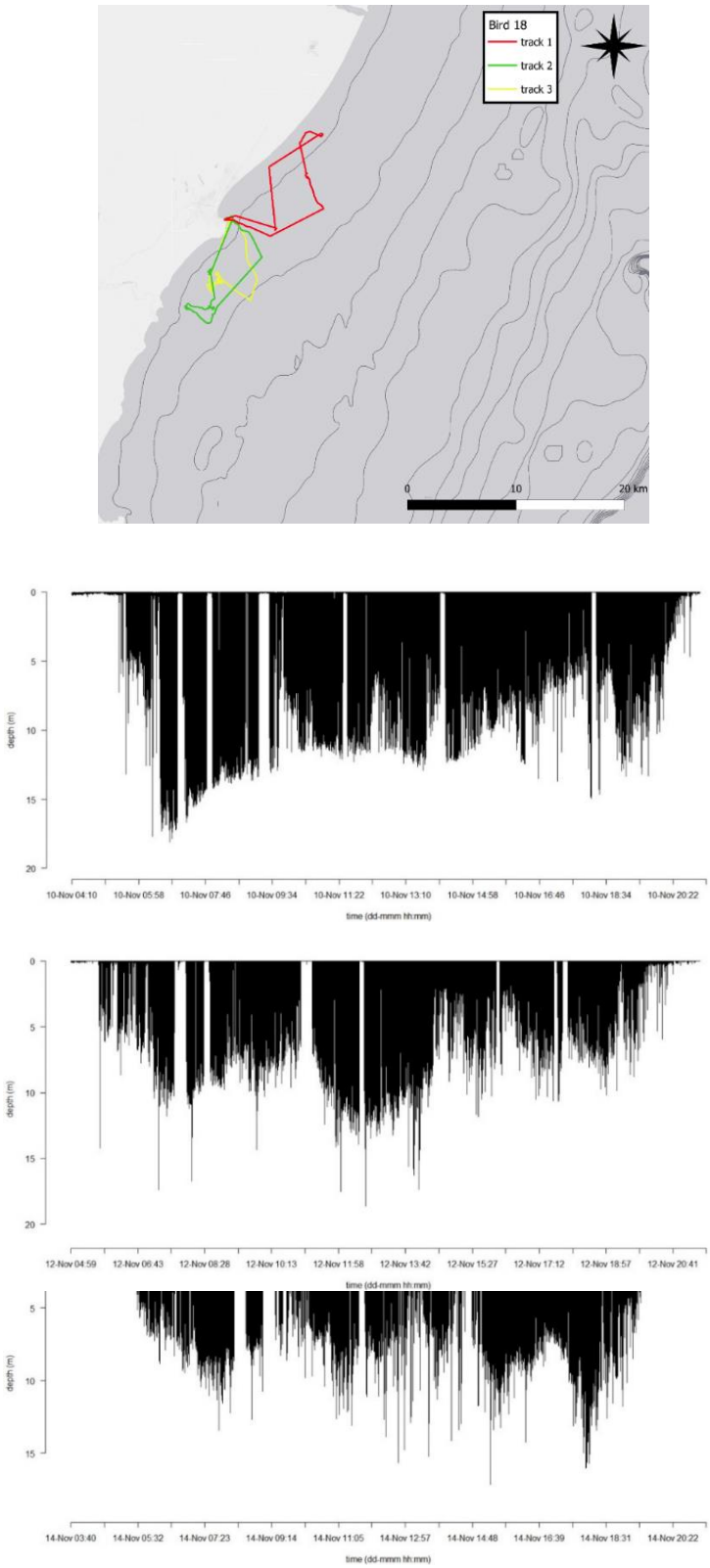

Fig. 3.21. Tracks and dive profiles for three consecutive foraging trips by bird 18. The contour lines show the water depth at intervals of 10 m. The top dive profile represents trip one, the centre profile trip two and the lower profile trip three.

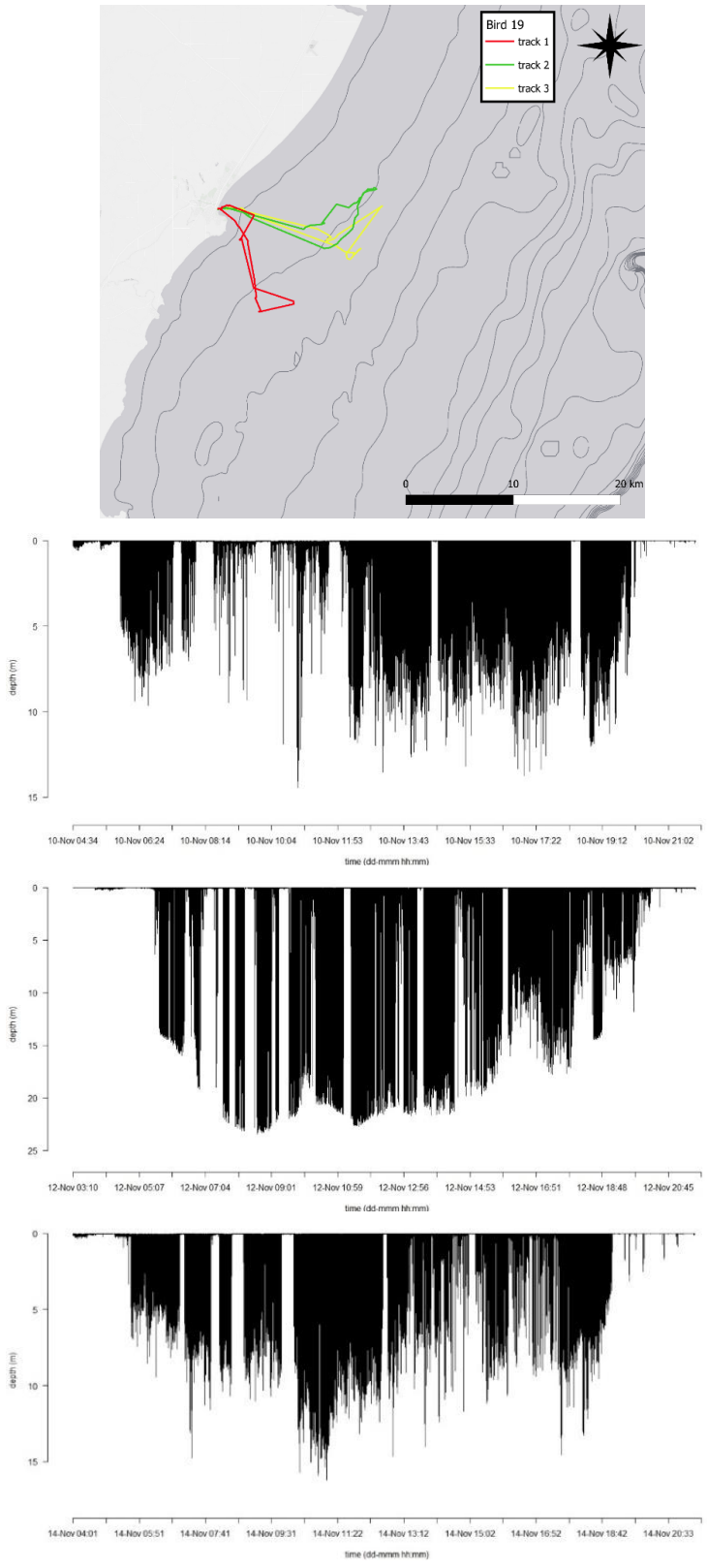

Fig. 3.22. Tracks and dive profiles for three consecutive foraging trips by bird 19. The contour lines show the water depth at intervals of 10 m. The top dive profile represents trip one, the centre profile trip two and the lower profile trip three.

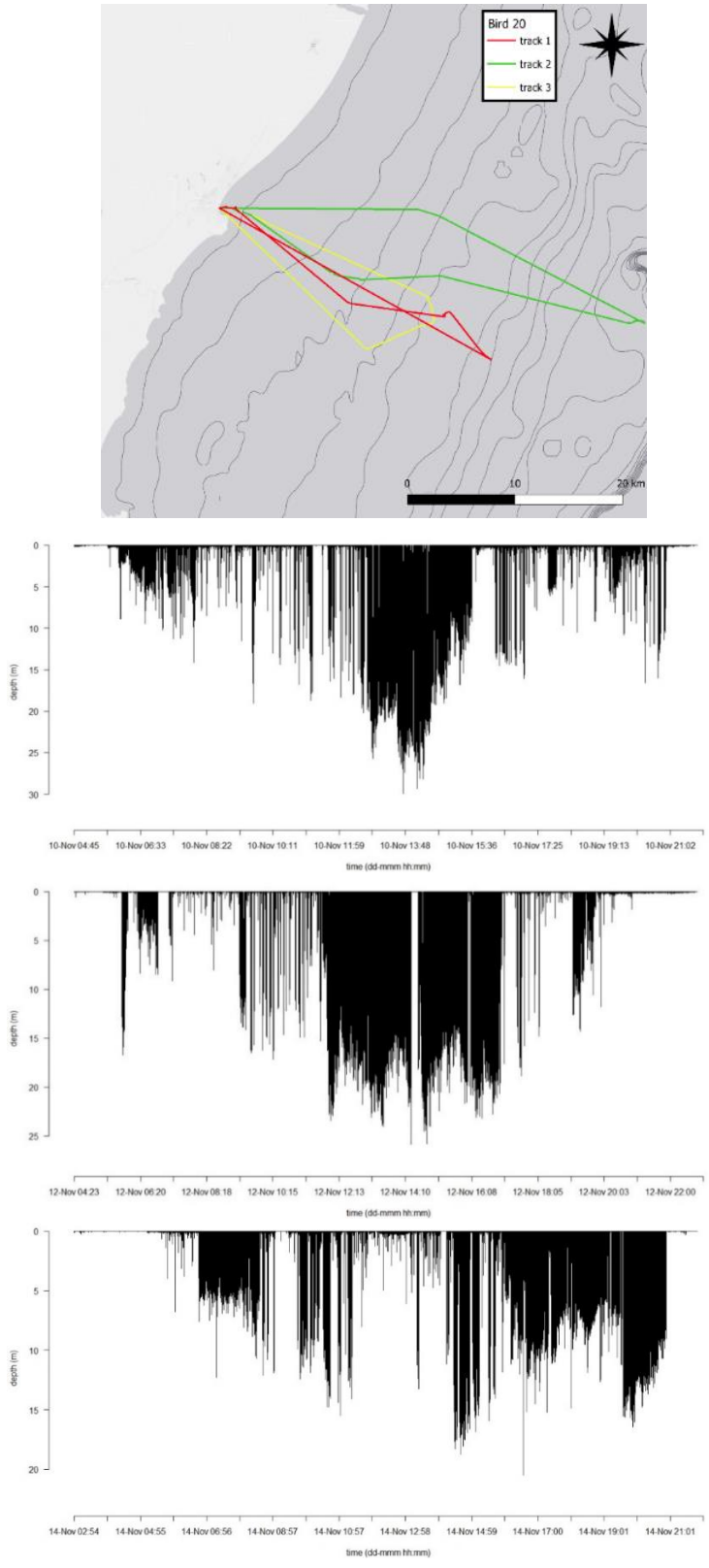

Fig. 3.23. Tracks and dive profiles for three consecutive foraging trips by bird 20. The contour lines show the water depth at intervals of 10 m. The top dive profile represents trip one, the centre profile trip two and the lower profile trip three.

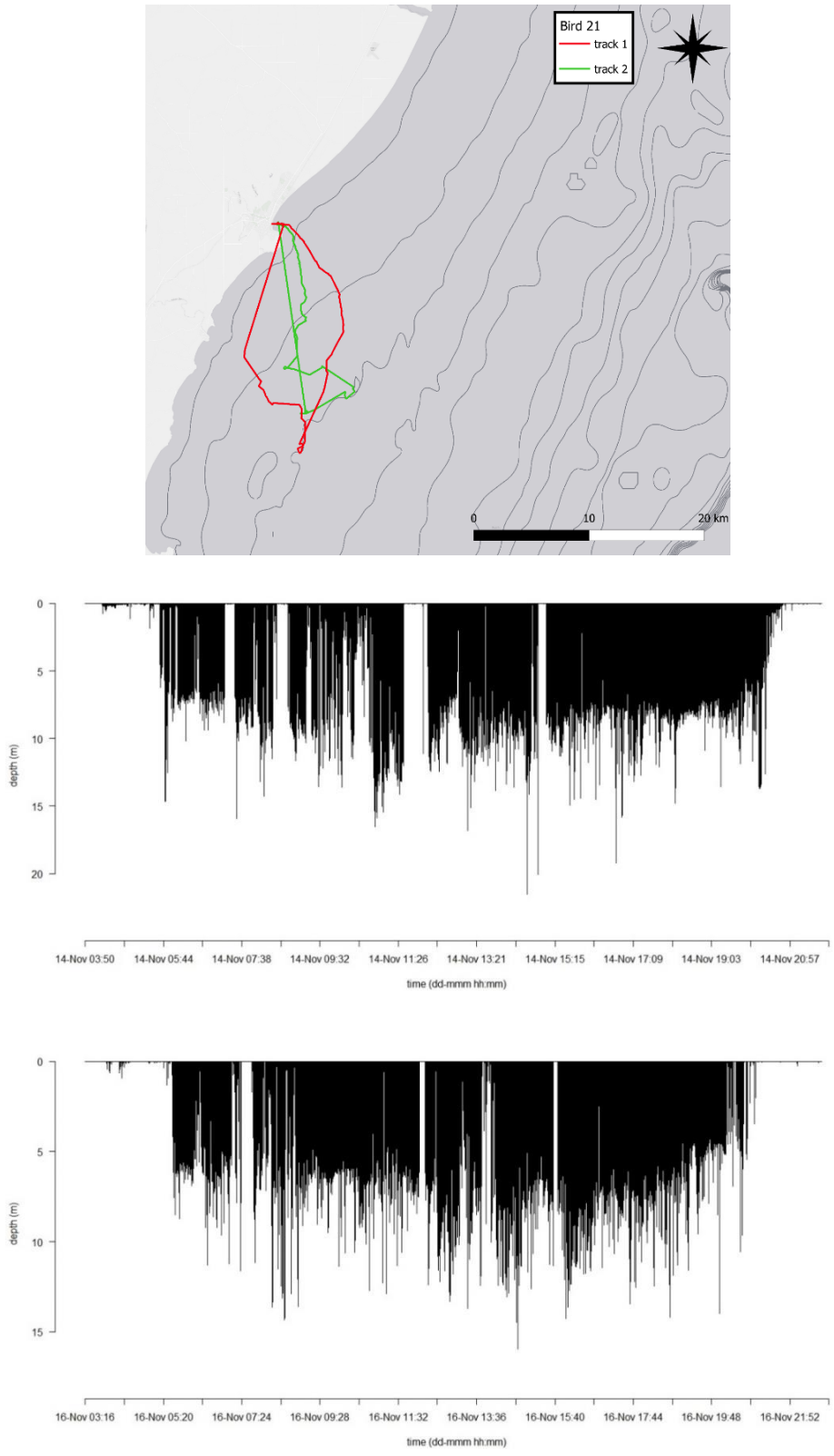

Fig. 3.24. Tracks and dive profiles for two consecutive foraging trips by bird 21. The contour lines show the water depth at intervals of 10 m. The top dive profile represents trip one and the lower profile is for trip two.

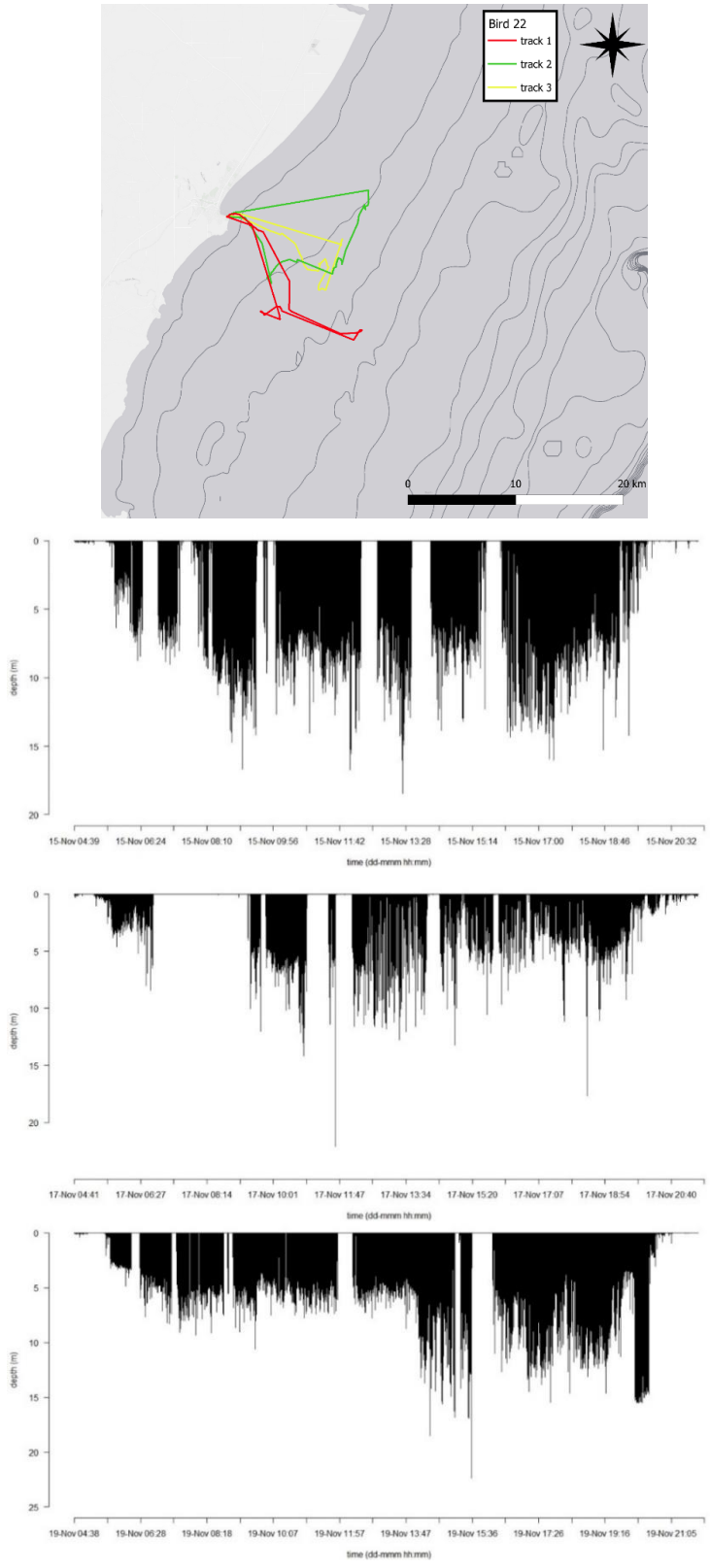

Fig. 3.25. Tracks and dive profiles for three consecutive foraging trips by bird 22. The contour lines show the water depth at intervals of 10 m. The top dive profile represents trip one, the centre profile trip two and the lower profile trip three.

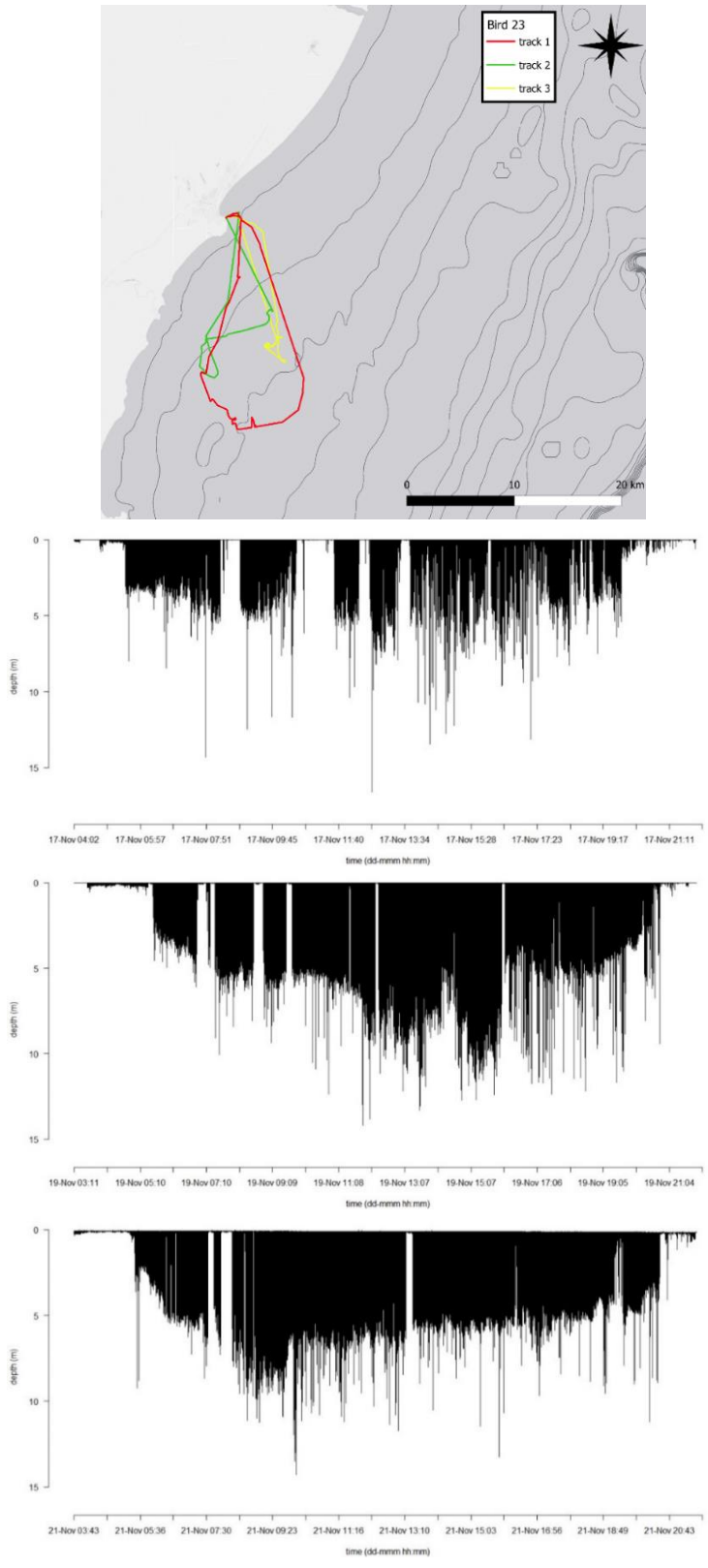

Fig. 3.26. Tracks and dive profiles for three consecutive foraging trips by bird 23. The contour lines show the water depth at intervals of 10 m. The top dive profile represents trip one, the centre profile trip two and the lower profile trip three.

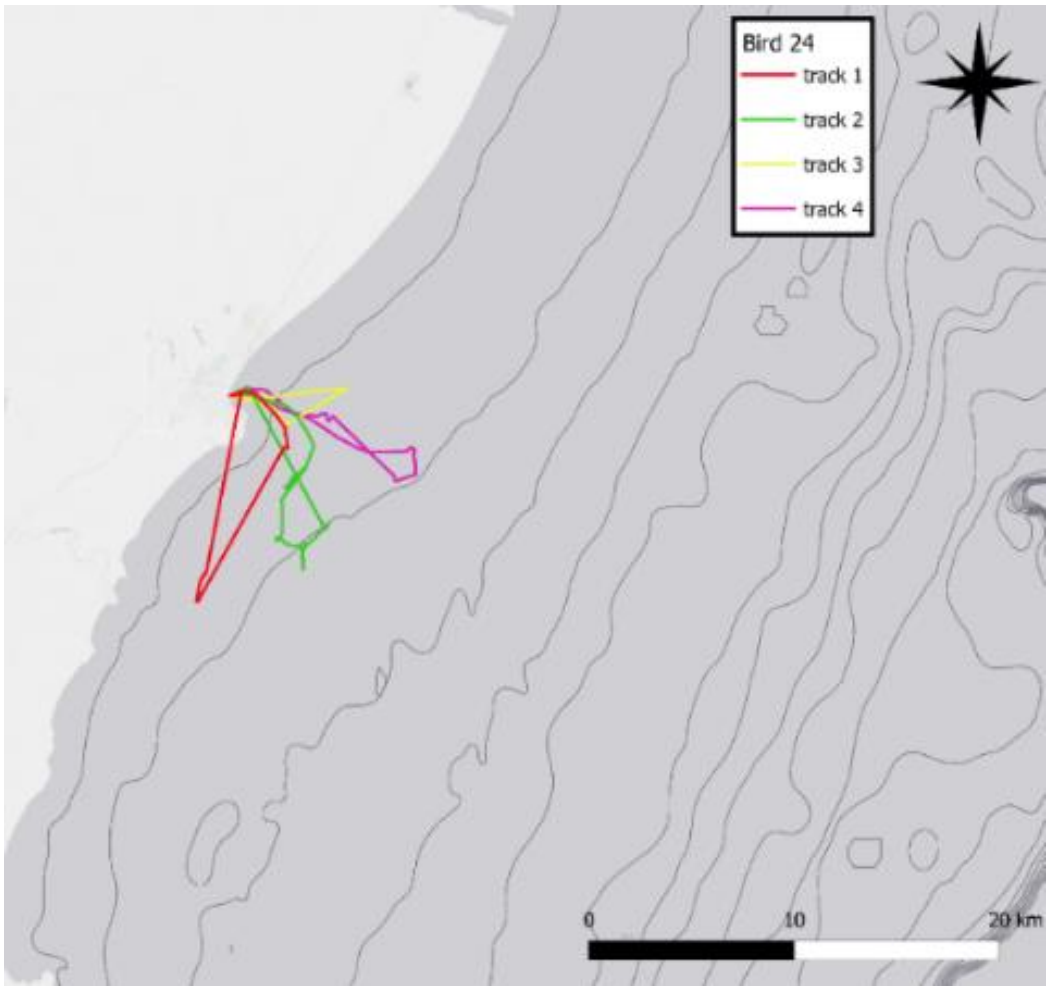

Fig. 3.27. Tracks four consecutive foraging trips by bird 24. The contour lines show the water depth at intervals of 10 m.

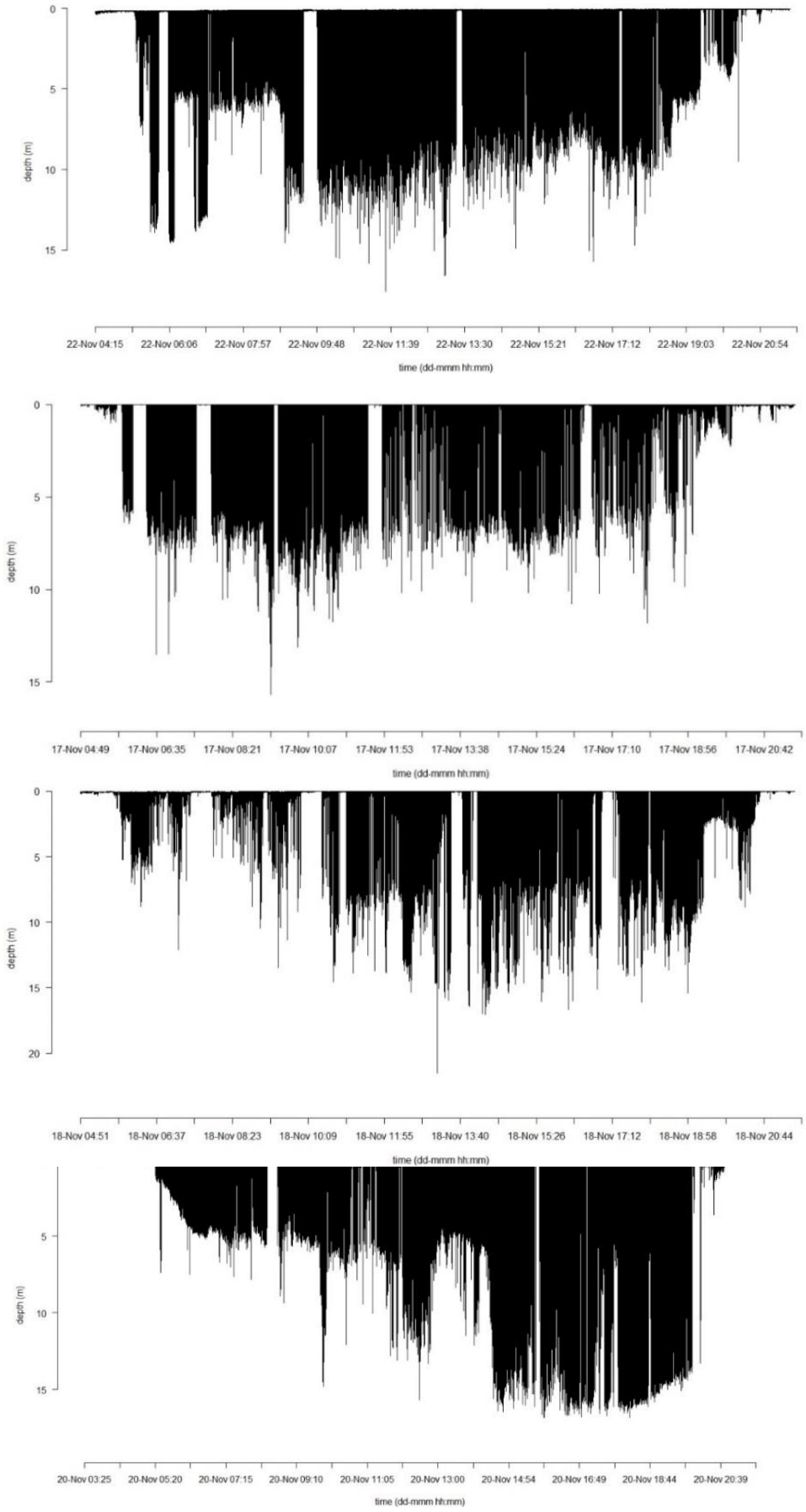

Fig 3.28. Dive profiles for four consecutive foraging trips by bird 24.

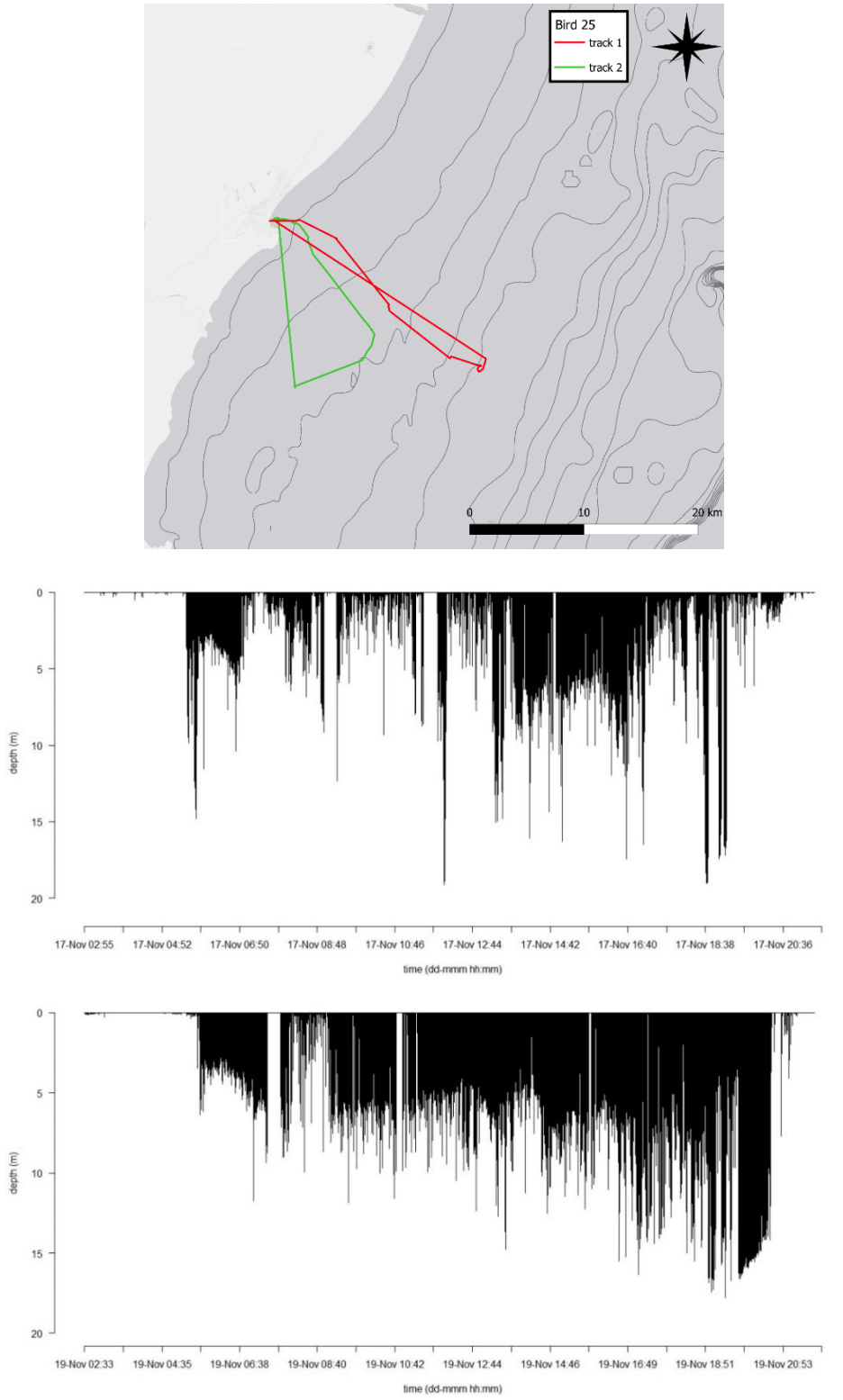

Fig. 3.29. Tracks and dive profiles for two consecutive foraging trips by bird 25. The contour lines show the water depth at intervals of 10 m. The top dive profile represents trip one and the lower profile is for trip two.

3.2 Trip distance and duration

Penguins typically remained within 20 km of their colony during a foraging trip (Fig. 3.1). No OBPC birds travelled greater than 20 km from the colony. Creek birds travelling large maximum distances from the colony (>25 km), tended to travel perpendicular to the coastline, so these birds swam into deeper water than other birds. Total distances travelled on each trip, maximum distances from colonies and durations of trips are shown in Fig. 3.30. Travelling distances ranged widely between trips. The longest total distance travelled was 85.3 km at the Creek and 57.4 km at the OBPC; the shortest distance travelled was 13.4 km and 25.2 km, respectively (Fig. 3.31). Minimum, maximum, and mean values are presented in Table 3.1, with statistical results for comparisons between colonies in Table 3.2. While the greatest maximum distance away from the colony was 41.2 km at the Creek and 19.8 km at the OBPC, mean maximum distances and mean total distances travelled did not differ significantly between colonies.

11 of the tracks were excluded from trip duration calculations as the departure time could not be determined as there was no GPS fix on land immediately before departure. All foraging trips began in the morning, ended in the evening, and had durations less than one day. The mean trip duration was longer for trips from the Creek than for trips from the OBPC, whereas foraging durations (duration between the first and last dive on each trip) did not differ between colonies (see Fig. 3.30 and Tables 3.1 and 3.2). The longest and shortest trip duration at the OBPC was 18.1 and 15.6 h, with corresponding durations at the Creek of 19.4 and 16.1 h. The greatest foraging durations were 15.4 and 15.3 h at the OBPC and Creek respectively, while the shortest foraging durations were 13.6 and 13.8 h.

The departure time from the colonies ranged between 3:31 am and 5:02 am at the OBPC (mean = 4:22 am) and between 2:22 am and 5:07 am at the Creek (mean = 4:05am). Return times to the colony were between 8:15 pm and 9:59 pm at the OBPC (mean = 9:03 pm) and 8:51 pm and 10:48 pm at the Creek (mean = 9:34 pm). Departure and return times were converted to times before sunrise and after sunset (see Fig. 3.32). Mean departure times were around 2 h before sunrise and did not differ between colonies. The mean return time for the OBPC was earlier than the mean return time for the Creek (0.5 ± 0.1 and 1.0 ± 0.1 h after sunset; see Tables 3.1 and 3.2). The earliest departure time was 3.00 h before sunrise at the OBPC and 3.52 h at the Creek. The latest departure time was 1.00 h before sunrise at the OBPC and 1.05 h at the Creek. The earliest return time was 0.03 h before sunset at the OBPC and 0.434 h after sunset at the Creek. The latest return time was 1.18 h after sunset at the OBPC and 2.12 h after sunset at the Creek.

There were no significant differences between males and females in mean trip distances, durations, or departure and return times (see Figs. 3.33 and 3.34, and Tables 3.3 and 3.4).

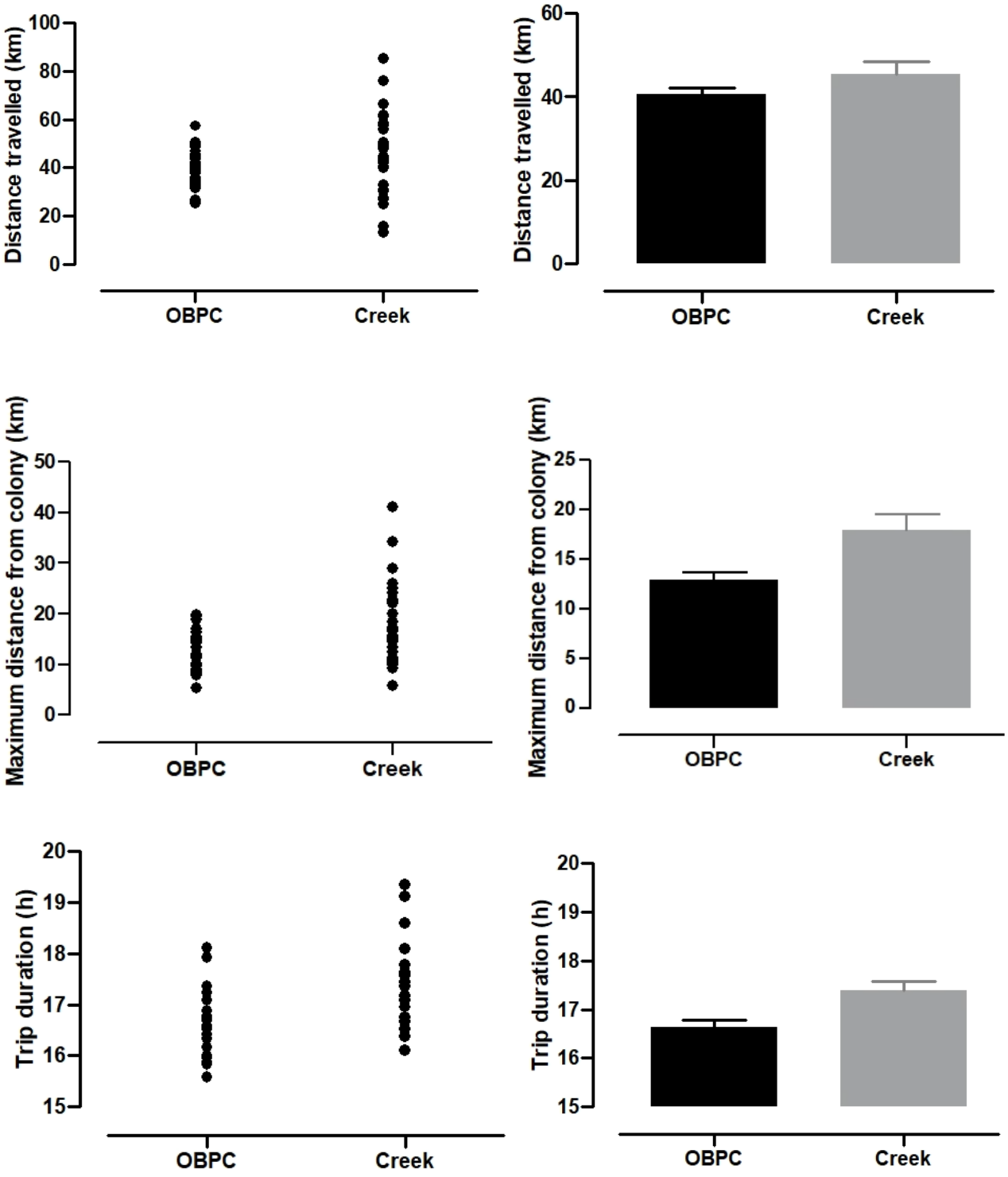

Fig. 3.30. Total distance travelled, maximum distance from the colony and trip duration at the OBPC and Creek colonies. Individual values are shown in the left column and mean ± SE in the right column.

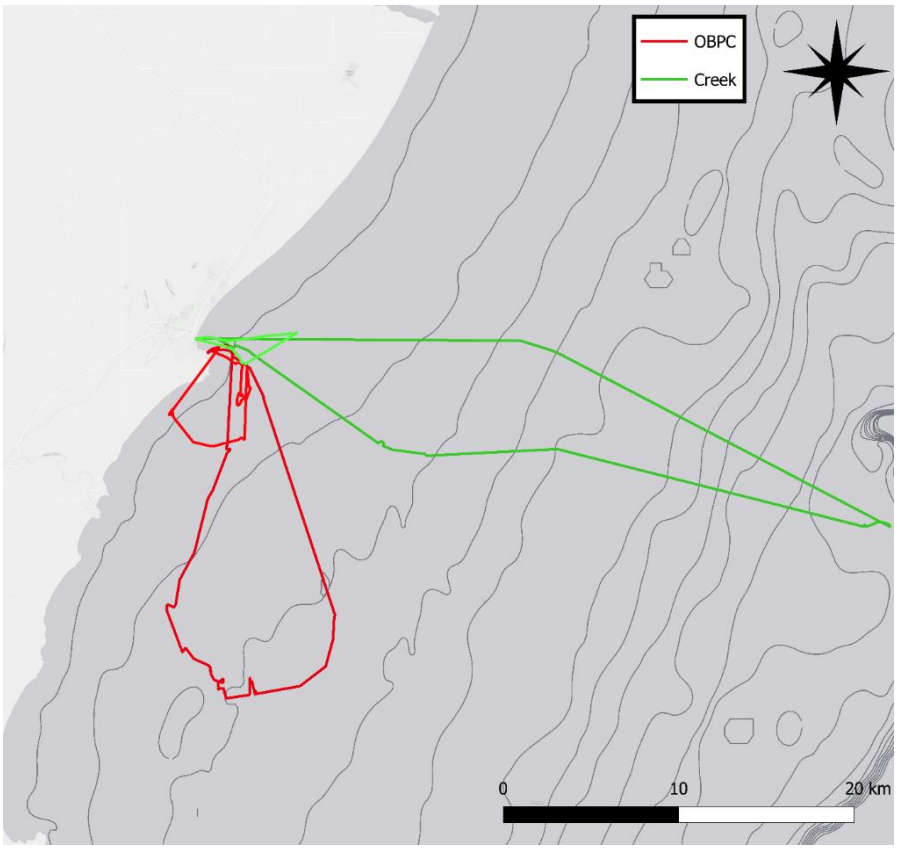

Fig. 3.31. Longest and shortest foraging trips from the OBPC (red) and the Creek (green) colonies. The longest Creek trip was seven times longer and the longest OBPC trip four times longer than the shortest trips from each colony. The contour lines show the water depth at intervals of 10 m.

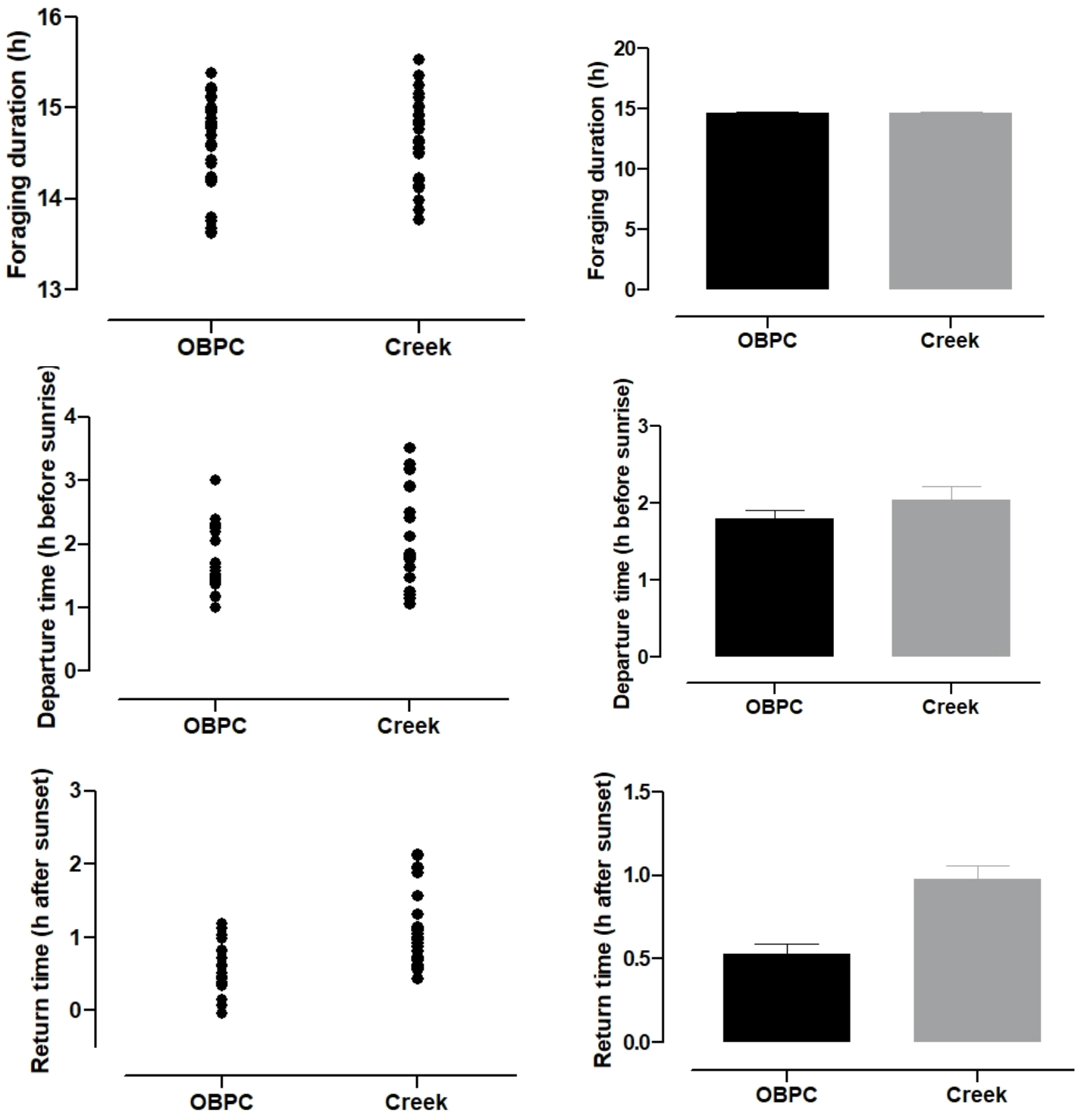

Fig. 3.32. Foraging duration and trip departure and return times for foraging trips from OBPC and Creek colonies. Individual values are shown in the left column and mean ± SE in the right column.

Table 3.1. Minimum, maximum and mean (± S.E.) distances, durations and trip departure and return times for penguin foraging trips from the OBPC and Creek colonies during the guard stage of breeding in October and November 2016

	Colony									
	OBPC					Creek				
	Min.	Max..	Mean	SE	*n*	Min.	Max.	Mean	SE	*n*
Maximum distance (km)	5.4	19.8	12.9	0.8	25	5.8	41.1	18.0	1.5	29
Total distance (km)	25.2	57.4	40.7	1.5	25	13.4	85.3	45.5	3.1	29
Total duration (h)	15.6	18.1	16.6	0.1	23	16.1	19.4	17.4	0.2	20
Foraging duration (h)	13.6	15.4	14.6	0.1	25	13.8	15.3	14.7	0.1	28
Trip departure (h before sunrise)	1.00	3.00	1.80	0.1	23	1.05	3.52	2.04	0.2	20
Trip return (h after sunset)	-0.03	1.18	0.526	0.1	25	0.434	2.12	0.979	0.1	29

Table 3.2. Results of nested *t*-tests for comparisons between colonies for distances, durations and trip departure and return times for penguin foraging trips from the OBPC and Creek colonies during the guard stage of breeding in October and November 2016.

	t	df	*p*
Log maximum distance	1.915	23	0.0680
Total distance	1.158	23	0.2586
Total duration	2.538	21	**0.0191**
Foraging duration	0.216	23	0.8312
Trip departure	1.11	21	0.2790
Log return time	3.619	23	**0.0014**

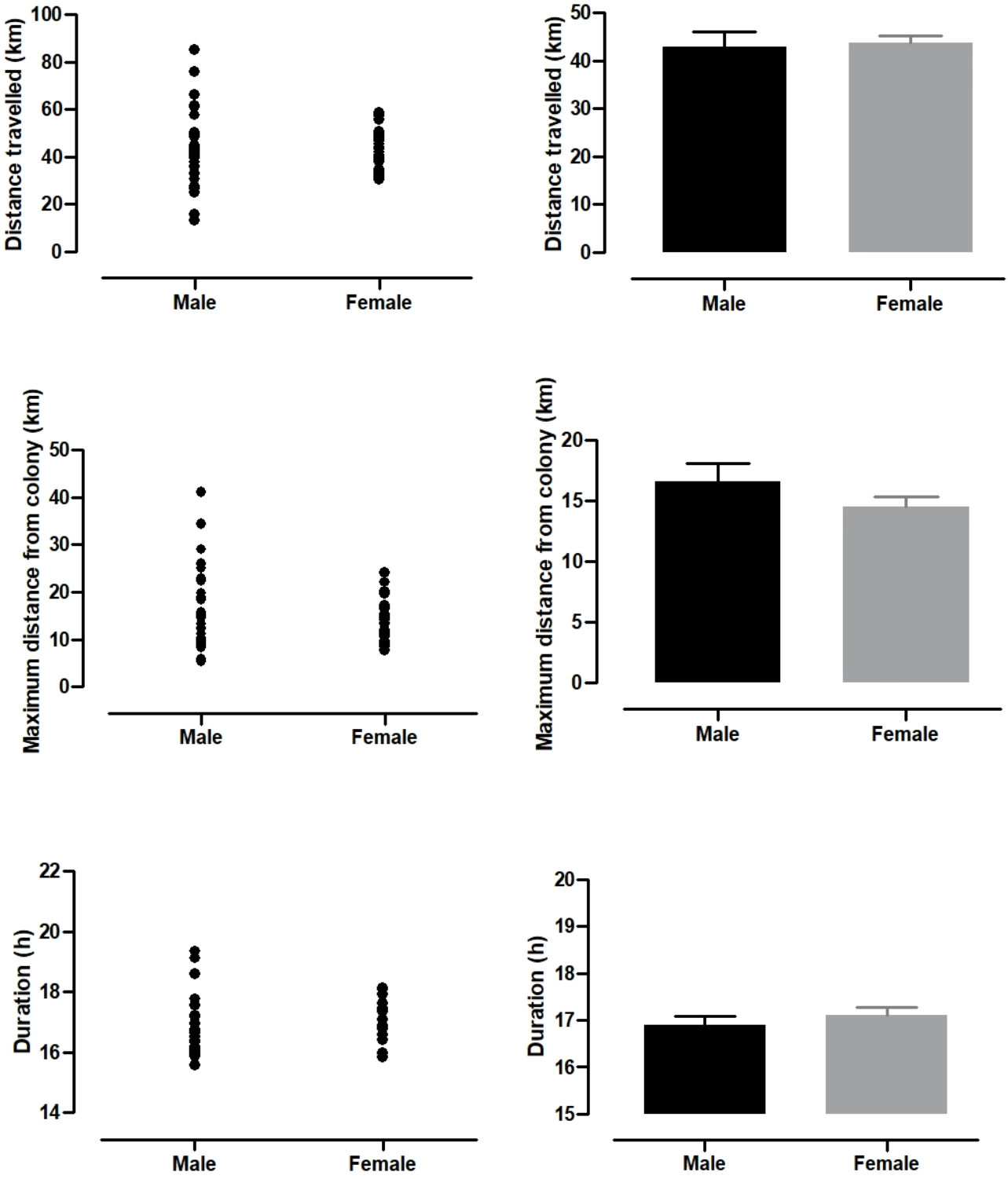

Fig. 3.33. Total distance travelled, maximum distance from the colony and trip duration for foraging trips by male and female penguins from the OBPC and Creek colonies. Individual values are shown in the left column and mean ± SE in the right column.

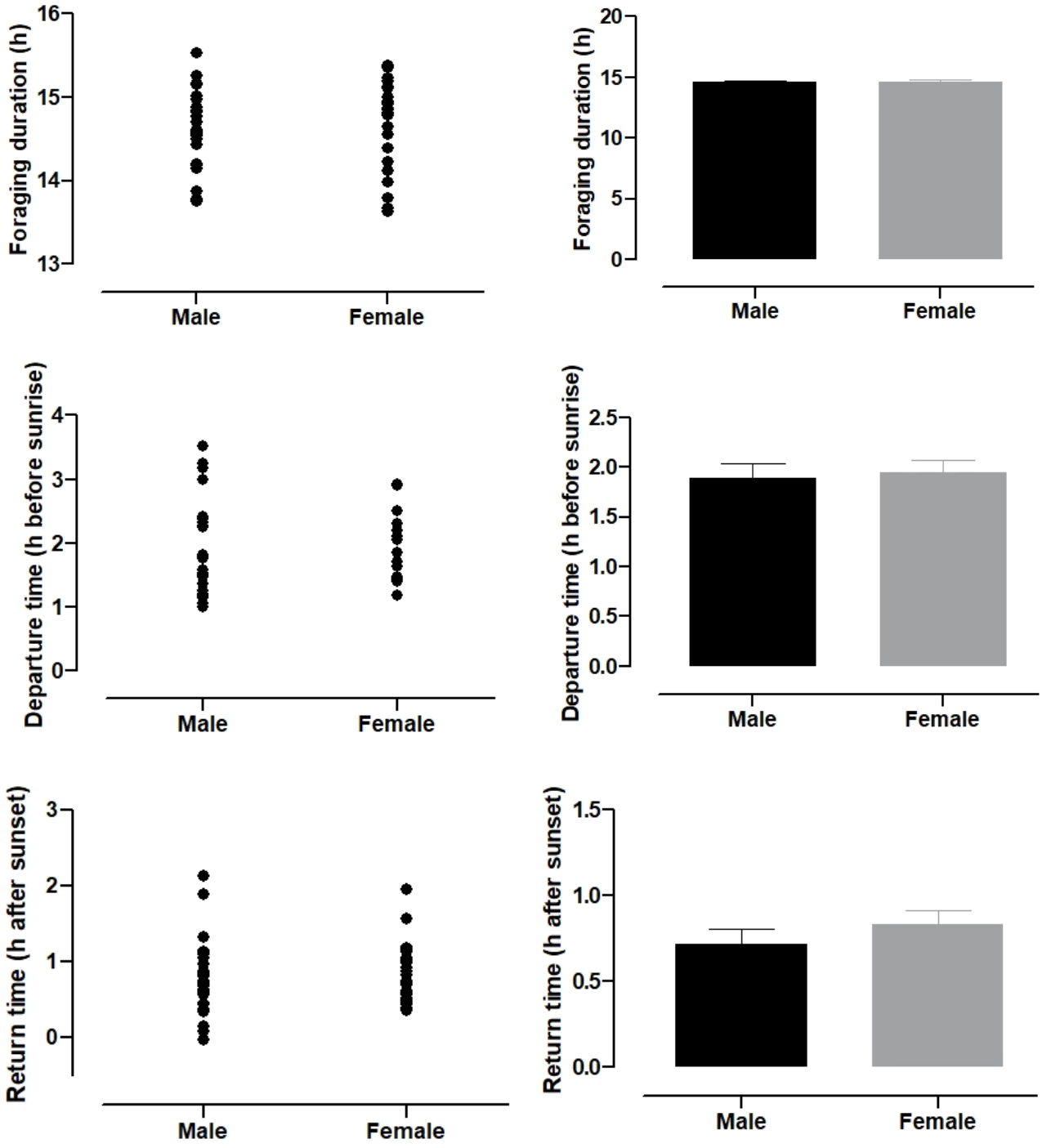

Fig. 3.34. Foraging duration and trip departure and return times for foraging trips by male and female penguins for penguin from the OBPC and Creek colonies. Individual values are shown in the left column and mean ± SE in the right column.

Table 3.3. Minimum, maximum and mean (± S.E.) distances, durations and trip departure and return times for foraging trips by male and female penguins for penguin from the OBPC and Creek colonies during the guard stage of breeding in October and November 2016.

	Sex									
	Male					Female				
	Min.	Max.	Mean	SE	*n*	Min.	Max.	Mean	SE	*n*
Maximum distance (km)	5.4	41.1	16.5	1.6	30	7.8	24.8	14.5	0.9	24
Total distance (km)	13.4	85.3	43.0	3.0	30	30.5	58.6	43.6	1.6	24
Total duration (h)	15.6	19.4	16.9	0.2	25	15.8	18.1	17.1	0.2	18
Foraging duration (h)	13.8	15.5	14.6	0.08	29	13.6	15.4	14.6	0.1	24
Trip departure (h before sunrise)	1.00	3.52	1.88	0.1	25	1.18	2.92	1.95	0.1	18
Trip return (h after sunset)	-0.03	2.12	0.715	0.09	30	0.351	1.95	0.836	0.08	24

Table 3.4. Results of nested *t*-tests for comparisons between sexes for distances, durations and trip departure and return times for foraging trips by male and female penguins for penguin from the OBPC and Creek colonies during the guard stage of breeding in October and November 2016.

	t	df	*p*
Log maximum distance	0.0387	23	0.9695
Total distance	0.3574	23	0.7240
Total duration	0.6932	21	0.4958
Foraging duration	0.2602	23	0.7970
Log trip departure	0.5183	21	0.6097
Log trip return	1.3430	23	0.1924

3.3 Foraging range

Estimates for home and core ranges were calculated for each trip, and for all trips together for each colony. The home range was calculated as the 95% kernel utilisation distribution (KUD), while the core range was calculated as the 50% KUD (see the methods section 2.2.2 for details of range calculations). Home and core ranges, and the tracks of trips used to calculate the ranges, are shown for all trips from each colony in Figs. 3.35 and 3.36. Individual and mean values for ranges are shown in Fig. 3.37.

Mean home and core ranges for trips recorded from the Creek colony during the guard stage of breeding in October and November 2016 were approximately twice as large as ranges for trips recorded from the OBPC colony, with significant differences between colonies in these ranges (Tables 3.5 and 3.6). Calculated range sizes varied widely between trips, with the largest calculated home range more than 20 times larger than the smallest (see Table 3.5). The larger calculated home ranges were for trips that were wide-ranging. Calculated core ranges also varied markedly.

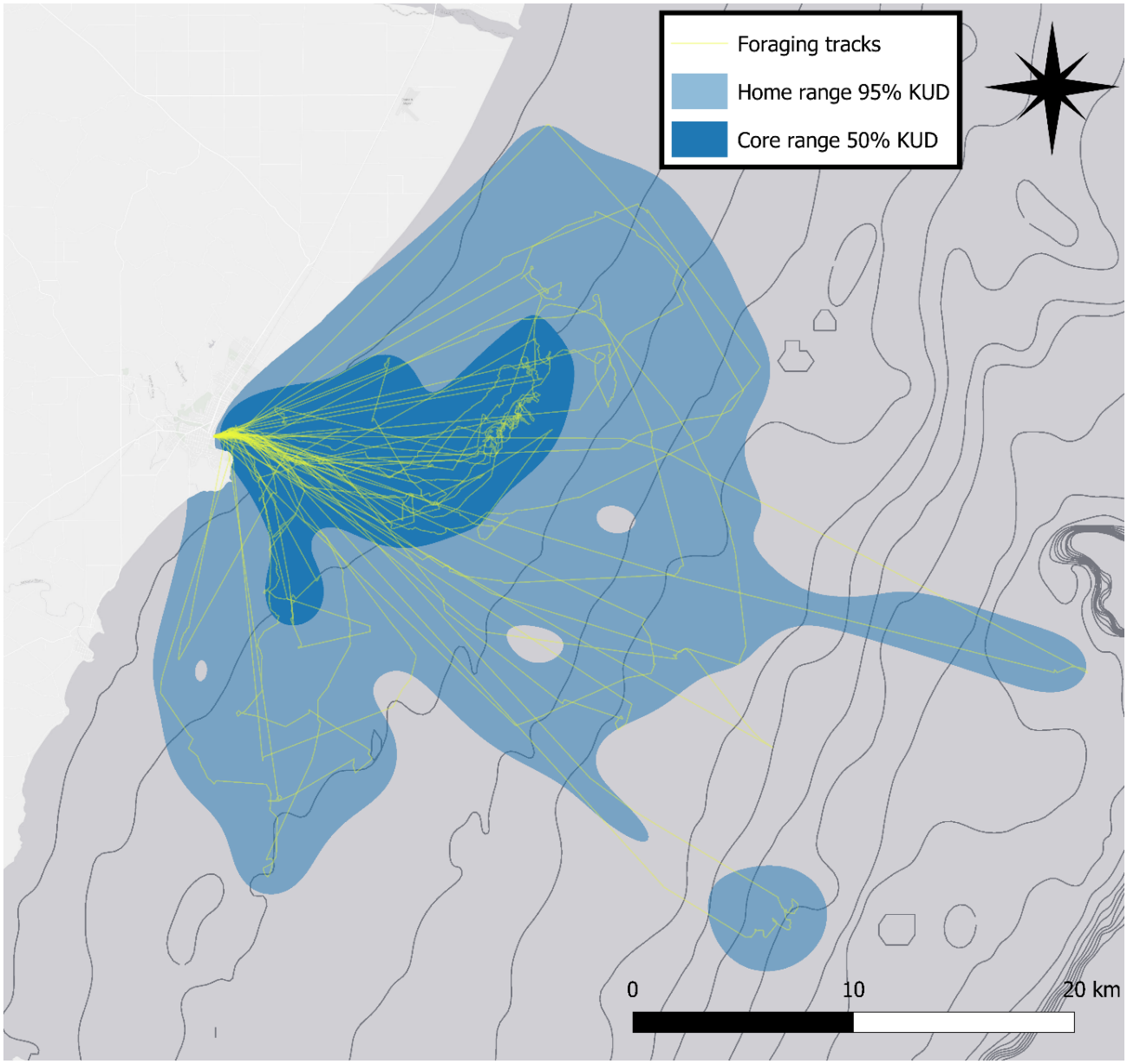

Fig. 3.35. Tracks of foraging trips and calculated mean home and core ranges for all foraging trips recorded from the Creek colony during the guard stage of breeding in October and November 2016. The contour lines show the water depth at intervals of 10 m.

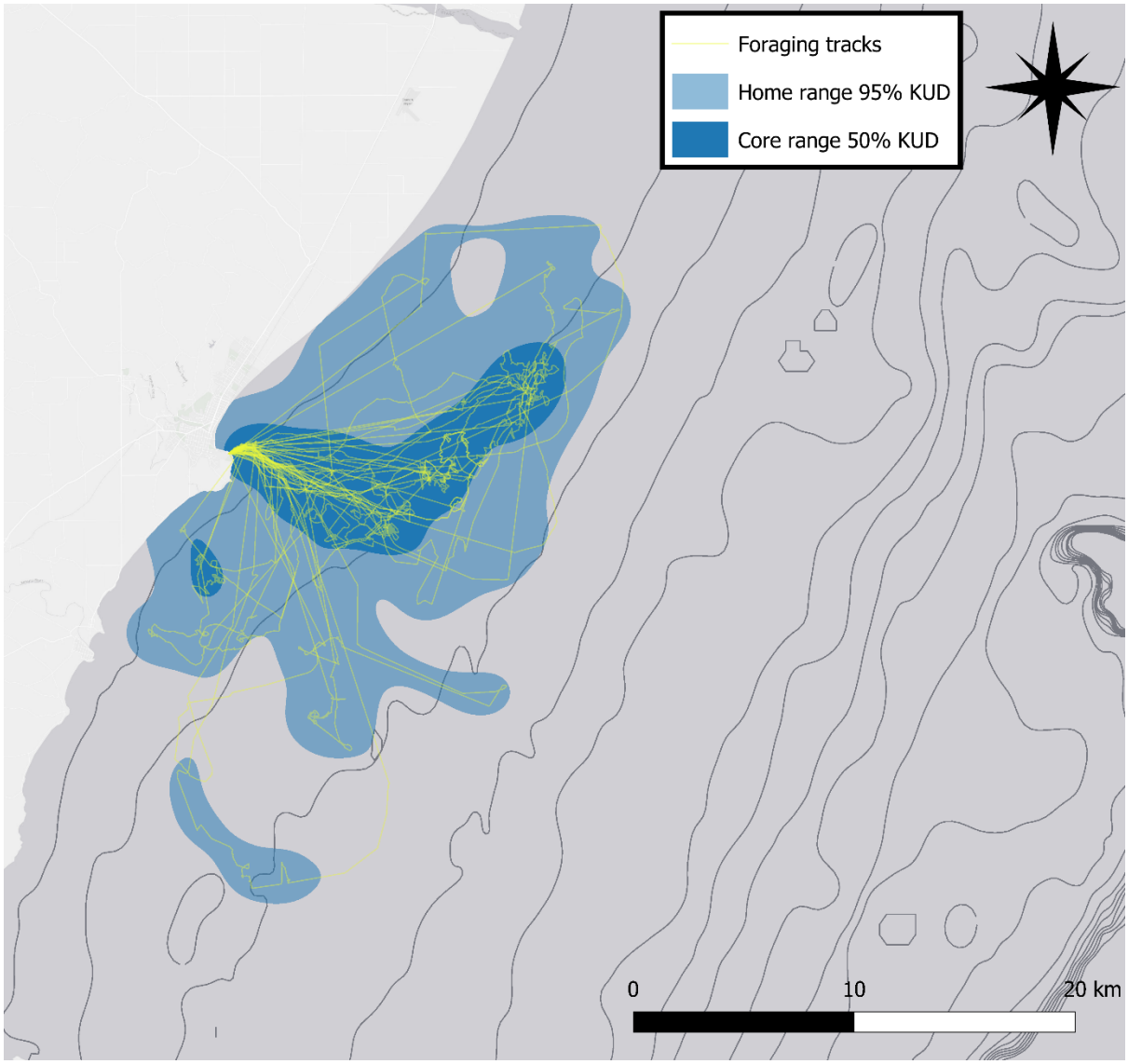

Fig. 3.36. Tracks of foraging trips and calculated home and core ranges for all foraging trips recorded from the OBPC colony during the guard stage of breeding in October and November 2016. The contour lines show the water depth at intervals of 10 m.

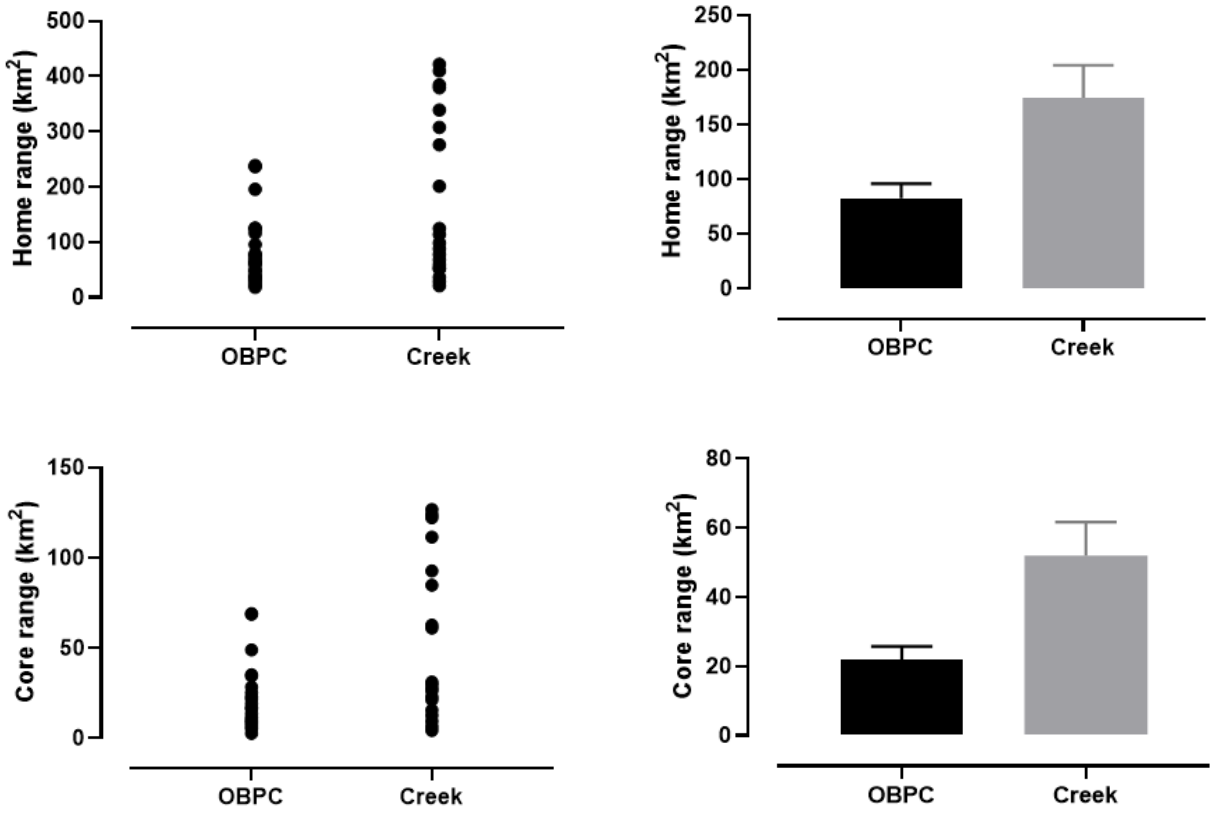

Fig. 3.37. Calculated home and core ranges for all foraging trips recorded from the OBPC and Creek colonies during the guard stage of breeding in October and November 2016. Individual values are shown in the left column and mean ± SE in the right column.

Table 3.5. Minimum, maximum and mean (± S.E.) calculated home and core ranges for penguin foraging trips from the OBPC and Creek colonies during the guard stage of breeding in October and November 2016.

	Colony									
	OBPC					Creek				
	Min.	Max.	Mean	SE	*n*	Min.	Max.	Mean	SE	*n*
Home range (km^2)	18.2	384.6	82.5	13.4	23	22.3	421.9	174.5	29.9	22
Core range (km^2)	2.8	127.6	21.8	3.9	23	4.4	122.2	52.0	9.7	22

Table 3.6. Results of nested *t*-tests for comparisons between colonies for calculated home and core ranges for foraging trips from the OBPC and Creek colonies during the guard stage of breeding in October and November 2016.

	T	df	*p*
Home range (95% KUD)	2.232	21	**0.0366**
Core range (50% KUD)	2.310	21	**0.0312**

Calculated home and core ranges for all recorded foraging trips combined for each colony during the guard stage of breeding were larger for the Creek than the OBPC colony (see Figs. 3.38 and 3.39 and Table 3.7). Differences between colonies in calculated core ranges for all trips combined were much less than differences in calculated home ranges. Several penguins from the Creek colony foraged in deep water far from the coast, with these trips accounting for the larger calculated home range for all trips combined for the Creek in comparison with the OBPC colony.

Despite the larger range of the Creek colony, foraging locations were similar between the 2 colonies. The foraging ranges did overlap, that is, there was no significant spatial segregation between each colony (Table 3.7). Each colony's home range had a similar southern extent, while the Creek colony had a northern boundary further from Oamaru than the OBPC. In addition, the eastern extent of the Creek home range was much greater than that of the OBPC home range. One section of the Creek home range extended 40 km from the colony due to a single long foraging trip. The core range extents were similar, with no significant spatial segregation. For both the home and core ranges almost the entire extent of the OBPC foraging area falls within the larger Creek range. The core range overlap was smaller than that of the home range overlap. This is despite a greater apparent overlap of the core ranges when viewing the mapped polygons, compared with the mapped home ranges. This is due to the UDOI method calculating overlap over the whole utilisation distribution. As the core range represents only 50 % probability of occurrence, the overlap value will be lower than the home range, which represents 95 % probability of occurrence. Penguins were very likely to be present in the larger home ranges, therefore overlap in these zones is more likely.

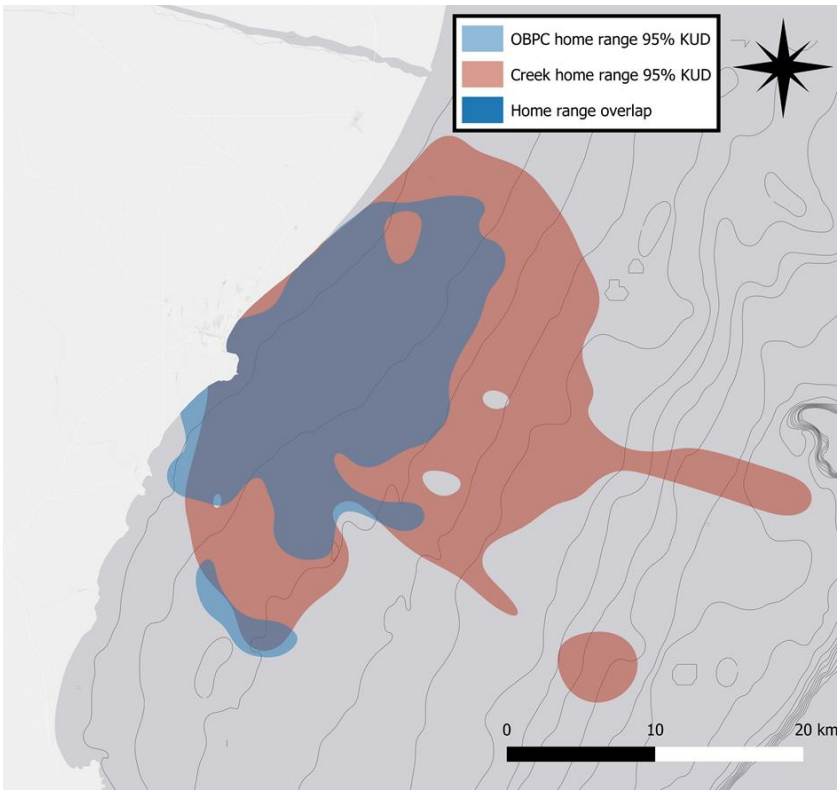

Fig. 3.38. Calculated home ranges, and overlap between the ranges, for all recorded foraging trips combined for the OBPC and Creek colonies during the guard stage of breeding in October and November 2016. Home range of OBPC and Creek colonies, illustrating both the difference in size and the degree of overlap. The contour lines show the water depth at intervals of 10 m.

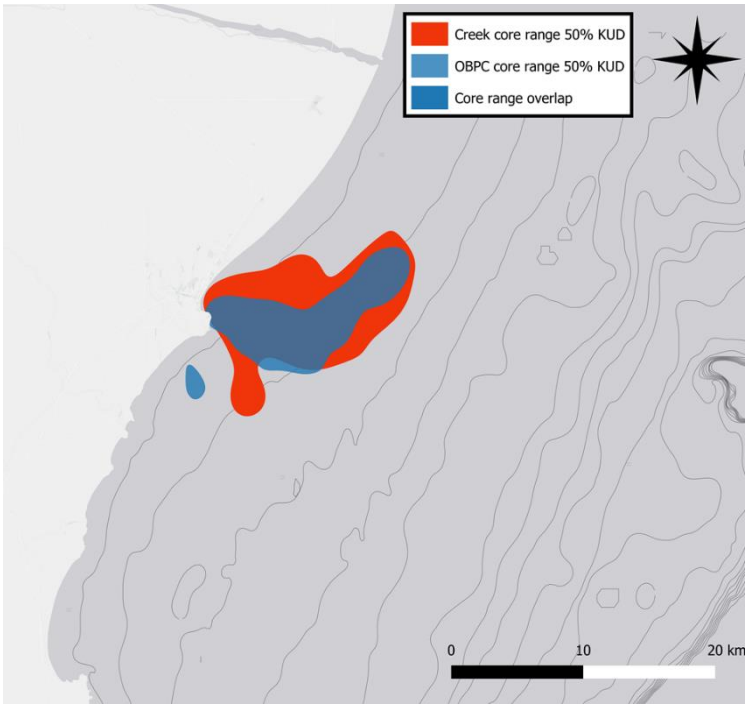

Fig. 3.39. Calculated core ranges, and overlap between the ranges, for all recorded foraging trips combined for the OBPC and Creek colonies during the guard stage of breeding in October and November 2016. Home range of OBPC and Creek colonies, illustrating both the difference in size and the degree of overlap. The contour lines show the water depth at intervals of 10 m.

Table 3.7. Calculated home and core range sizes and calculated utilisation distribution overlap index between colonies for all foraging trips made by penguins from the OBPC and Creek colonies during the guard stage of breeding in October and November 2016. The proportion of randomised overlap values less than the observed overlap value was used to test for significance of spatial segregation. A proportion < 0.05 was considered to indicate an observed overlap value less than expected by chance.

	OBPC	Creek	Observed overlap (UDOI)	Mean random overlap	Proportion of randomised UDOI values < observed UDOI value
Home range (km^2)	325.0	681.5	0.99	1.12	0.133
Core range (km^2)	71.8	115.4	0.15	0.15	0.464

3.4 Diving behaviour

Dive data were recorded for 53 foraging trips made by 25 penguins. 25 447 dives were identified for penguins from the OBPC colony, and 26 031 dives were recorded for penguins from the Creek colony. Penguin dives consist of a descent from the sea surface, followed in many dives by a period when the bird is swimming with small increases and decreases in its depth below the surface, then an ascent back to the surface of the sea (see Fig. 3.40). The durations of the three phases of a dive, called the descent, bottom and ascent periods, were calculated for each dive. The sum of the descent, bottom and ascent durations is the total duration of each dive. The durations of the periods of time on the surface between dives (called the post-dive phase) were also calculated.

The duration of the bottom phase and the patterns of changes in depth during the bottom phase vary between dives. Dives can be categorised as V shape, when there is no bottom phase, U shape when a relatively constant depth was maintained while a penguin was swimming in the bottom phase, and W shape when there were large undulations in depth during the bottom phase (Halsey *et al.* (2007). V, U and W shaped dives were recorded for little penguins at Oamaru (Fig.3.41), as seen in other studies of little penguin diving behaviour.

Diving behaviour was similar for penguins from the two colonies (see Figs. 3.42, 3.43 and 3.44). Minimum, maximum, and mean values for diving variables are presented in Table 3.8. Minimum and maximums are the mean values from a single trip. There were no significant differences between colonies for any of the diving variables (see Table 3.9).

The longest single dive duration at the OBPC was 94 seconds, and 85 seconds at the Creek. No dive exceeded 30 m in depth for penguins from either colony, with maximum depths of 24.8 m and 29.9 m from the OBPC and Creek, respectively. The longest time spent in the bottom phase was 63 seconds for an OBPC bird and 53 seconds for a Creek individual. The greatest proportion of a dive spent in the bottom phase was 84 % at the OBPC and 86 % at the Creek. While the maximum post-dive durations reached 52 and 31.5 minutes for the OBPC and Creek respectively, these values represent inter-bout intervals, rather than resting between dives within a single diving bout.

Throughout a trip, little penguins dived approximately 1000 times (OBPC: 1017.9, Creek: 929.7), The greatest number of dives performed in a day was 1607 by a Creek penguin (OBPC max= 1525), while the fewest was 496, also by a Creek individual (OBPC min = 573). The average daily diving time was 7.1 and 6.5 hours for birds from the OBPC and Creek colony. The total time spent underwater varied considerably between trips. Total daily diving time varied between 3.8 – 9 hours at the OBPC and 4 – 8.5 hours at the Creek. Total diving time was influenced by both the number of dives, and the average dive duration throughout a trip. For example, a single trip with 671 dives at an average duration of 36 seconds (depth = 15m) resulted in a similar total diving duration to a trip with 1 182 dives at a dive duration of 20 seconds (depth = 7 m), 6.8 and 6.7 h, respectively.

Furthermore, the number of dives was negatively correlated with mean diving duration and depth. Birds that dived longer and deeper during a trip tended to dive less often than shallow divers (Fig 3.48). The average diving rate was 69.4 dives/hour and 63.4 dives/hour at the OBPC and Creek, with no significant difference between colonies. Diving rates were lower than those expected from calculations using the mean dive duration and the post-dive

duration. This is because all post-dive durations greater than 100 seconds long were removed from the dataset. These intervals likely represent inter-bout periods, rather than resting time between dives within a single bout. Therefore, a diving rate calculated using these values will overestimate the number of dives per hour, as little penguins do not sustain this rate for the entirety of a trip but have periods of reduced diving intensity between bouts.

Little penguins covered a vertical distance of 20.4 ± 0.9 km and 18.3 ± 0.8 km for the OBPC and Creek, respectively. The total vertical distance swum also varied greatly at both colonies; 8 – 28.1 km at the OBPC and 8.3 – 24.6 km at the Creek.

Diving behaviour was similar for male and female penguins (see Figs. 3.45, 3.46 and 3.47). Mean values for diving variables are presented in Table 3.10. The bottom time was greater for males than females, with no other significant differences between sexes (see Table 3.11).

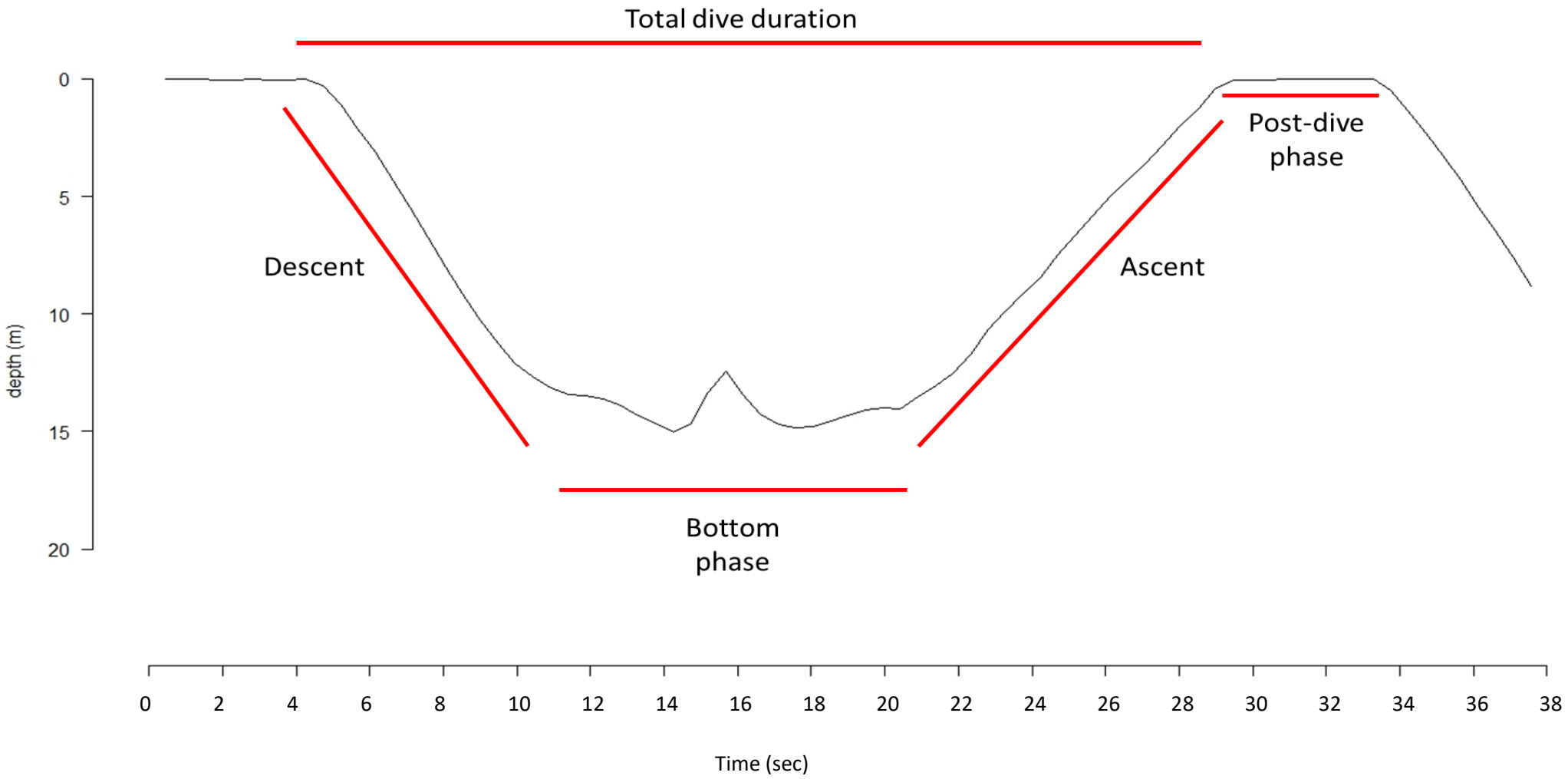

Fig. 3.40. A single dive profile illustrating the phases of a dive. A dive begins with descent, followed by a bottom phase, then ascent to the surface. These stages contribute to the total dive duration. Each dive is seperated by a post-dive phase on the surface.

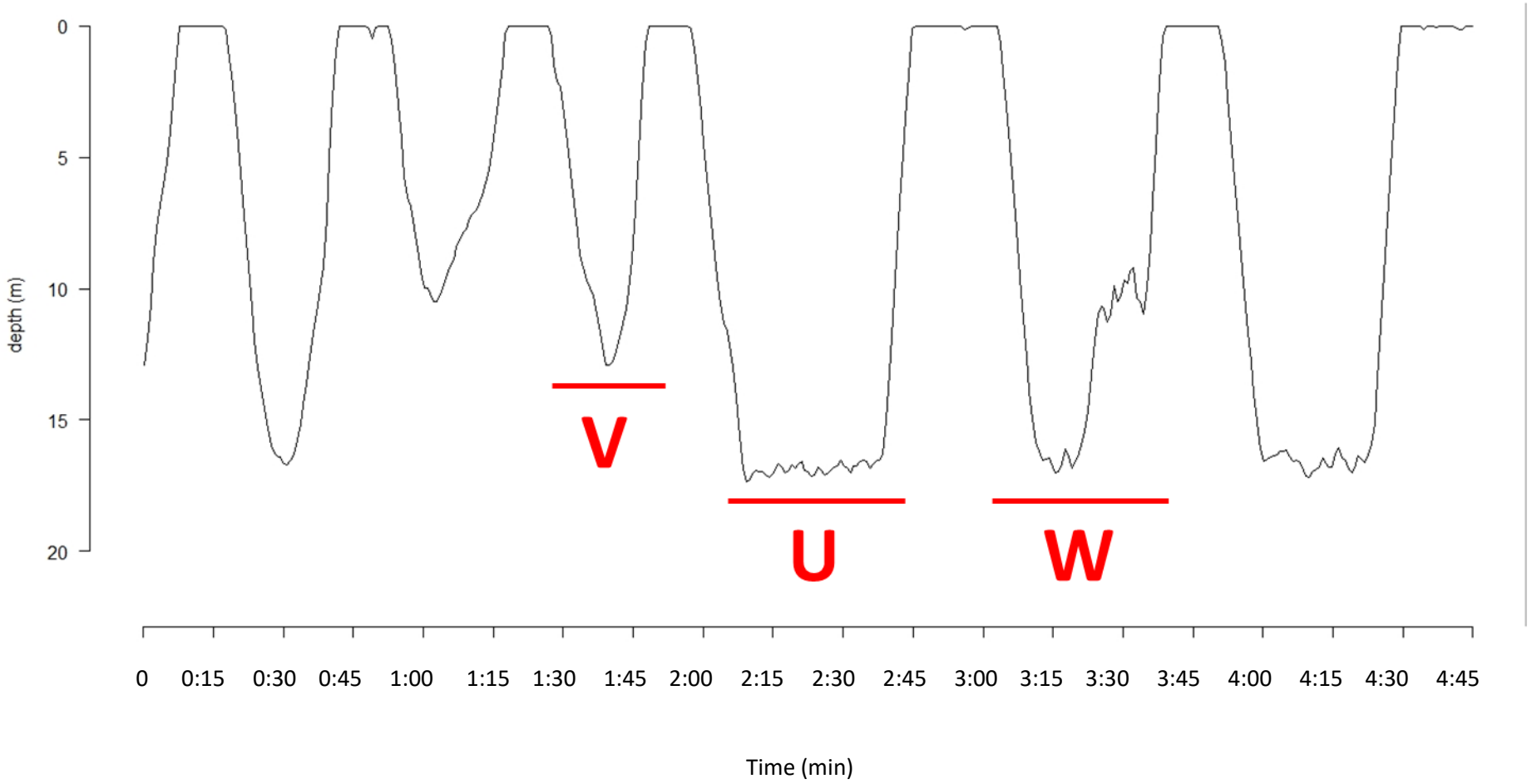

Fig. 3.41. Individual dive profiles can can vary greatly. Dives may be 'V' shape within no bottom time, 'U' dives with a longer bottom time, or 'W' dives with large undulations during the bottom phase.

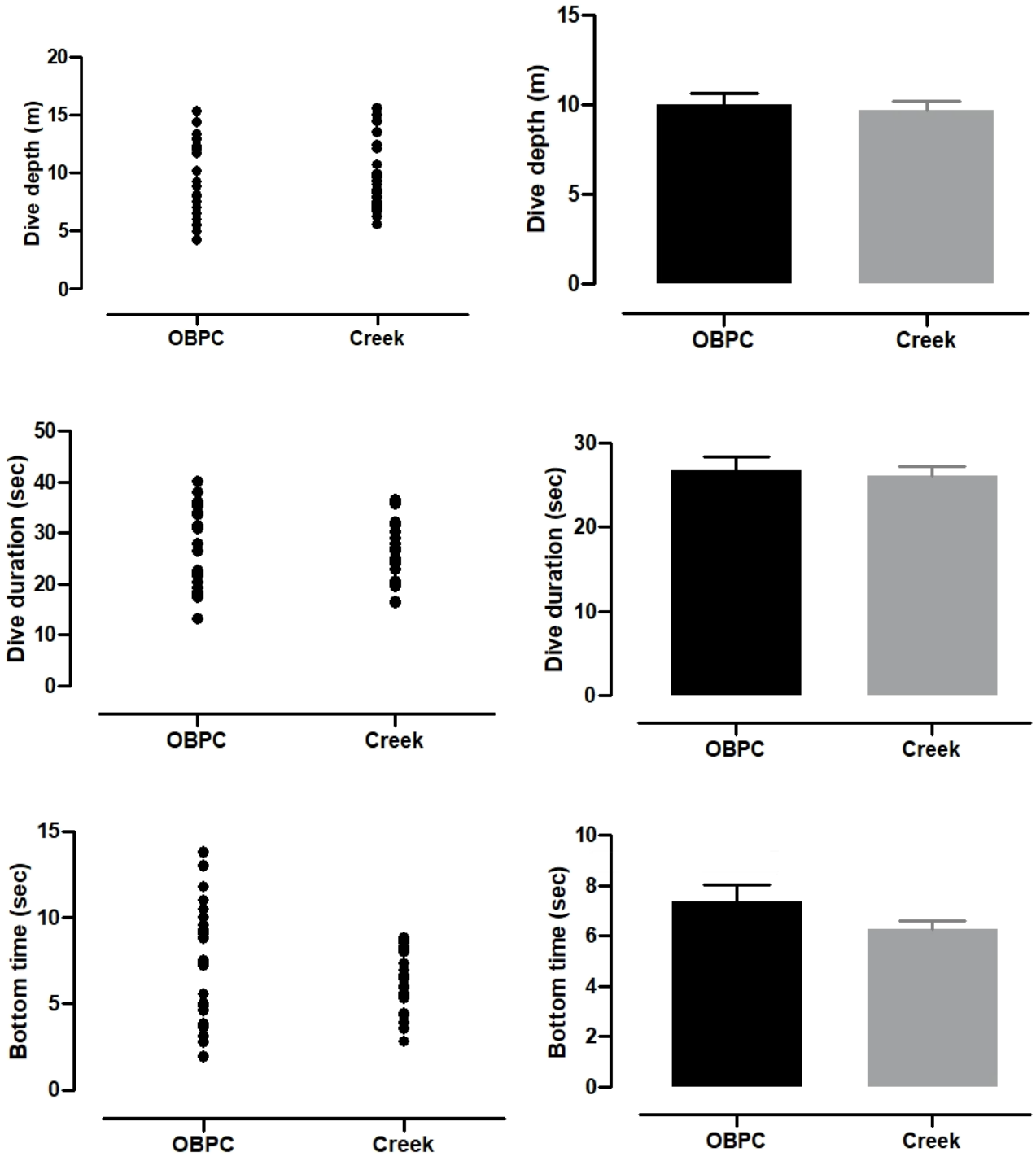

Fig. 3.42. Dive depth, dive duration, and bottom time for all foraging trips recorded from the OBPC and Creek colonies during the guard stage of breeding in October and November 2016. Individual values are shown in the left column and mean ± SE in the right column.

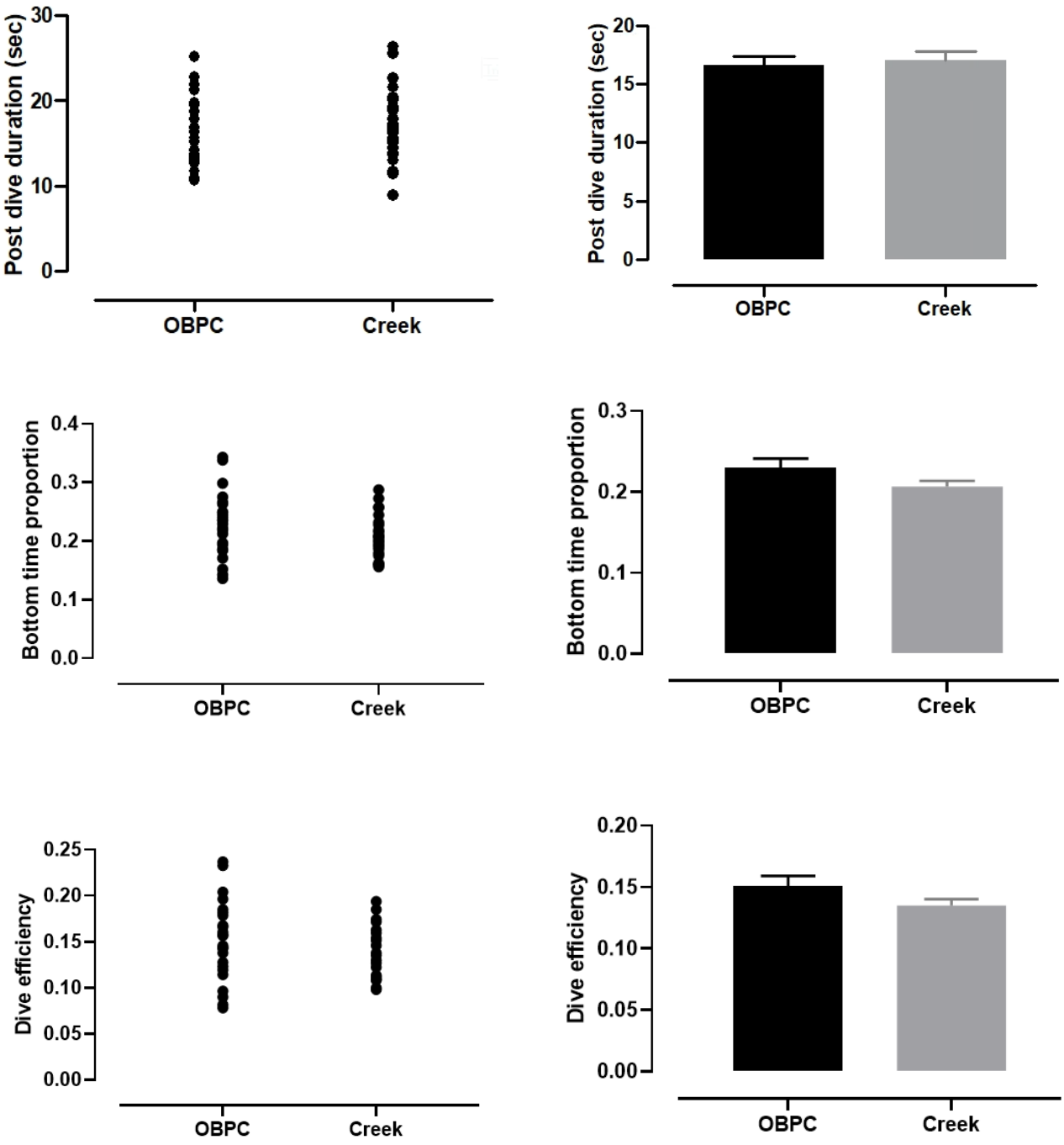

Fig. 3.43. Post-dive duration, bottom time proportion (bottom time/dive duration), and dive efficiency (bottom time/ (dive duration + post dive duration)) for all foraging trips recorded from the OBPC and Creek colonies during the guard stage of breeding in October and November 2016. Individual values are shown in the left column and mean ± SE in the right column.

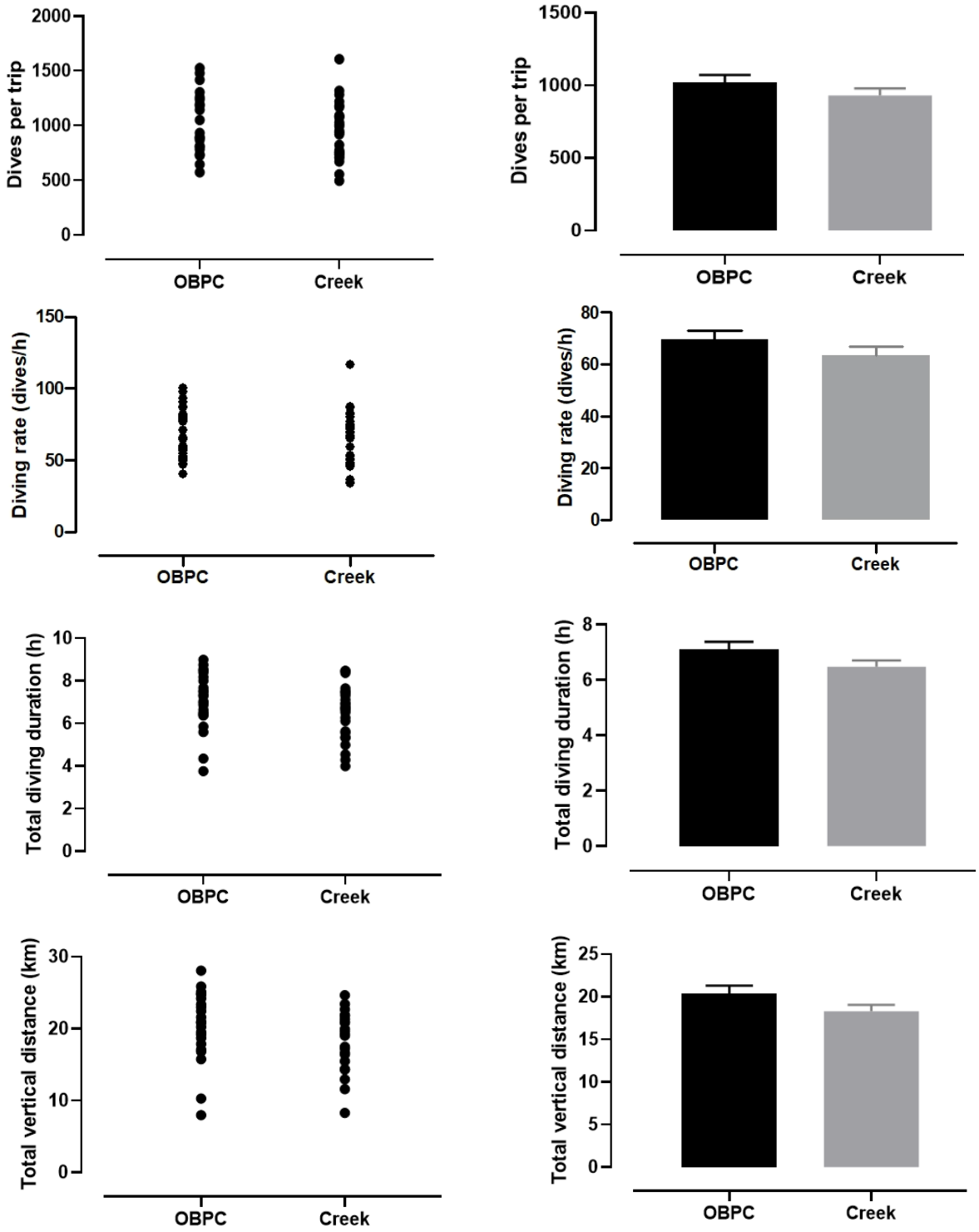

Fig. 3.44. Number of dives per trip, diving rate (total dives/foraging duration), total diving duration, and total vertical distance dived for all foraging trips recorded from the OBPC and Creek colonies during the guard stage of breeding in October and November 2016. Individual values are shown in the left column and mean ± SE in the right column.

Table 3.8. Mean (± S.E.) values for diving variables for penguin foraging trips from the OBPC and Creek colonies during the guard stage of breeding in October and November 2016. Minimum and maximum mean values from individual foraging trips are also presented.

	Colony									
	OBPC					Creek				
	Min.	Max.	Mean	SE	*n*	Min.	Max.	Mean	SE	*n*
Dive duration (sec)	13.1	40.0	26.8	1.6	25	16.4.	36.5	26.2	1.1	28
Dive depth (m)	4.2	15.4	10.0	0.69	25	5.5	15.6	9.7	0.6	28
Bottom time (sec)	1.9	13.8	7.3	0.7	25	2.8	13.9	6.2	0.3	28
Bottom time proportion	0.14	0.34	0.23	0.01	25	0.16	0.29	0.20	0.01	28
Post dive duration (sec)	10.7	25.2	16.6	0.8	25	8.9	26.4	17.1	0.8	28
Dive efficiency (bottom time/dive time + post dive time)	0.08	0.20	0.15	0.01	25	0.10	0.20	0.14	0.01	28
No. of dives per trip	573	1525	1017.9	53.9	25	496	1607	929.7	48.5	28
Daily diving time (h)	3.8	9.0	7.1	0.3	25	4.0	8.5	6.5	0.2	28
Diving rate (dives/h)	40.3	100.4	69.4	3.5	25	34.2	116.7	63.4	3.4	28
Vertical distance (km)	8.0	28.1	20.4	0.9	25	8.3	24.6	18.3	0.8	28

Table 3.9. Results of nested *t*-tests for comparisons between colonies for diving variables for foraging trips from the OBPC and Creek colonies during the guard stage of breeding in October and November 2016.

	t	df	*p*
Dive duration	0.6376	23	0.5300
Dive depth	0.6833	23	0.5013
Bottom time	1.465	23	0.1565
Bottom time/dive time	1.705	23	0.1017
Post dive duration	0.1509	23	0.8814
Dive efficiency	1.492	23	0.1492
No. of dives	0.6761	23	0.5057
Daily diving time	1.839	23	0.0789
Diving rate	0.6601	23	0.5157
Vertical distance squared	0.1115	23	1.655

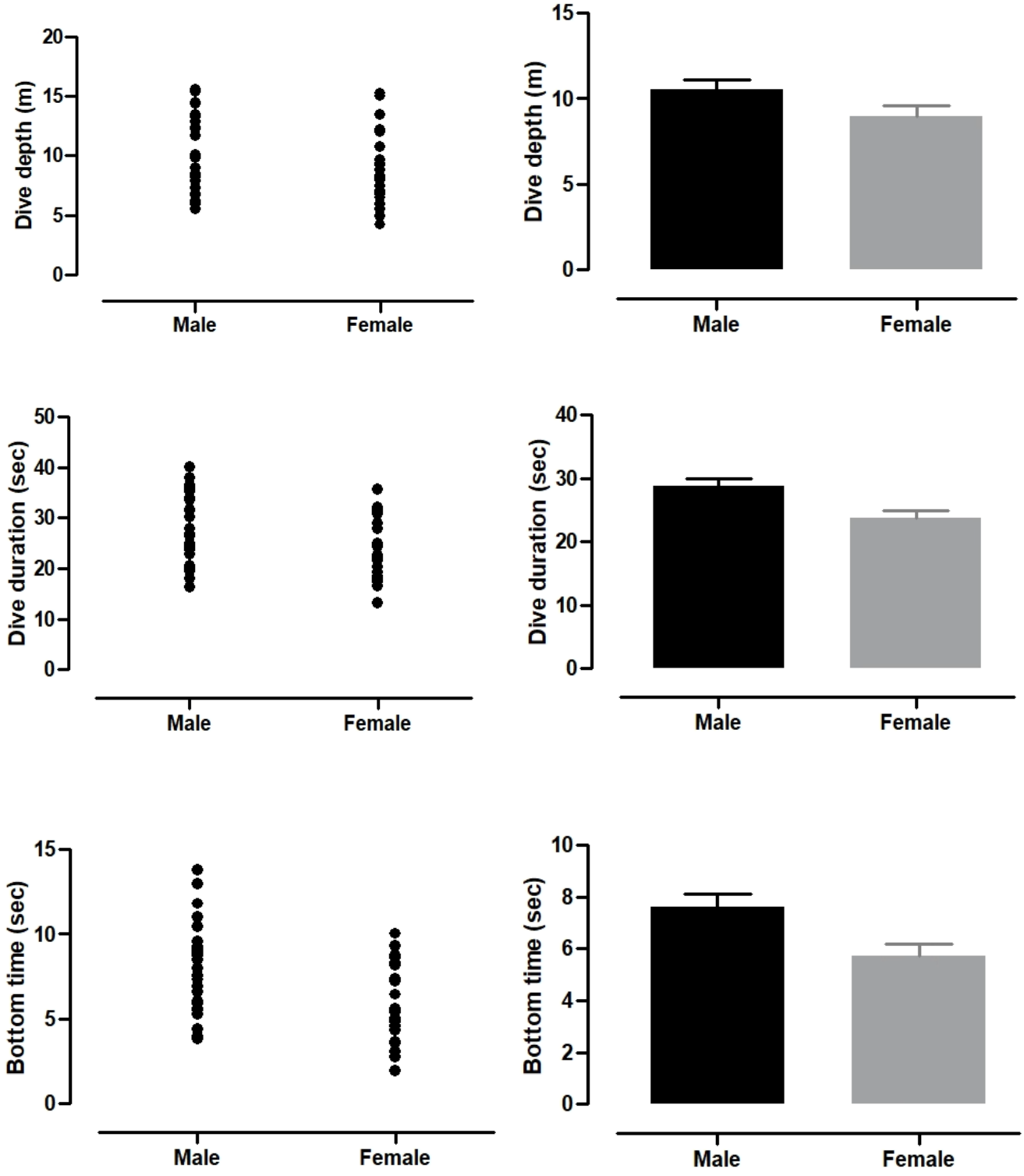

Fig. 3.45. Dive depth, dive duration and bottom time for foraging trips by male and female penguins from the OBPC and Creek colonies. Individual values are shown in the left column and mean ± SE in the right column.

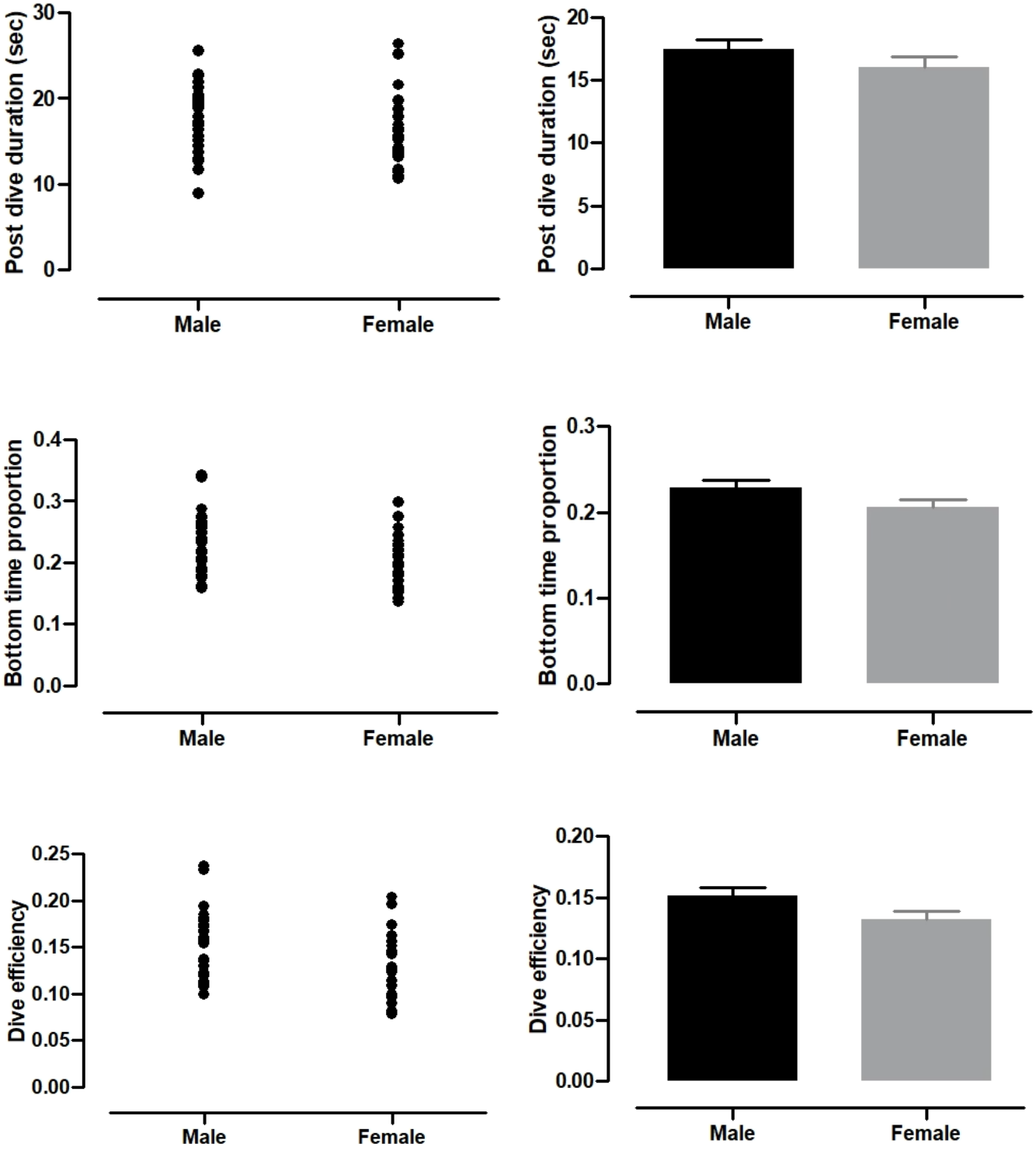

Fig. 3.46. Post-dive duration, bottom time proportion (bottom time/dive duration) and dive efficiency (bottom time/ (dive duration + post dive duration)) for foraging trips by male and female penguins from the OBPC and Creek colonies. Individual values are shown in the left column and mean $\pm$ SE in the right column.

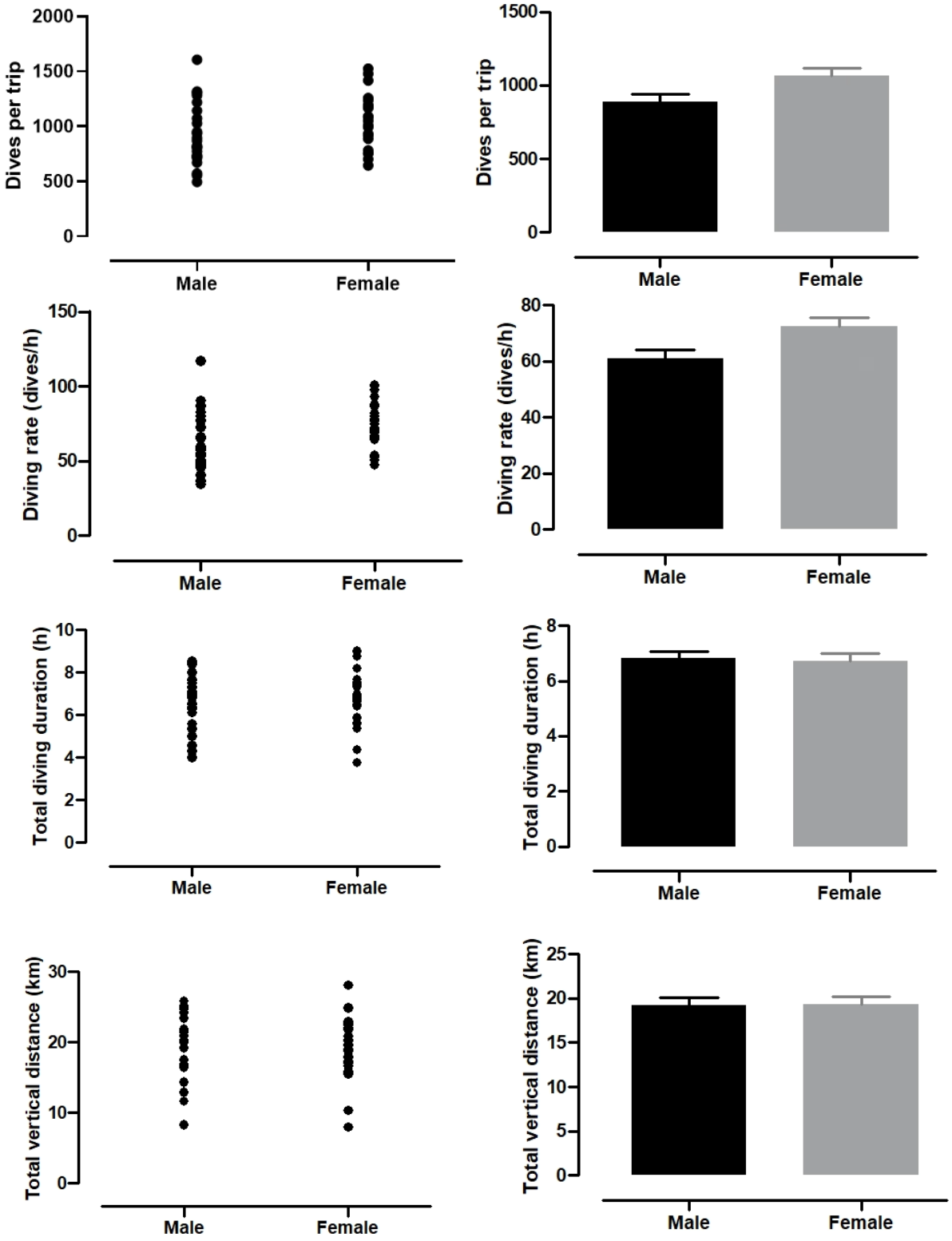

Fig. 3.47. Number of dives per trip, diving rate (total dives/foraging duration), total diving duration and total vertical distance dived for foraging trips by male and female penguins from the OBPC and Creek colonies. Individual values are shown in the left column and mean ± SE in the right column.

Table 3.10. Mean (± S.E.) values for diving variables for foraging trips by male and female penguins for penguin from the OBPC and Creek colonies during the guard stage of breeding in October and November 2016.

	Sex					
	Male			Female		
Diving Parameter	Mean	SE	*n*	Mean	SE	*n*
Dive duration (sec)	28.8	1.2	29	23.6	1.3	24
Dive depth (m)	10.5	0.6	29	9.0	0.6	24
Bottom time (sec)	7.6	0.5	29	5.7	0.5	24
Bottom time/dive time	0.23	0.009	29	0.21	0.009	24
Post dive duration	17.5	0.7	29	16.1	0.8	24
Dive efficiency (bottom time/dive time + post dive time)	0.15	0.007	29	0.13	0.007	24
No. of dives per trip	891.4	48.4	29	1067.8	48.9	24
Daily diving time (h)	6.8	0.25	29	6.7	0.25	24
Diving rate (dives/h)	61.0	3.3	29	72.6	3.1	24
Vertical distance (km)	19.2	0.8	29	19.3	0.9	24

Table 3.11. Results of nested t-tests for comparisons between sexes for diving variables for foraging trips by male and female penguins for penguin from the OBPC and Creek colonies during the guard stage of breeding in October and November 2016.

	t	df	p
Dive duration	2.054	23	0.0516
Dive depth	1.222	23	0.2734
Bottom time	2.228	23	**0.0360**
Bottom time/dive time	1.496	23	0.1483
Post dive duration	0.9259	23	0.3641
Dive efficiency	1.735	23	0.0962
No. of dives	1.7	23	0.1026
Daily diving time	0.1997	23	0.8435
Diving rate	1.662	23	0.1101
Vertical distance squared	0.1323	23	0.8959

Mean dive durations for trips were inversely related to the number of dives per trip (Fig. 3.48; $r^2 = 0.52$, $p < 0.0001$), indicating that the durations of dives were shorter when penguins made many dives per day in comparison with trips when penguins made relatively few dives.

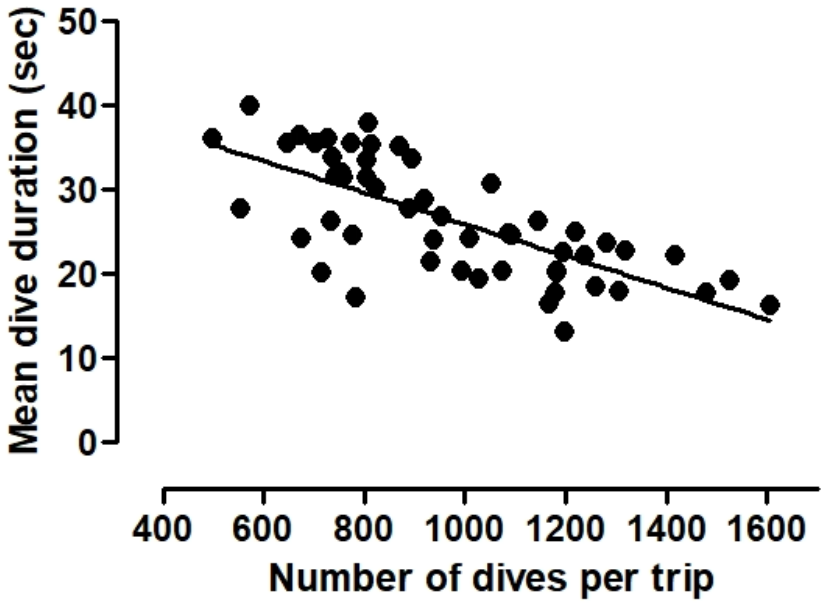

Fig. 3.48. Relationship between mean dive duration and the number of dives per trip. The line is a linear regression line.

The mean number of dives per trip increased over the 33-day period of the study (Fig. 3.49A), mean duration of dives (Fig. 51B) and mean dive depth (Fig. 3.49C) all declined over the study period ($r^2 = 0.35$, $p = 0.0013$; $r^2 = 0.32$, $p = 0.0023$; $r^2 = 0.4$, $p = 0.0004$).

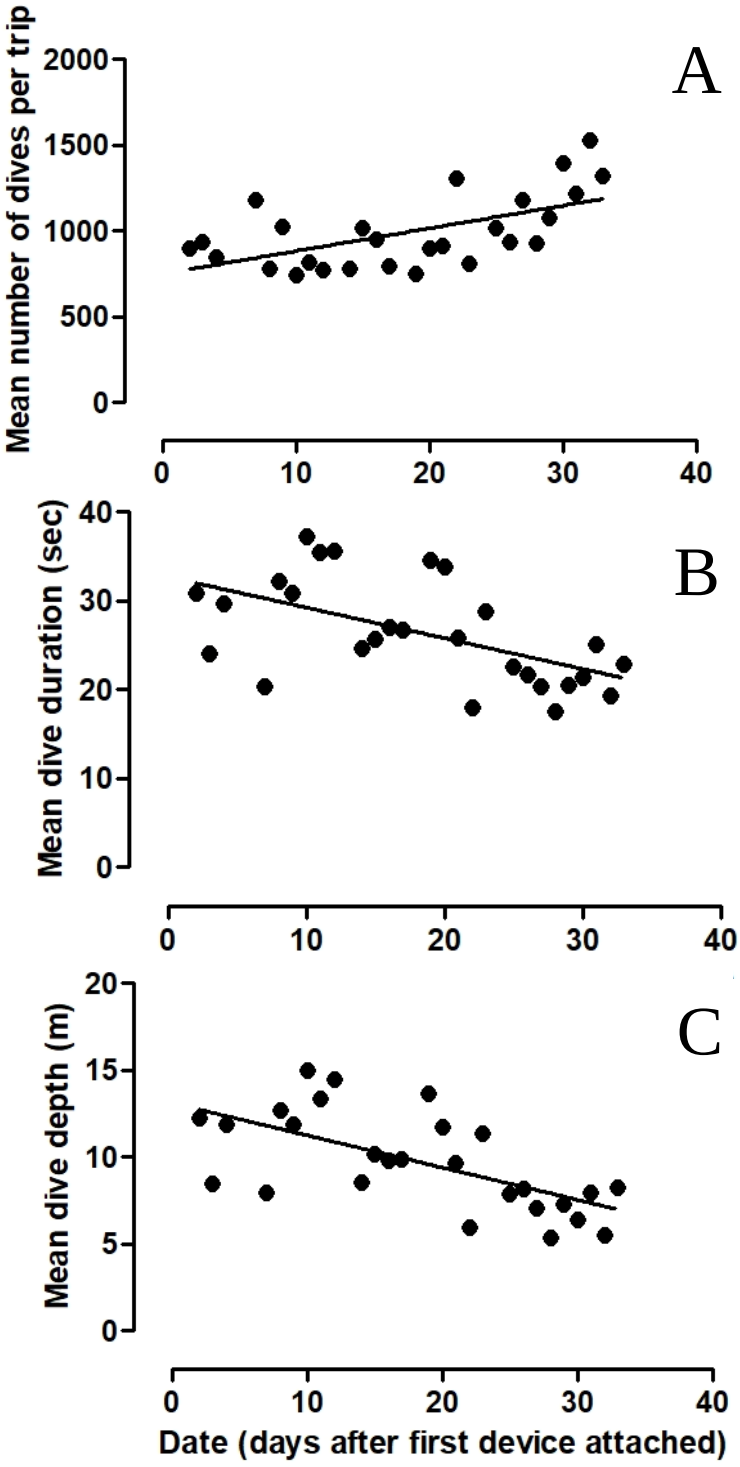

Fig. 3.49. Relationships between the mean number of dives per trip (A), mean duration of dives (B) and mean dive depth (C), and time (days from the start of the study). The lines are linear regression lines.

Mean diving depths changed during the day at each colony (see Fig. 3.50; Kruskal-Wallis test: OBPC $p < 0.0001$, Creek $p < 0.0001$). Depths increased during the morning to a peak near midday and decreased in the late afternoon. This pattern corresponded to the birds swimming out to sea in the morning then returning to the colony at the end of the day.

There was also a significant difference in diving rate throughout the day at both the OBPC and Creek (see Fig. 3.51; Kruskal-Wallis test: OBPC $p < 0.0001$, Creek $p < 0.0001$). Dunn's multiple comparisons tests were used to test for significant differences between paired columns. There were significant differences only for the first and last hours of the day. For these periods, diving rates were very low compared to the rest of the day.

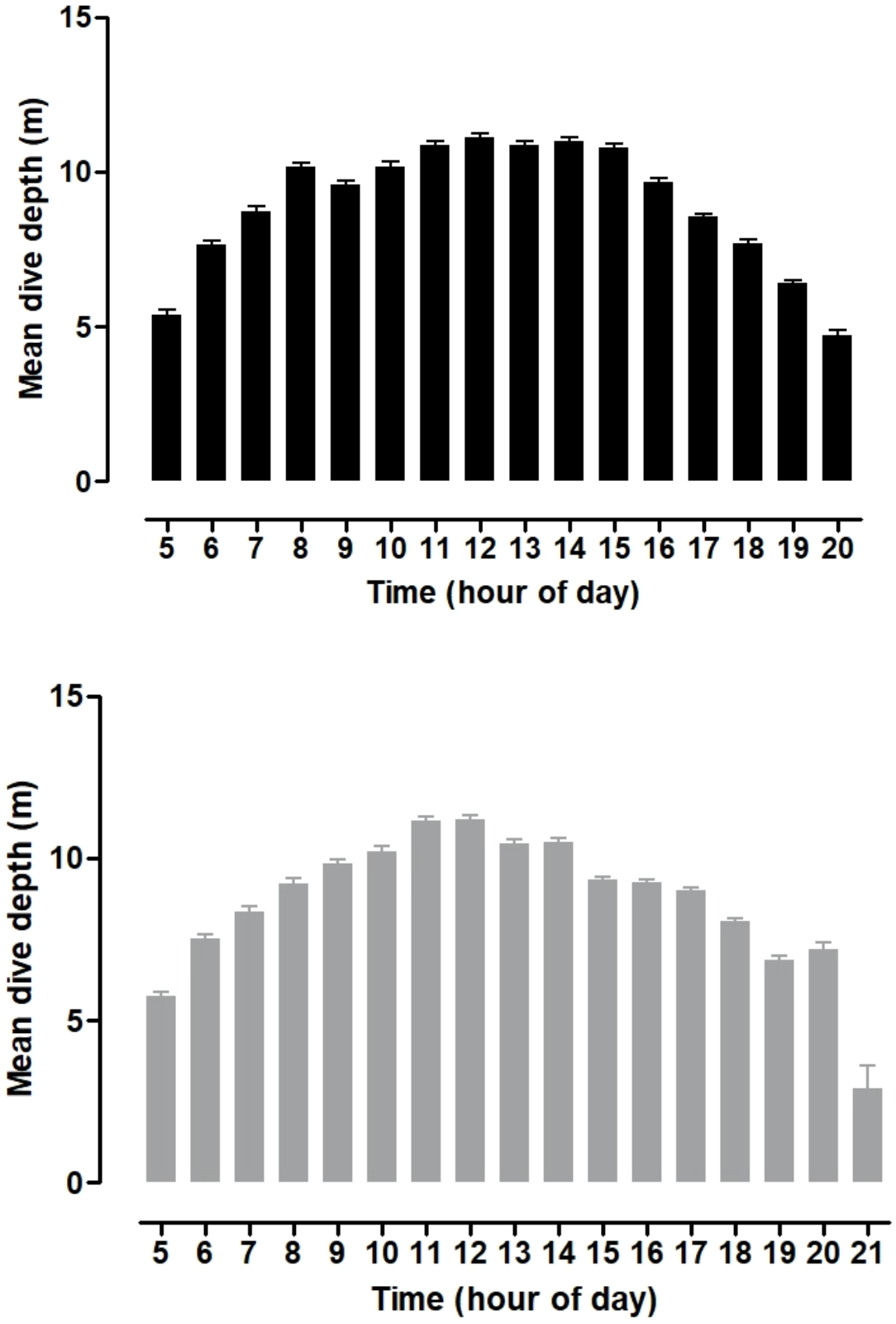

Fig. 3.50. Dive depth in relation to time of day at the OBPC (black bars) and the Creek (grey bars). Data are shown as mean ± S.E.

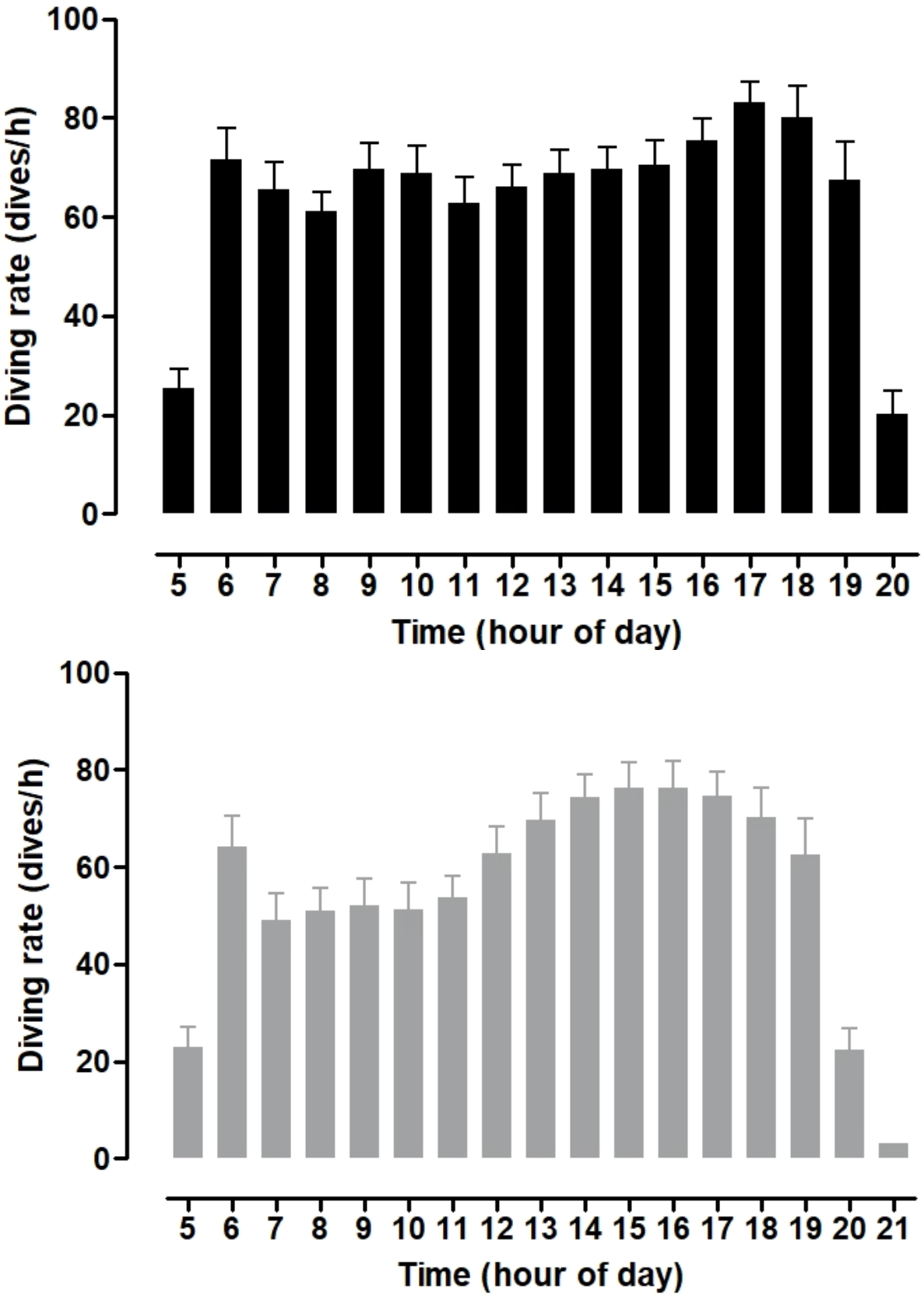

Fig. 3.51. Number of dives in relation to time of day at the OBPC (black bars) and the Creek (grey bars). Data are shown as mean ± S.E.

3.4.1 Variation in diving behaviour

Diving behaviour varied between trips of individual penguins and between penguins. Figs. 3.53 and 3.54 show examples of two patterns of diving behaviour in relation to depth of the water. Fig. 3.53 shows the dive profile and the track of a penguin that made increasingly deep dives as it swam away from the shore. The penguin spent time diving regularly to about 20 m while in an area where the sea was about 20 m deep, then the diving depth steadily decreased as the penguin swam back towards the shore. The dive profile and the track suggest that this penguin often foraged along the seabed. Fig. 3.54 shows a different pattern of diving in relation to the depth of the water. This penguin generally dived to depths of around 5 m while it swam into water more than 30 m deep, indicating that the bird was not foraging along the seabed.

Three foraging trips were recorded for bird 10 (Fig. 3.13), in which many dives appeared to match the bathymetry of the seafloor throughout the trip. Fig 3.52 illustrates the first trip from this bird. When departing the colony, dive depth increased as the seafloor depth also increased. This continued until the penguin reached the 20 m depth contour. The middle portion of the trip was spent near the 20 m depth contour. During this phase, dive depth remained relatively consistent, and dives were often to depths of approximately 20 m. Once the penguin began to return to the colony and encounter shallower water, the dive depths decreased. It appears the dive depths were related to water depth in this trip, and it is likely that there were many benthic dives.

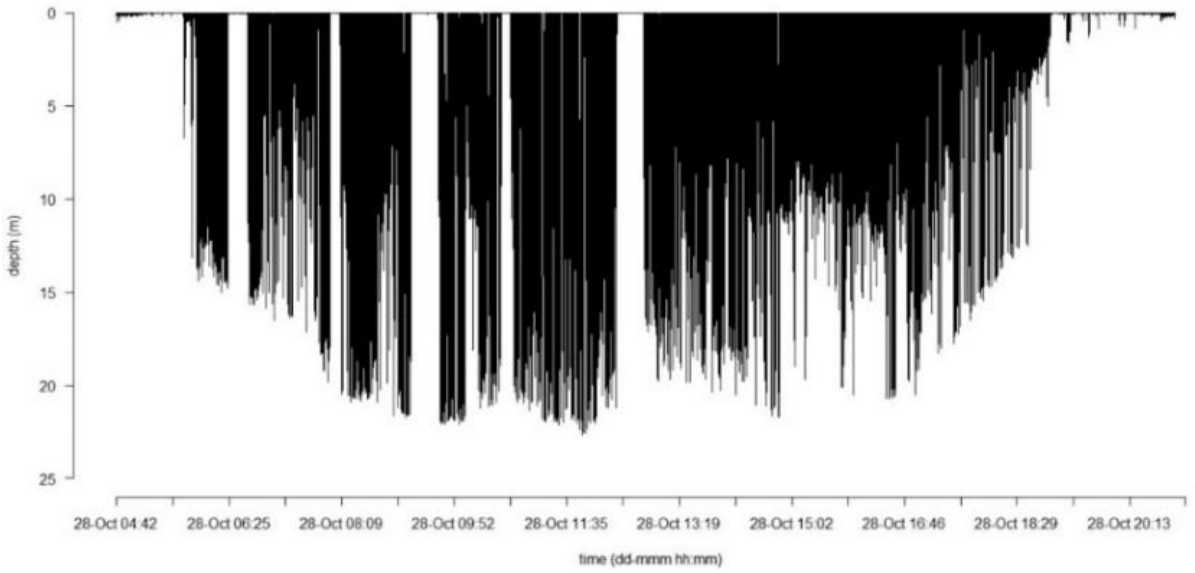

Fig. 3.52. A daily dive profile from bird 10 (trip 1) shows that the dive depths increased as during the morning as the bird departed the colony and decreased as they returned to the shore in the evening.

The same pattern was observed for other trips. During bird 14's third trip (Fig. 3.17 and Fig. 3.55), the dive profile appears to match the ocean water depth for the entirety of the trip. After departing the colony at 3:11 am, diving began at 5:27 am. Dive depth increased as the penguin swam away from the colony and reached a maximum of approximately 22 m. This increase matches the change in seafloor depth along the tracked path for this bird. Furthermore, this penguin spent a long period of the day around the 20 m depth contour, and the dive depths appear to correlate with this. Before this period of deeper dives, there was a 26 minute rest from diving, and during this phase a 30 minute rest also occurred. From 4:40 pm, dive depths began to decrease, while at the same time the bird began swimming back towards the shore.

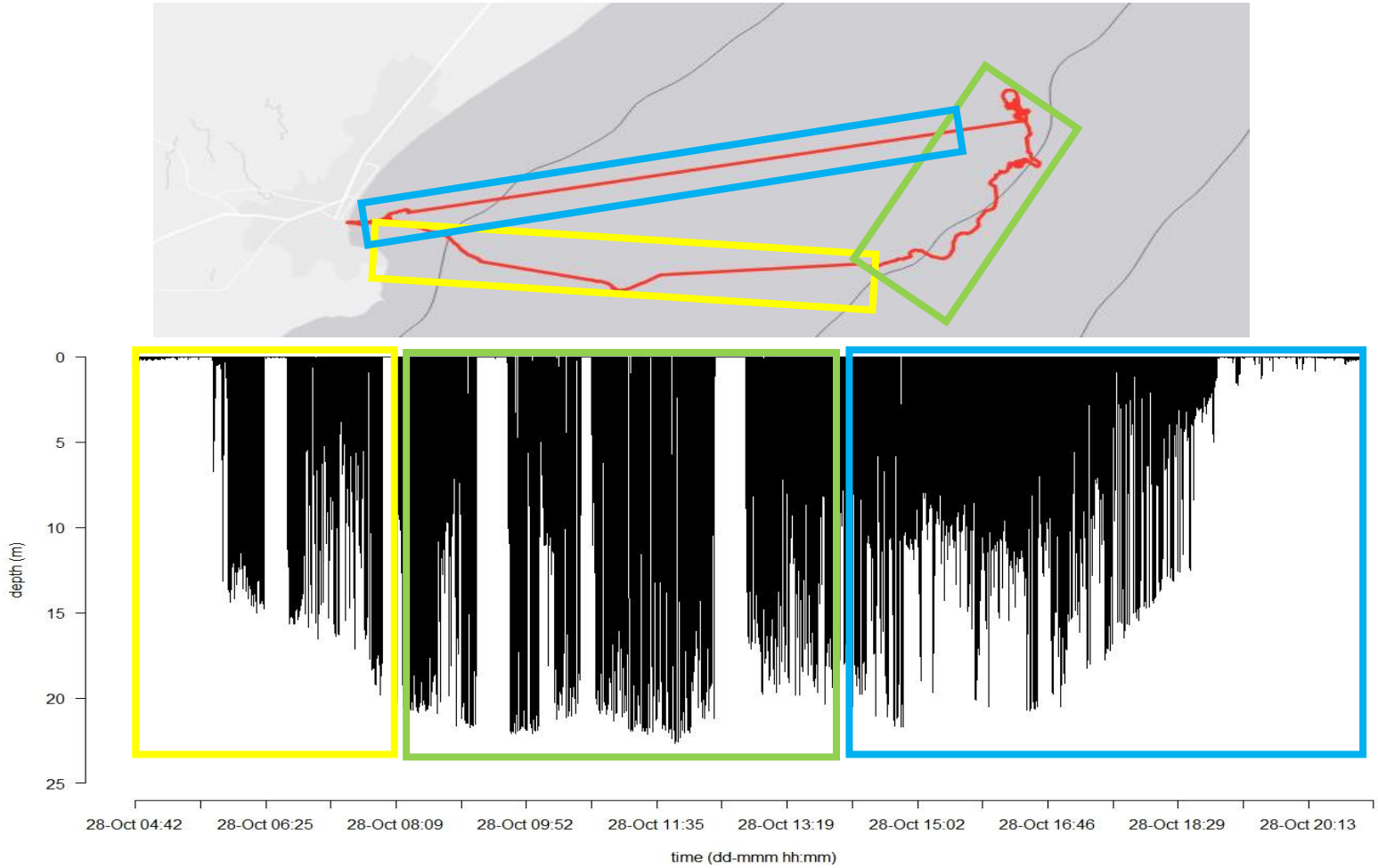

Fig. 3.53. Track and diving profile of a penguin that often dived to a depth that was similar to the water depth. Water depth contours are at 10 m intervals.

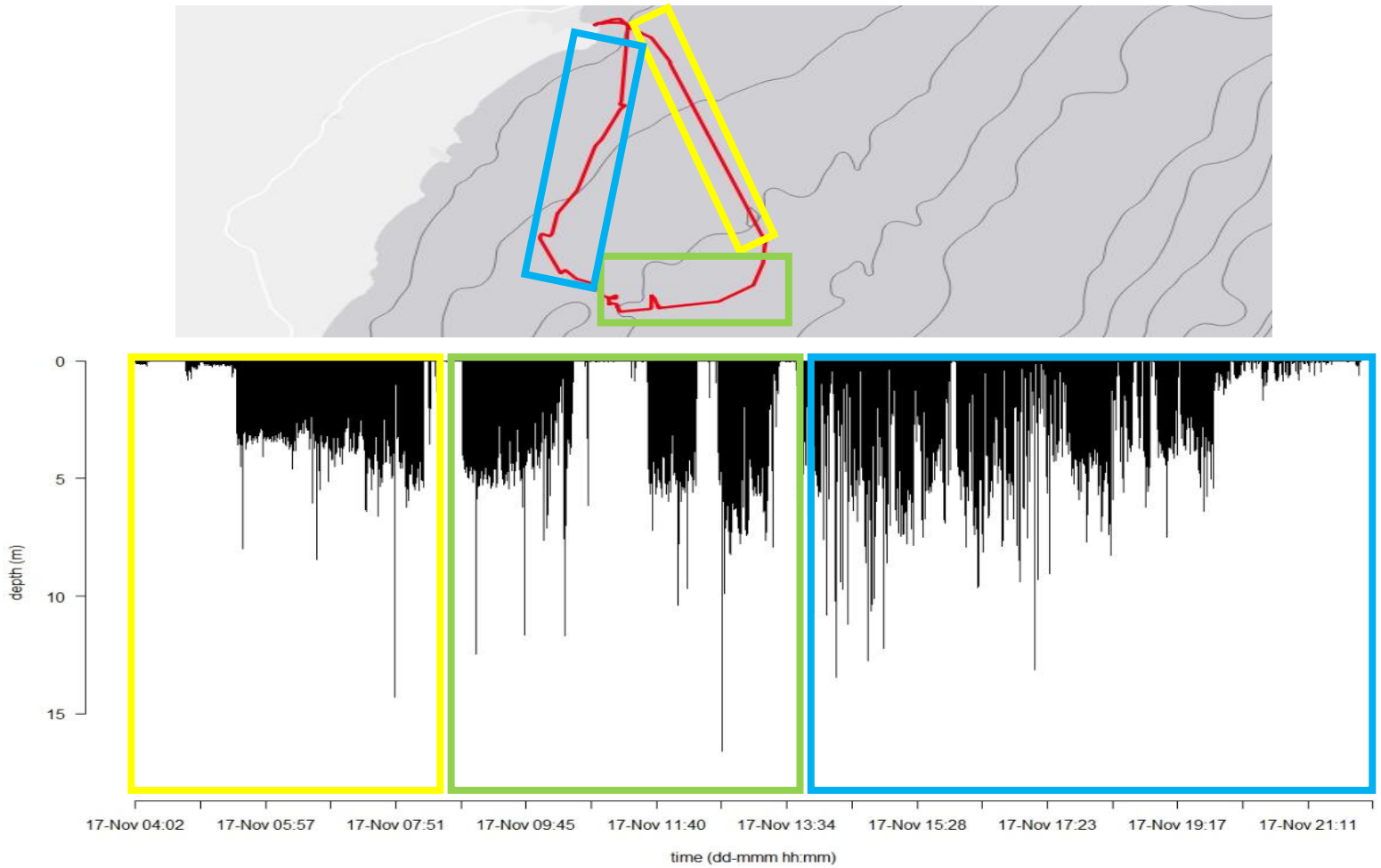

Fig. 3.54. Track and diving profile of a penguin that dived to depths that were shallower than the water depth. Water depth contours are at 10 m intervals.

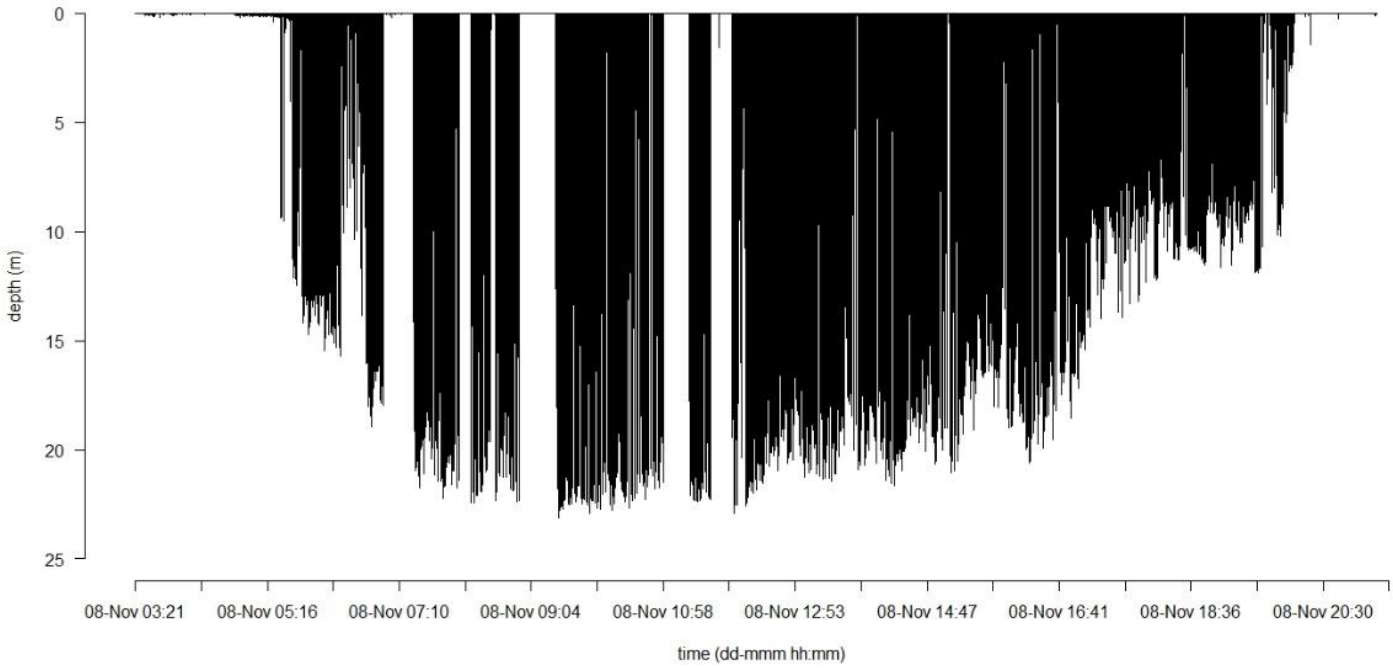

Fig. 3.55. Dive profiles from bird 14 (trip 3). Diving pattern shows an increase in depth as the bird departs the colony, a consistent dive depth during the day and a decrease as it returns in the evening.

In contrast, some trips showed little correlation between dive depth profiles and water depths. Bird 23 (Fig. 3.26) encountered relatively deep water on its first trip but dived to very shallow depths. Throughout the trip mean dive depth was only 4.2 m, the shallowest of all recorded trips. The first dive was conducted at 5:31 am, over 1.5 hours after the departure time of 3:52 am. The bird was approximately 4 km from the colony when diving begun. From 5:28 to 8:20 am, there was a gap in GPS fixes. However, during this period the penguin swam from water 15 m deep to water over 30 m deep. Despite this, dive depths remained shallow. Average dive depth was only 3.4 m, and only one dive was greater than 10 m. Shallow diving remained common while the penguin was foraging in water > 30 m deep. Diving depth increased after 1:30 pm, with was a higher proportion of dives between 5-10 m. This coincided with the penguin beginning to swim back towards the shore into shallower water. However, shallow dives were still commonplace. 65% of dives from 1:30

pm until the final dive were less than 5 m deep, while only 10 dives deeper than 10 m were recorded. The final bout of diving finished at 7:58 pm, and the penguin returned ashore at 9:59 pm. Dive depths certainly did not match water depths, and almost all dives must have been pelagic.

Shallow diving was observed on other trips, with some birds making shallow dives while other birds were making deeper, benthic dives. Bird 22 was a very shallow diver during its second trip (Fig. 3.56). This bird departed the colony at 4:28 am, and the first dive was 2 hours later at 5:31 am. Dive depths initially followed water depths, becoming deeper as the penguin travelled from the colony. However, while travelling from the colony diving depth did not generally exceed 10 m, despite the fact the penguin was foraging in water deeper than 20 m from 7:30 am. Deeper dives only occurred after 2 pm, and shallow dives were still commonplace. 53% of dives were less than 10 m. The only period of consistent diving to depths greater than 10 m was from 8:05 – 8:30 pm, just before the final dive at 8:39 pm.

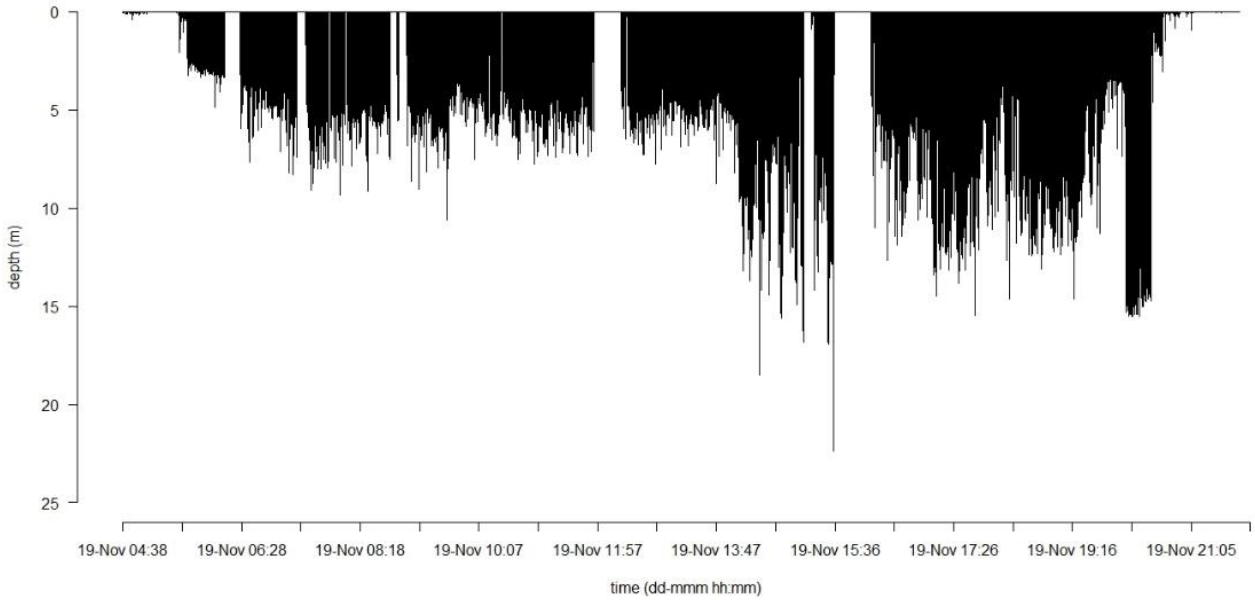

Fig. 3.56. Bird 22 (trip 3). This trip indicates a shallow pattern of diving throughout the day. Most dives occurred in water >15m, indicating most dives are pelagic.

Another example of shallow diving was bird 17's second trip (Fig. 3.57). After departing at 5:02 am, the first dive was at 5:43 am. This bird was a relatively shallow diver during this trip, with a mean dive depth of 6 m. Less than 5% of dives were 11 m or deeper. This bird also dived very often, with 90.4 dives per hour and a total of 1305 dives. This was consistent with expectations that when penguins have a shallower mean dive depth they tend to dive more often. The largest break from diving was 18 minutes and it occurred just prior to the bird reaching the maximum distance from the colony. Unlike many other trips by other penguins, this bird did not forage in water deeper than 20 m on this trip. Furthermore, between 1 pm and 5 pm this bird foraged in water 10 m or less in depth and foraged within 1 km of the coastline. Diving ceased by 8:09 pm and the penguin returned ashore at 8:37 pm.

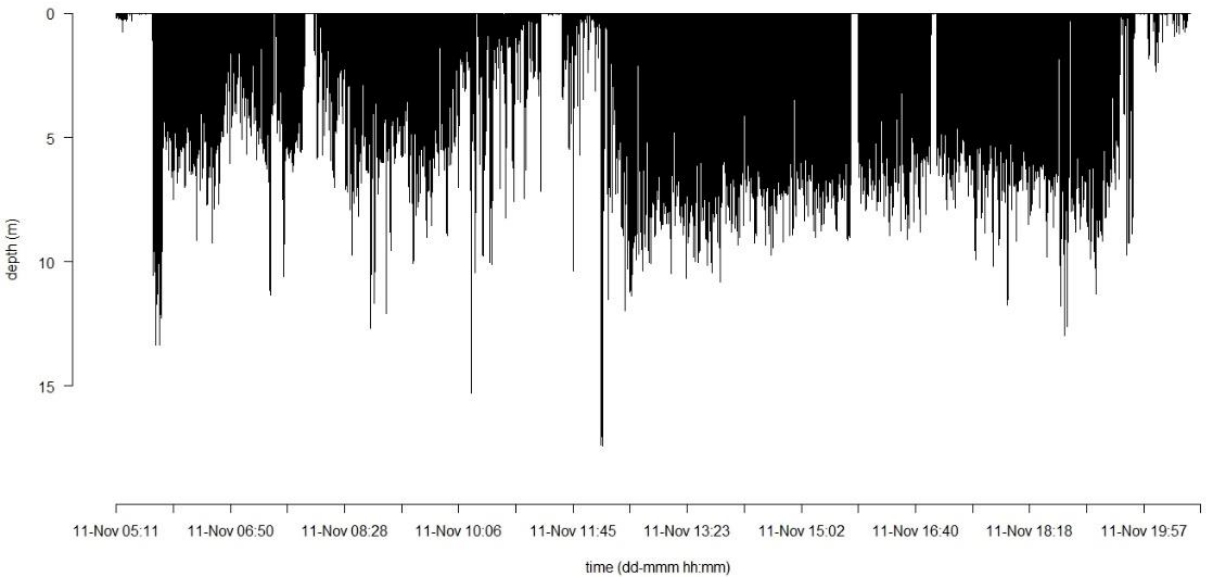

Fig. 3.57. Bird 17 (trip 2). Dive pattern showing a consistent shallow dive depth throughout the day.

From visual inspection of the dive patterns and the foraging tracks, it appears that little penguins often have periods of deep and periods of shallow diving. Furthermore, there may be periods of benthic or pelagic diving. Dive profile patterns can change significantly

throughout a trip. For example, bird 3 departed for its only recorded trip at 4:04 am. Diving began at 5:55 am, when the bird was approximately 5 km from the colony. From 6:00 am to 9:30 am, dives were relatively deep (Fig. 3.58). Mean dive depth was 12.6 m, while 55% of dives were deeper than 15 m. Within this period, foraging was occurring in water between 15 and 20 m deep. However, once the penguin reached water more than 20 m deep, diving depth reduced markedly. Although dive depth slowly increased, dives never exceeded 16 m during this period. Following a rest of 11 minutes, dives tended to become shallower as the bird returned towards the shore. This pattern contrasts with many other dive profiles in which benthic diving around the 20 m depth contour zone. It appears this bird was diving benthically at the beginning of its foraging trip, then pelagically in water greater than 20 m deep.

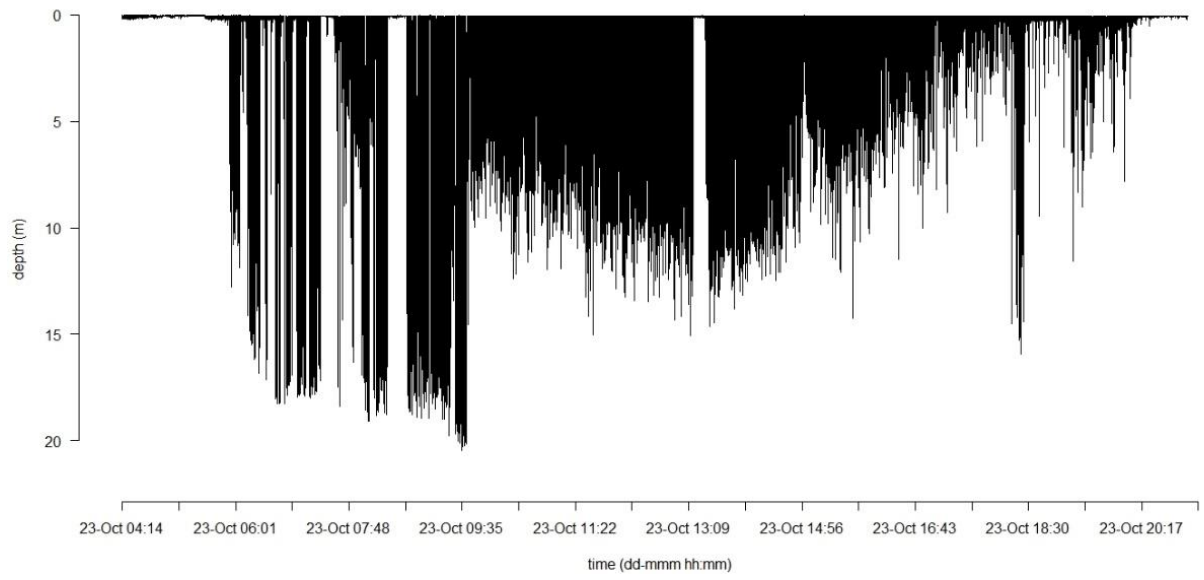

Fig. 3.58. Bird 3 (trip 1). A large change in maximum dive depth between different periods was observed in this daily diving pattern. The shallowest period of dives was while the penguin was foraging in the deepest water.

Bird 6 departed for its second trip at 4:51 am and begun diving 1 hour later. Initially, diving depth matched the water depth and benthic dives were common as the penguin travelled away from the colony. However, once water deeper than 20 m was reached, diving depths decreased. As the penguin swam in water between 20 and 30 m deep mean dive depth was 6.8 m, and the maximum dive depth was 11.8 m. Dive depth then increased as this bird travelled back to shallower water and deeper diving occurred in water 20 m deep. Following this deep diving phase there was a gap in GPS fixes during a period of non-benthic dives, then a second sustained period of deeper diving occurred. After this phase, dive depth decreased as the penguin swum towards the shore.

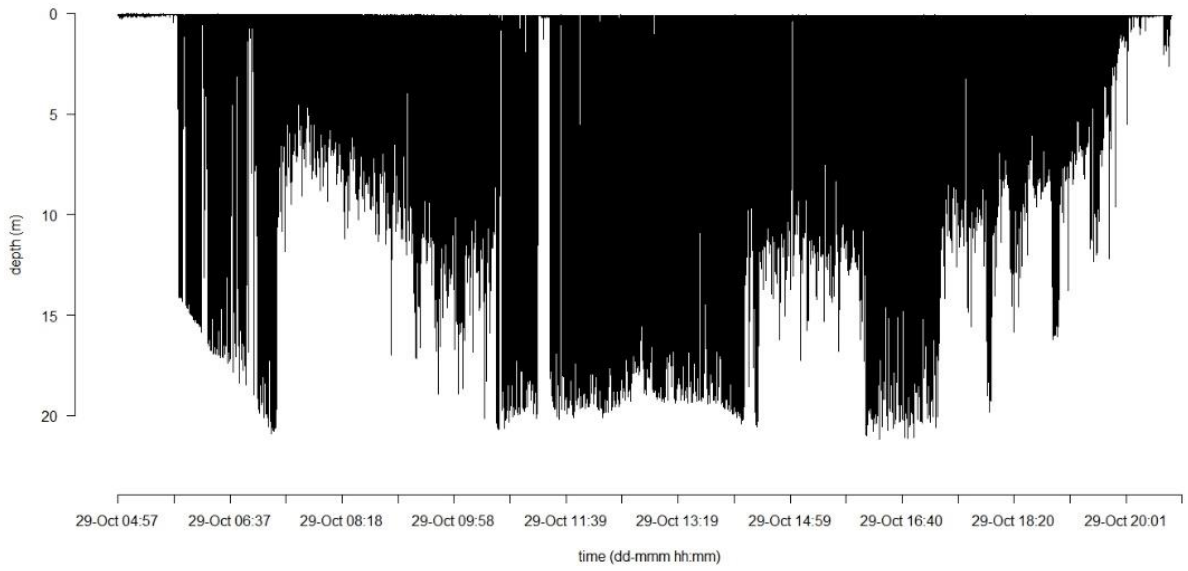

Fig. 3.59. Bird 6 (trip 2). Daily dive pattern with changes in maximum dive depth throughout the trip. There were periods of both benthic and pelagic diving.

Visual inspections of dive profiles revealed variation in diving behaviour at finer temporal scales also. Often, diving behaviour was consistent and consecutive dives were often to the same depths (Fig. 3.60). This was often observed when penguins were foraging in water around 20 m deep and were diving to this depth. Given that consecutive dives to similar

depths are often considered as benthic, and that the water depth was estimated to be 20 m, it is likely that penguins were diving benthically during these periods. At other times dives varied greatly within a short time period, with consecutive dives reaching different maximum depths (Fig. 3.61). These dives are typically defined as pelagic dives. Birds that stayed in water less than 20 m deep appeared to dive benthically more often than birds that ventured further from the coast into deeper water where the water depth was greater than the usual maximum dive depth of approximately 25 m.

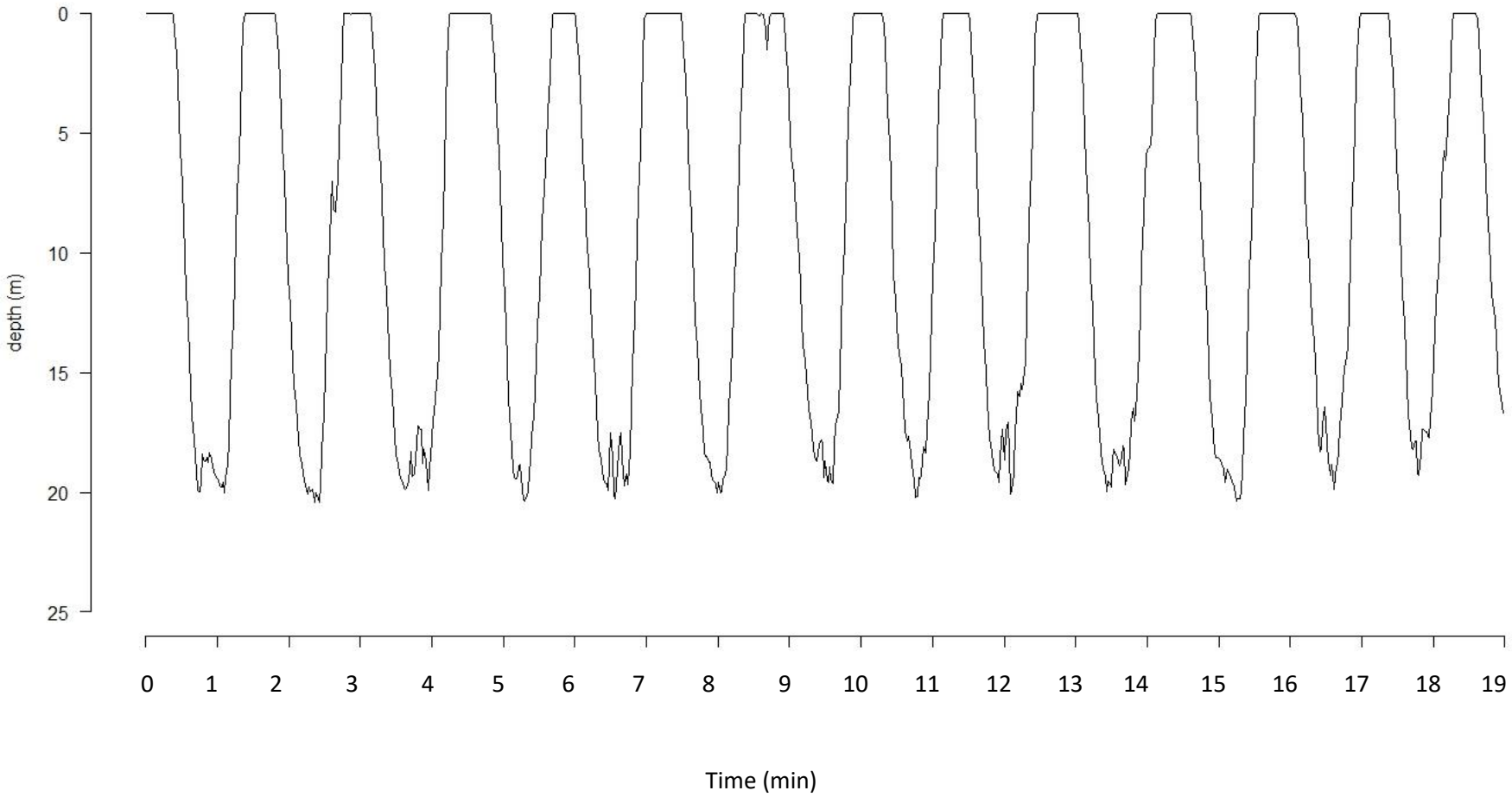

Fig. 3.60. Diving behaviour over 19 min when a penguin consistently dived to the same depth. The water depth was estimated from bathymetry data to be approximately 20 m where the dives were recorded, indicating that the dives where likely to be benthic dives.

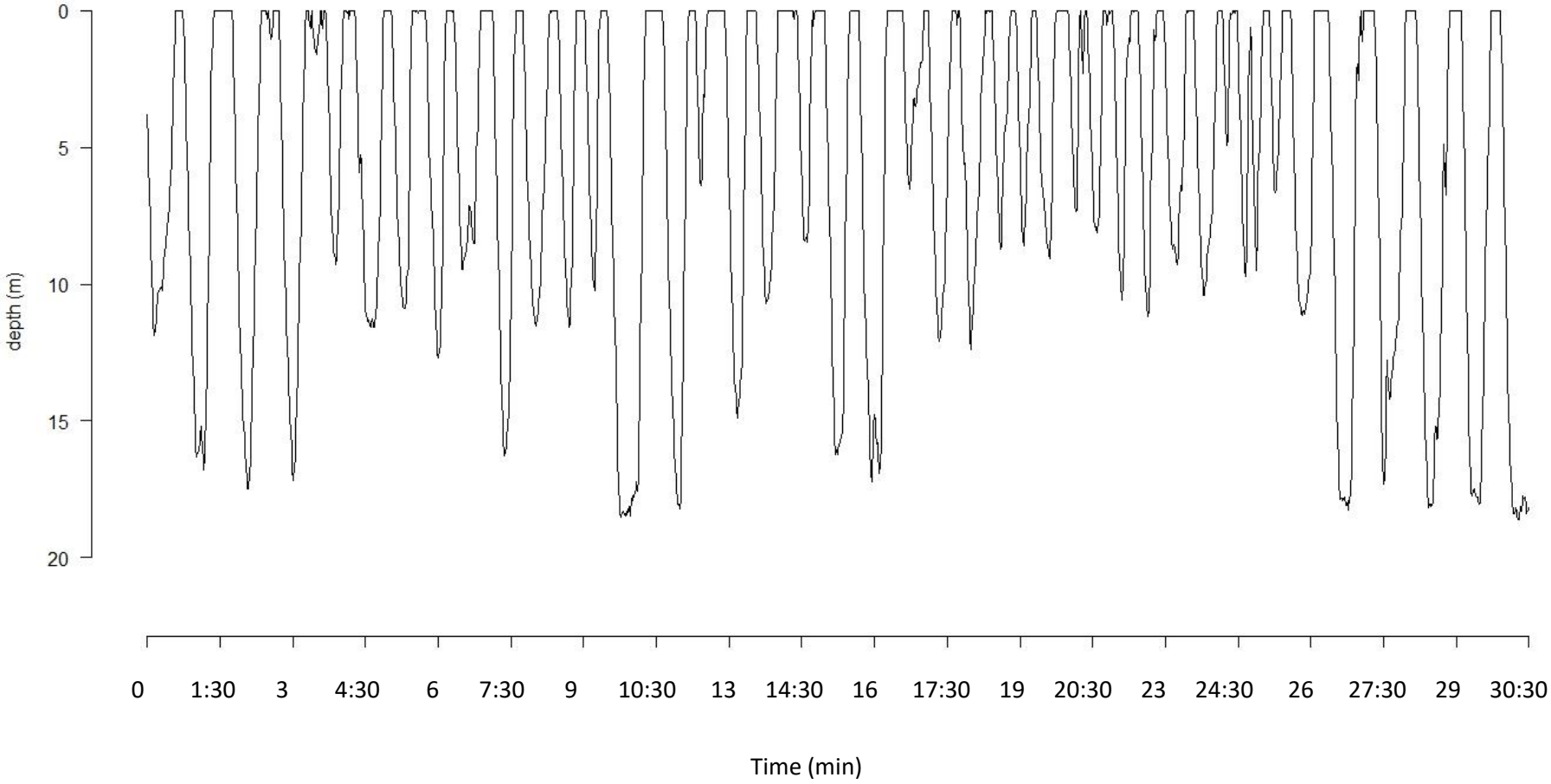

Fig. 3.61. Diving behaviour over 30 min when the maximum depth of dives differed between dives. The water depth was estimated from bathymetry data to be approximately 20 m where the dives were recorded. Therfore, many of these dives were pelagic dives.

4. Discussion

This is the first study comparing the foraging and diving behaviour of two neighbouring little penguin colonies in New Zealand. Individuals from each site had similar foraging behaviour and generally foraged in the same area. Furthermore, diving behaviour did not differ between colonies. However, individuals from the Creek colony had a greater mean trip duration and a later mean return time to the colony, than their OBPC counterparts. In addition, the mean foraging area per trip was larger for Creek colony individuals compared to OBPC birds. This was associated with a higher number of wide-ranging trips from Creek individuals. However, wide-ranging trips are unlikely to be characteristic of birds from the Creek colony, and the larger mean range may be due to the relatively small sample size. While seabirds from neighbouring colonies will often forage in distinct areas, for the Oamaru penguins the foraging ranges of each colony broadly overlapped. There was considerable individual variation in foraging and diving behaviour. Some birds travelled twice the total distance of others whilst foraging, and diving effort varied greatly between individuals.

4.1 Foraging

4.1.1 Trip duration

Single day foraging trips were recorded during the guard stage of breeding. During the guard stage, little penguins are constrained by the need to feed their offspring daily. Parents usually alternate nest attendance with one day foraging trips to meet the nutritional demands of the chicks. While one parent forages, the other remains at the nest to meet the chick's thermoregulatory requirements. The penguins in this study deviated from this nest attendance pattern on only three occasions, twice when a parent returned to sea the day after a foraging trip, and once when a parent remained in the nest box for three consecutive days.

There was a significant difference in trip duration between the OBPC and Creek colonies. Creek colony birds had a mean trip duration 0.8 h longer than OBPC birds. In contrast, the foraging duration (period between the first dive and the last dive) did not differ between the colonies. It is unsurprising that the foraging duration did not differ between colonies. Little penguin diving behaviour is highly influenced by light intensity, with birds performing fewer dives at lower light levels (Cannell and Cullen, 1998). In addition, studies have shown little penguins conduct very few dives early and late in the day, when light levels are lowest (Mattern, 2001). Furthermore, little penguins do not usually dive during the night when undertaking multi-day trips. In this study, penguins rarely dived during the earliest and latest hours of a foraging trip. The difference between colonies in trip duration was related only to the total time spent at sea, rather than actual time spent foraging. Given that the colonies are only 1 km apart and that penguins experience the same daylength at each colony, it is surprising that trip duration differed. However, Wiebkin (2012) found little penguins from Troubridge Island departed over 3 hours before sunrise and returned 1.5 hours after sunset, while individuals from Pearson Island 350 km away departed and arrived 1.33 hours before sunrise and 0.67 hours after sunset. Furthermore, foraging duration did not vary between these colonies. Mean departure times did not differ between the OBPC and Creek, whereas OBPC birds returned approximately 30 minutes earlier than their Creek colony counterparts.

At Phillip Island, delayed arrival times have been associated with years of reduced breeding success. Average arrival time was delayed by 30 min in years of low breeding success, compared to more successful years (Daniel, 2005, as cited in Chiaradia *et al.*, 2007a). A sharp change in mean arrival time was also observed during a strong fog event at Phillip Island. The peak arrival time was 2 h later on the fog day, after the fog had subsided, than on

previous and subsequent days. The authors suggest two explanations: that little penguins would be unable to detect predators due to the reduced visibility and remained at sea to avoid predation, or penguins could not navigate to the colony due to poor visibility. The navigational ability of little penguins at sea is poorly understood. However, if penguins could not navigate to the colony in heavy fog, this would suggest that visual cues may be important. At the OBPC, artificial lighting is used so visitors may view the penguins when they arrive ashore. Lights from the OBPC will be visible some distance out to sea, whereas the Creek colony has no artificial lighting. However, little penguins in Oamaru will often swim to within a few hundred metres of the colony before sunset and then wait until darkness before coming ashore. In this scenario, they have navigated to the colony area while it is still light, therefore the artificial lighting at the colony will have had no effect in aiding their ability to find the colony. It has been suggested that the presence of lighting used for ecotourism may also influence little penguin behaviour. When lighting was introduced to a previously unlit area at Phillip Island, little penguins exhibited a preference for lit pathways on land, rather than the dark routes they may typically take to their nests. However, changes in light intensity had no effect on the arrival time of penguins at the artificially lit Penguin Parade section of the Phillip Island colony (Rodríguez *et al.*, 2018). While the impact of artificial lighting is apparent for some seabirds and many petrel species which are attracted to or disoriented by street lighting and will land in urban areas (Rodríguez *et al.*, 2017), there does not appear to be a strong effect on little penguin arrival and departure patterns from the colony. Finally, departure and arrival times can vary by over 2 h between individuals on any given night (Chiaradia *et al.*, 2007a; Rodriguez *et al.*, 2016). Any interpretation of inter-colony differences in trip duration, arrival times or departure times, should be based on larger sample sizes than those in this study. Further investigations on whether trip duration is consistently different between colonies should be conducted.

4.1.2. Trip distance

For most trips, individuals remained within 25 km of their colony. For little penguins, maximum and total trip distance is highly constrained by chick-rearing responsibilities during the breeding season when penguins must leave the colony in the morning and return in the evening on the same day. It has been suggested that a mean maximum distance of 25 km from the colony during the guard stage (Collins *et al.*, 1999; Preston *et al.*, 2008; Agnew, 2014) is the greatest distance that penguins can reach on day trips. The mean maximum distances from the colony at the OBPC and Creek were 12.9 km and 18.0 km. respectively. This is comparable with other studies at Oamaru, which recorded mean maximum distances between 11.7 km and 22.6 km when penguins were conducting one day foraging trips (Mattern, 2001; Agnew, 2014). Furthermore, studies from other colonies show little penguins remain within 20 km of the colony on average during guard stage. However, maximum distances for single day trips have been reported as far as 36 km from the colony (Hoskins *et al.*, 2008). Previously the greatest reported distance from the colony for a single day trip from Oamaru was 35.2 km (Mattern, 2001). The greatest distance in this study was 41.2 km from the colony.

Total trip distances were similar to previous Oamaru studies, in which mean distances between 33.6 km and 57.6 km were reported (Mattern, 2001; Agnew, 2014). OBPC penguins travelled a mean distance of 40.7 km, while Creek birds swum 45.5 km. Total travel distances have been reported up to 80.9 km for a single day trip in Australia (Wiebkin, 2012), and trips up to 75.5 km have been recorded for Oamaru (Agnew, 2014). The greatest distance travelled in this study was 85.3 km by a Creek colony individual.

Little penguins do not forage uniformly within a radius surrounding the colony, as foraging patterns are influenced by prey distribution. Prey is patchily distributed, due to the spatially and temporally dynamic nature of the marine environment. Seabirds will often forage about oceanographic features which facilitate prey aggregation. For example, African penguins forage in cooler waters associated with upwelling which are known to aggregate forage fish species (van Eeden *et al.*, 2016). In addition, local environmental features may impose limitations on foraging. For example, the available foraging habitat can vary in size between colonies due to geographical constraints. At Phillip Island, the ocean accounts for 89% of the area within 20 km of the colony, whereas in Oamaru only 51% of this area is ocean (Chiaradia *et al.*, 2007b). At Motuara Island, penguins remained within Queen Charlotte Sound during single day trips, possibly due to deep water outside the sound (Mattern, 2001; Poupart *et al.*, 2017).

Because environmental features are site-specific, foraging behaviour differs between colonies. Travelling distances vary between colonies, as distances to profitable prey patches will differ between colonies. These inter-colony differences may be more pronounced outside of the guard stage when parents are not limited to single day trips. Poupart *et al.* (2017) compared little penguin foraging behaviour across three colonies during both incubation and chick rearing. Inter-colony variability was greatest during incubation. During chick-rearing, most penguins foraged inshore, less than 20 km from their respective colonies. This is consistent with single day foraging behaviour throughout New Zealand and Australia. Trip distances have been more variable between studies of foraging during incubation in comparison with studies of single day guard stage foraging trips. For four colonies in New Zealand, mean maximum distance ranged between 11 km and 155 km during incubation, while mean total distance travelled was between 33.6 km and 482 km (Agnew, 2014; Poupart

et al., 2017). These distances were much greater than for single-day guard trips, from New Zealand and Australian colonies for which mean maximum distance has been reported up to 22.7 km from the colony, while the greatest reported mean total distance travelled is 64.4 km (Wiebkin, 2012; Phillips *et al.*, 2019). Several studies have shown that trip duration is more variable outside of the guard stage. Greater variation in trip duration was correlated with more variable total trip distances at Phillip Island between 1991 and 1993 (Collins *et al.*, 1999).

As both the OBPC and Creek penguins encounter the same marine environment, it may be expected that trip distances would be similar. Foraging behaviour is constrained by chick demands during the guard stage, so differences between colonies and foraging behaviour are less likely during the guard stage than during other stages of the annual cycle. Future studies at Oamaru should consider foraging behaviour outside the guard stage, and tracking should be conducted over multiple years. A single year study can only report foraging behaviour that reflects the environmental conditions that year, with studies repeated for three to five years at one location needed to be able to make generalisations about foraging behaviour at different stages of the annual cycle at a location.

4.1.3. Individual variation

There was considerable variation between individual trips from the Oamaru colonies. Maximum distances ranged from 5.3 km to 41.2 km, and total distance travelled from 13.4 km to 85.3 km. There were differences between individuals foraging on the same day, and differences between consecutive trips made by individual penguins. A wide range of distances for single day trips was observed by Agnew (2014), with a maximum distance from the colony of 35.2 km and a shortest distance of only 5.6 km. Similarly, Zhang *et al.* (2015)

reported distances ranging from 3.5 km to 27.4 km among chick-rearing penguins at Matiu/Somes Island in Wellington harbour.

In addition to variation in travelling distances, two foraging strategies were observed: short-range trips, where individuals remained close to the colony and foraged within a small area, and wide-ranging trips, in which individuals travelled further from the colony and swam in a large circular pattern (see Fig. 4.1). These dual foraging strategies were previously observed at Oamaru by Mattern (2001).

Among seabirds, sex related differences in foraging behaviours are more prevalent in species with greater sexual dimorphism. Little penguins exhibit only minor morphological differences between sexes (Arnould *et al.*, 2004), and no difference in trip distances has been previously reported between the sexes. However, females have been reported to forage over a larger range during the non-breeding period (McCutcheon *et al.*, 2011). There were no differences between males and females at Oamaru in trip distances. Age related differences have been reported in foraging range and diving behaviour (Zimmer *et al.*, 2011a; Pelletier *et al.*, 2014), but no difference in trip distances have been reported. Many individuals in this study were banded as adults, so age could not be determined.

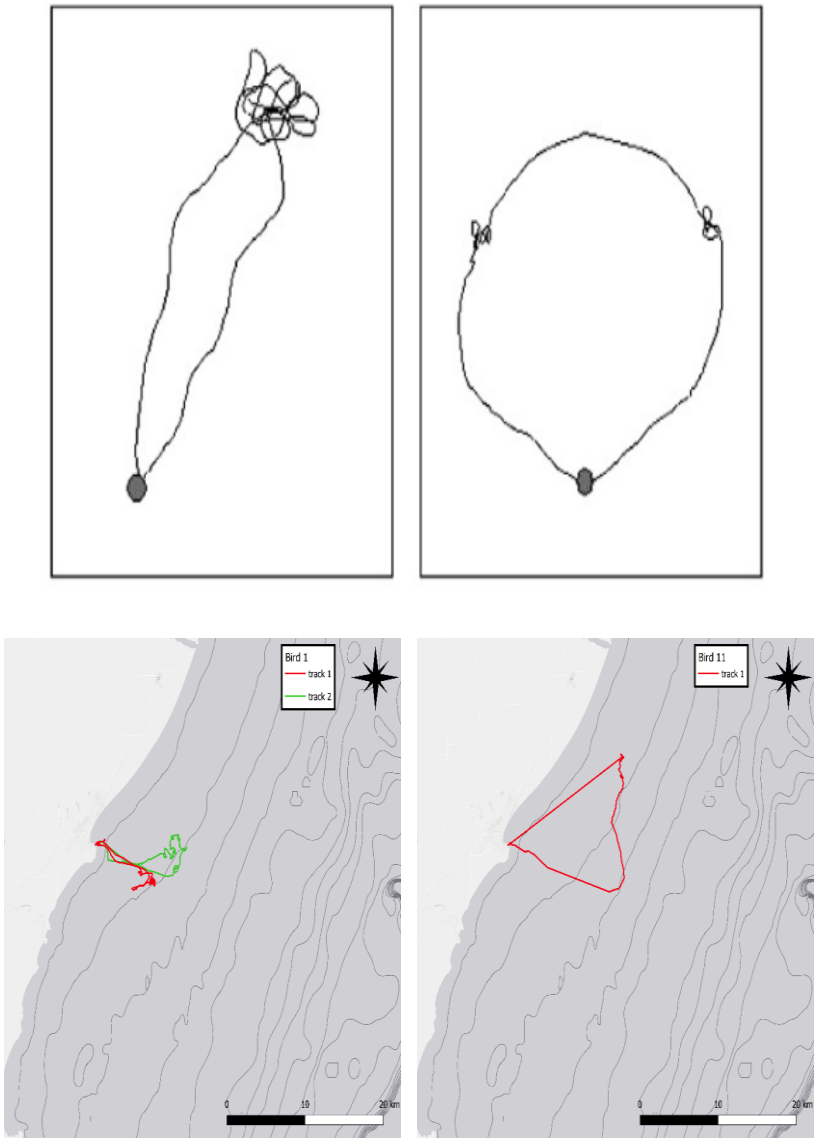

Fig. 4.1. Example of a short-range track (left panel) that was similar to the commuting pattern described by Weimerskirch (2007) and a wide-range track (right panel) similar to the looping pattern described by Weimerskirch (2007).

Differences between trips in foraging behaviour may result from differences between individuals and their foraging characteristics and from differences in environmental conditions from day-to-day and on longer timescales. Little penguins have plasticity in their foraging behaviour and are adaptable to changes in the marine environment. Changes in foraging behaviour have been associated with inter-annual variation in many environmental parameters. For example, increased foraging effort was associated with greater SST at London Bridge and Gabo Island (Berlincourt and Arnould, 2015), while Kowalczyk *et al.* (2015a) reported relationships between distance travelled from a colony and local water salinity and river outflow rate. More recently Phillips *et al.* (2019) showed that little penguins can respond to fine-scale environmental changes. Changes in behavioural states within a trip were correlated with SST, wave height anomaly and salinity. Fine-scale environmental processes can influence prey aggregations. For little penguins, responding to environmental cues and adjusting their foraging behaviour may assist in locating and capturing prey.

As little penguins can respond to fine-scale changes in their environment, a particular foraging strategy may reflect the conditions encountered during the tracking period. Phillips *et al.* (2019) noted two distinct foraging strategies conducted by little penguins at Wedge Island. These included short range trips with a large proportion of time spent searching for prey, indicated by area restricted search (ARS), and long-range trips with little time spent in ARS. Long range trips correlated with high wind gust speeds. High wind speeds are thought to reduce foraging success by disrupting the thermocline in the ocean. The thermocline may promote prey aggregation and assist in prey capture (Ropert-Coudert *et al.*, 2009; Saraux *et al.*, 2016). High winds can also reduce water clarity by increasing the amount of suspended sediment, which may reduce little penguin foraging success (Agnew, 2014). In contrast,

Mattern (2001) did not find any correlation between trip type and weather conditions, nor individual preferences, and proposed that trip type is driven by prey distribution. That is, individuals that encounter a prey patch early in the day will follow its movements and forage in a small area. While prey distribution certainly will affect foraging patterns, environmental conditions may influence how likely individuals are to locate and capture prey. Consequently, this may impact foraging patterns. In this study, over 70 % of wide-ranging trips were recorded during a 6-day period. It is possible that individuals tracked in this period were less likely to encounter prey early in trip due to the environmental conditions during this period. However, environmental data during this period were not assessed.

The two foraging patterns are comparable to the 'commuting' and 'looping' patterns described by Weimerskirch (2007). The looping pattern is thought to reflect a bird continuously searching for prey, while a commuting trip occurs when a bird travels to a known prey patch location (Fig 4.1.). These foraging patterns have been reported as individual-specific behaviours, and also as alternate strategies in one individual. Whether little penguins in Oamaru responded to temporally fine-scale environmental changes throughout the study period cannot be confirmed without fine-scale environmental data. Moreover, understanding whether individuals are behaviourally consistent could help to determine whether there is an intrinsic element to these behaviours. Further work could also investigate whether individuals undertaking wide ranging trips have reduced foraging efficiency compared to those conducting short range trips, as this could have implications for their reproductive success.

4.2 Foraging range

4.2.1 Trip level

Trip foraging areas differed between colonies. Individuals from the Creek covered a larger range per trip (mean 95% KUD 174.5 km^2), compared to OBPC birds (mean 95% KUD 82.5 km^2). In addition, Creek birds also had a larger core range per trip (Creek 52 km^2, OBPC 21.8 km^2). These range sizes are comparable to a study of little penguin foraging behaviour in Australia. Berlincourt and Arnould (2015) reported mean home range sizes between 93.5 km^2 and 207.7 km^2 for two colonies, with foraging areas (50% KUD) from 24.9 km^2 to 53.6 km^2. As was the case for trip distance parameters, the Creek colony had a wider range of foraging area sizes than the OBPC colony. The largest home range for an OBPC trip was 238.7 km^2, while on seven occasions Creek individuals exceeded 250 km^2.

Inter-colony variation in trip range has been reported previously among seabirds. European shags (*Phalacrocorax aristotelis*) exhibited differences between breeding sites in mean foraging area for individual trips. Individuals from the Ledge site at the Puffin Island colony in Great Britain had a mean foraging area almost twice as large as individuals at the Beach site 1 km away km away (Soanes *et al.*, 2014). Similarly, Cory's shearwaters from different sub-colonies less than 2.5 km apart varied in foraging areas. Mean foraging area was larger at one sub-colony, for 25, 50 and 75% kernel densities. The population home ranges from these sites were spatially segregated, and there were significant differences in SST and chl-α between their respective ranges (Ceia *et al.*, 2015b). These environmental covariates are proxies for ocean productivity, which can influence prey distribution, so variation in prey distribution may have influenced foraging behaviour and the size of the area explored during a foraging trip. Birds from the sub-colonies had the same potential foraging areas for single day trips, as is the case for the OBPC and Creek little penguin colonies which are

approximately 1 km apart. However, in contrast to the shearwaters, colony home ranges were not spatially segregated in Oamaru (see section 4.2.3 Range overlap). The larger mean foraging area at the Creek, for both 95 and 50% kernel densities, is possibly related to a higher occurrence of wide-ranging trips from Creek colony birds, compared to OBPC individuals. 10 trips were defined as wide-ranging, and 7 were recorded by Creek colony individuals. Birds that forage in a looping pattern on wide-ranging trips cover greater areas than birds foraging on short-range trips. In addition, the core range is spread more widely across the entire trip, with no localised feeding hotspot.

Often the mean foraging area per trip is not reported for little penguins, but rather just the population home range. This makes it difficult to determine whether individuals are exploring a large area in search of prey during each foraging trip or whether a large population home range is caused by individual penguins consistently foraging in different areas. For example, individuals may have a small foraging range per trip but often travel in different directions on different trips, so these individuals would contribute to a large population home range in comparison with birds that consistently foraged in a small area. Berlincourt and Arnould (2015) reported the mean home range and foraging area (95 and 50% KUD respectively) for little penguins at two colonies. Gabo Island individuals consistently had a larger mean home range and foraging area during the guard stage across three seasons, compared to their London Bridge counterparts. At Oamaru, Creek colony birds were foraging over a larger area per trip than their OBPC counterparts. The greater trip range arose from some individuals conducting wide-ranging trips, in which they travelled in a large looping pattern. The difference between colonies in the current study may reflect a difference between colonies during the year of the study, or a difference between colonies in foraging behaviour during the guard stage that is present each year. Alternatively,

differences between colonies in mean values may have been due to the chance inclusion of some wide-ranging trips by a small number of penguins. If it had been possible to have a much larger sample size, then there may not have been a significant difference between the colonies.

Soanes *et al.* (2014) highlighted the importance of a sampling regime which accounts for individual, temporal, and spatial variability within a population. The composition of the population sample and timeframe over which tracking is conducted affect foraging parameters. Tracking at both the OBPC and Creek colony has revealed greater variability among Oamaru penguins than would have been reported for just the OBPC site. For example, no trips greater than 20 km were recorded for OBPC birds. In addition, inter-colony variation in trip range was also observed. This highlights the importance of sampling individuals from multiple colonies, even when they are close together, to ensure total local variability in foraging behaviour is depicted. However, greater variability in foraging behaviour may have been recorded at the OBPC with a larger sample size. To limit confounding factors created by temporal variation in the marine environment, individuals were tracked from each site throughout the same period. However, as sampling was only conducted for one season, it cannot be determined whether the larger foraging area per trip at the Creek colony is a consistent characteristic of individuals from this site. Foraging ranges can vary between years among many seabirds. For example, mean home range size for little penguins varied significantly across three seasons at both Gabo Island and London Bridge. At Gabo Island, during the guard stage, individuals foraged over an area twice as large in 2013 compared to 2011 (Berlincourt and Arnould, 2015). Furthermore, demographic parameters such as fledge weights and median lay dates have varied between the OBPC and Creek colony in some years, but there were no differences between sites for data from 1994

to 2014 for these variables (Agnew and Houston, 2020). It is possible that this may be the case for foraging behaviours also. Future study should consider foraging in multiple years to determine whether Creek birds do indeed consistently forage over a larger area than OBPC birds.

4.2.2 Population level

There was a difference in population home range size between each colony. The Creek colony home range was 681.5 km ^{2} compared to the OBPC home range of 325 km^2. Both the northern and southern extents of each colony home range were similar. However, the eastern extent of the Creek home range was further from the coastline compared to the OBPC range. Some Creek colony individuals conducted trips with maximum distances >30 km from the coastline, resulting in a home range extending much further to the east than home ranges for OBPC birds.

Many studies have reported maximum or mean maximum distance from the colony as estimates for the potential home range radius. These methods may overestimate home range size, and do not illustrate focal areas within the potential range. Studies that do report home and core range usually report either a mean range size across all recorded trips, or a pooled population range, but not both. Both the OBPC and Creek population home range size falls within the range of values previously reported. Sánchez *et al.* (2018) reported guard stage home range sizes of 438 km^2 and 716 km^2 for two sub-sections of the colony at Phillip Island. However, these estimates were calculated from kernel densities of prey-capture locations only. A larger home range at Phillip Island than Oamaru could be expected, as 89% of the surrounding area is ocean, compared with 52% in Oamaru. In New Zealand, Wellington and

Buller populations had home ranges of 228 km^2 and 278 km^2 for single day trips during chick rearing, respectively (Poupart *et al.*, 2017).

Comparisons of range sizes between multiple studies are challenging as a variety of methods are used for the estimation of range sizes. Both sample size and sample composition can influence parameter estimates. Small sample sizes can underestimate the size of the population home range (Soanes *et al.*, 2013). Although the appropriate sample size may vary between species, previous studies of little penguins have possibly underestimated home range area due to small sample sizes. Soanes *et al.* (2016) extrapolated the sample home range size to create a population range size estimate. Foraging parameter estimates can depend on the age (Pelletier *et al.*, 2014) and sex of penguins (Soanes *et al.*, 2014) and can differ between sub-colonies (Sánchez *et al.*, 2018). Without a sample that represents a wide range of individual characteristics, home range size may be underestimated. In addition, tracking methodology can affect results. Preston *et al.* (2010) highlighted how GPS fix rates can alter foraging parameter estimates. A more rapid fix rate will allow more precise estimates to be made. However, there are trade-offs between fix rates and battery consumption. In contrast, Poupart *et al.* (2017) found no significant difference in the utilisation distribution calculated from data with a consistent GPS fix rate (how often a location is recorded) compared to data with fix rates ranging from 1 to 60 minutes. Furthermore, the choice of smoothing parameter can affect KUD estimates. Large smoothing parameters can 'over-smooth' and expand the area, while smaller values can 'under-smooth' and create smaller disjointed range estimates (Schuler *et al.*, 2014). Among little penguin studies, smoothing parameter selection has included the 'reference bandwidth' method, average ARS size, or selection based on visual inspection of the data (Poupart *et al.*, 2017; Carroll *et al.*, 2018; Sánchez *et al.*, 2018).

Therefore, when comparing studies, care should be taken when drawing conclusions about inter-colony differences.

Due to the large distances travelled by some Creek individuals, this colony had a home range larger than the available foraging habitat previously predicted for the Oamaru population (Chiaradia *et al.*, 2007b). This estimate was calculated using the mean maximum distance little penguins travelled on one day trips at Phillip Island (Collins *et al.*, 1999). The fact that part of the home range falls outside of this radius supports the results from Soanes *et al.* (2016) that this method may exclude parts of the home range area. However, the larger foraging area contrasts with the suggestion that this method will overestimate home range size for little penguins. Both colonies made wide use of the available foraging area by travelling in a range of different directions away from the colony. The northern and southern extents were approximately 20 km from the colony and the eastern extent for the Creek home range was > 30 km from the colony.

The use of the entire available foraging area contrasts with the results of Kowalczyk *et al.* (2015b), which showed little penguins foraged selectively within their potential range. It was suggested that penguins were targeting areas of high primary productivity. Indeed, the home range had higher levels of chl-α compared to the non-foraging area of the potential range. Furthermore, many studies show that the home range is often localised within a section of the full potential range. Habitat selection may be related to SST, chl-α (as a proxy for productivity) and water depth, and penguins may localise their foraging efforts in zones where prey abundance could be highest (Hoskins *et al.*, 2008). The extent to which a little penguin population spreads its home range throughout its full potential foraging zone can vary between years. Little penguins at London Bridge and Gabo Island foraged in a localised

zone during the 2011 breeding season, but dispersed more widely during 2012 and 2013, (Berlincourt and Arnould, 2015). Data from 3 to 5 years would be needed to determine if the wide foraging area reported in the current study occurs consistently from year to year. Data on ocean productivity or prey distribution surrounding the colonies could help to explain the wide distribution. Possibly the marine environment to the north, east and south of Oamaru is relatively consistent in terms of marine productivity. This was observed at Kanowna Island, where SST was consistent across the entire potential little penguin foraging zone (Hoskins *et al.*, 2008). However, productivity might be higher inshore. Agnew (2014) noted a trend for Oamaru penguins to forage inshore, where chl-α concentration was highest, in comparison with further offshore, but no significant correlation was found.

OBPC birds did however forage within an area smaller than their full potential range. These individuals remained further inshore and did not travel greater than 20 km from the coastline. Presumably, OBPC individuals are capable of travelling as far as Creek penguins and could reach the same offshore distances. Agnew (2014) tracked OBPC individuals travelling up to 35.2 km from the colony, with a maximum total distance of 75 km during single day trips and foraging locations that were outside the eastern boundary of the home range in the current study.

The limited sample size in the current study means that the home range estimate applies only to the studied birds during the study period in the study year. The home ranges of Oamaru penguins will differ between years, will be much larger during incubation than the guard stage of chick rearing, and are likely to be much larger in autumn and winter than during the guard stage. Although small sample sizes limit estimates of home range for seabirds with large home ranges, estimates for smaller foraging ranges are also affected by sample size

(Soanes *et al.*, 2013). For example, breeding European shags travel up to 30 km while foraging, so have a similar potential foraging range size as little penguins for single day trips (Soanes *et al.*, 2014). However, to represent the full area of active use of the population at a certain time of year, Soanes *et al.* (2013) suggested that at least 20% of individuals in a population should be tracked when only a single trip is recorded from each individual. This would represent approximately 60 and 40 individuals for the OBPC and Creek during the 2016 guard stage. However, multiple trips were recorded from many individuals, which may reduce the required sample size of individuals (Soanes *et al.*, 2013). The importance of recording multiple trips from different individuals to estimate the population home range may vary between species, along with the amount of variation within and between individuals. For example, individuals with high foraging site fidelity may reveal only a small portion of the total population home range, even if they are tracked multiple times. In this instance, with a larger sample size the wide arc of the OBPC range would be unlikely to change but the home range might extend further from the coast. Conversely, small sample sizes can also over-represent the importance of a single foraging track. Trips by one bird could lead to an area being highlighted as a hotspot despite no other individuals travelling to that region (BirdLife International, 2004). This can be seen in the Creek home range, as a section protrudes out to the east due to a single trip. A larger sample size would likely remove this zone from the home range if no other individuals travelled there. This excessive weighting of single trips could create differences in foraging areas between population samples that are not indicative of true population differences.

Due to the Creek home range extending further offshore, this range included water that was deeper than the OBPC home range. The OBPC home range was almost entirely in water < 30 m deep, whereas the Creek individuals foraged in water up to 50 m deep.

Although the home range was much larger at the Creek compared to the OBPC, the two colonies had a similar core range. The Creek core range was slightly larger than the OBPC, however it was localised in the same area, inshore and near each colony. Most of the core range was within water < 20 m deep and the mean depth was 16.3 m for both colonies. Similarly, little penguins breeding in different sub-colonies at Phillip Island exhibited differences in median home range depth, but not core range depth, during the guard stage (Sánchez *et al.*, 2018).

The locations of the core Oamaru ranges are similar to findings from Agnew (2014). During chick rearing in 2010, 2011 and 2012, most recorded GPS locations were in the home range estimated from the 2016 data. Little penguins in Oamaru are preferentially inshore, in shallow waters, near the colony. Colonies surrounded by deeper water often have reduced reproductive success, compared to colonies with shallow surrounding water (Chiaradia *et al.*, 2007b), presumably because food is more readily available in shallower water. Both Phillip and Motuara Islands have a high proportion of surrounding waters deeper than 20 m. Individuals from these sites exhibit high diving effort and low breeding success compared to individuals from Penguin Island and Oamaru, which have access to relatively shallow waters.

Little penguins make both benthic and pelagic dives. Although little penguins are capable of diving to depths up to 70 m (Ropert-Coudert *et al.*, 2006a), they are more likely to undertake benthic dives in shallow water (Preston *et al.*, 2010). When making benthic dives, the seafloor may act as a physical barrier, which penguins can use to entrap prey by reducing the prey species' field of escape (Ropert-Coudert *et al.*, 2006b). Benthic dives also tend to have a greater proportion of time spent on the bottom phase, the phase commonly associated with

prey encounters (Ropert-Coudert *et al.*, 2006b), than pelagic dives. In addition, prey capture for little penguins has been shown to be most efficient when fish aggregations are dense and occur in the top 20 m of the water column (Carroll *et al.*, 2017). In deeper water, prey aggregations may occur deeper than this and be more dispersed.

Although penguins in Oamaru did explore most of their available habitat, they mostly foraged in shallow water. Previous studies have suggested that the high fledging success in Oamaru may be related to food availability in nearby relatively shallow water (Chiaradia *et al.*, 2007b). Oamaru's coastal sea floor slopes gently away from the shore, so a large proportion of the available foraging area for penguins is < 20m deep and most foraging during the guard phase was in water < 20m deep. Prey distribution is the primary driver of foraging decisions, and little penguins have been shown to match the distribution of prey capture events to the distribution of their prey (Carroll *et al.*, 2017). Penguins are thought to conduct longer trips, travelling over a larger range in search of prey when it is scarce. Foraging near the colony indicates prey is most likely abundant nearby. The proximity of prey to the colonies has most likely benefitted the reproductive success here. Fledge weights and breeding success at both the OBPC and Creek are among the highest observed for the species (Agnew and Houston, 2020).

Despite the inshore core range, many Creek individuals did venture relatively far from the coast, raising the question of why some individuals would travel long distances from the colony if prey were abundant nearby. Future studies could investigate whether these longer, wide ranging trips correlate with any weather events or are primarily individual characteristics, and whether these individual penguins have lower foraging success when undertaking long compared with short trips.

4.2.3 Range overlap

Penguins from each colony foraged in the same areas and the estimated home and core ranges for each colony overlapped. Numerous seabird studies have shown that individuals from neighbouring colonies often forage in different areas. While data for close little penguin colonies are scarce, Sánchez *et al.* (2018) did report different foraging areas for sub-colonies at Phillip Island. Each population foraged preferentially in the area adjacent to their own colony. During guard and post-guard each sub-colony had different estimated core foraging ranges. However, foraging ranges were calculated from prey capture locations, rather than all locations traversed while foraging, as was the case in this study.

Distinct foraging areas for birds from adjacent colonies have been reported in several penguin species (Bolton *et al.*, 2019). For example, multiple colonies of neighbouring chinstrap and gentoo penguins exhibited greater intra-specific segregation between colonies, compared to inter-specific segregation (Lee *et al.*, 2021). However, this behaviour is not ubiquitous within taxonomic groups. For example, European shags breeding around Britain and Ireland did not exhibit spatial segregation between breeding colonies, although other *Phalacrocorax* species did (Wakefield *et al.*, 2017).

The hinterland model, proposed by Cairns (1989), suggests that the foraging areas of adjacent colonies will be separate, and that individuals will forage closer to their own colony than to their neighbours' colony. However, this does not always occur. For example, Ainley *et al.* (2004) found that the degree of overlap between adjacent Adelie penguin colonies varied depending on the size of the colonies. Pairs of small colonies showed greater foraging area overlap, compared to medium sized colonies, and segregation was more common for large than small colonies. A density-dependent model has been proposed which considers the sizes

of the colonies and their distance from each other (Wakefield *et al.*, 2013). Independent foraging areas are thought to be driven by inter-colony competition. The degree of competition is a function of the size of each colony, the distance they are apart, and the abundance and distribution of prey. Large colonies close to each other that have low prey abundance in the adjacent ocean will experience higher competition, whereas smaller colonies experiencing little inter-colony competition may not segregate their foraging ranges. The Oamaru colonies are very close to each other and are relatively small, although they are among the largest little penguin colonies in New Zealand. Colonies in Australia, such as at Phillip Island, may have over 25 000 individuals (Sutherland and Dann, 2014). The OBPC and Creek colony had 144 and 103 breeding pairs respectively, during the 2016 breeding season. Competition between sites may not be strong enough to drive inter-colony segregation. In addition, it is likely that prey is abundant surrounding the Oamaru sites. Both the OBPC and Creek colonies have high reproductive success, early lay dates, and heavy chick fledge weights, compared to other colonies (Agnew and Houston, 2020). These positive demographic parameters likely reflect a favourable marine environment. In addition, pre-breeding tracking in a single year has shown little penguins in Oamaru can remain close to the colony when free of breeding constraints (Agnew, 2019).

Foraging overlap between neighbouring colonies may occur within areas of high productivity (Bolton *et al.*, 2019). Foraging in these zones of high prey abundance could provide a net benefit in energy gain, compared to foraging in areas of lower productivity, despite greater competition with conspecifics in these areas, compared to areas where foraging areas do not overlap. However, studies often describe colonies which generally exhibit segregation, but overlap in distant areas at foraging hotspots (Ramos *et al.*, 2013; Paredes *et al.*, 2014). In the

current study, little penguins foraged in the same area very close to their respective colonies, indicating that prey was probably abundant near the colonies.

4.3. Diving parameters

There were no differences between colonies in mean values of diving parameters (dive depth, duration, bottom-time, proportional bottom time, dive effort, total diving duration, vertical distance, diving rate, and the number of dives per trip). The mean dive depth of approximately 10 m falls within the range of previously reported dive depths for little penguins. Mean dive depth differs between years at Oamaru. For example, between 2010 and 2012 median dive depth ranged from 5.06 to 12.67 m during chick rearing (Agnew, 2014). Chiaradia *et al.* (2007b) reported mean dive depth of 5 m during the guard stage at Oamaru in 2000. Mean dive depth varied significantly between years at both Gabo Island and London Bridge from 2011 to 2013 (Berlincourt and Arnould, 2015). Mean dive depth during the guard stage varied across five weeks at Phillip Island, indicating that diving behaviour changes in response to short term environmental variation. Phillip Island individuals dived deeper than their Penguin Island counterparts and this was thought to be related to differences between colonies in the depth of water near each colony (Chiaradia *et al.*, 2007b).

Mean dive depth varied during the day for penguins from both colonies. Dives were deepest near midday, and shallowest at the beginning and end of a foraging trip. Little penguins are visual predators that need sufficient light to see their prey. Under experimental conditions, the number of prey pursuits and captures was positively correlated with light levels (Cannell and Cullen, 1998). Dive depth appears to be associated with light levels for many penguin species. Deeper dives often occur near midday, with overnight diving shallower and rare

(Wilson *et al.*, 1993). This pattern has been reported for little penguins previously (Mattern, 2001). As light can penetrate the water column further at midday than earlier or later in the day, little penguins could hunt successfully at greater depths in the middle of the day. Diving depth is also influenced by the water depth as penguins swim away from the shore in the morning and return to the shore in the evening. Analysis of dive data from long term trips, where penguins begin diving when they are already in deep water could reveal if light influences dive depth throughout the day.

Whilst mean dive depth was greater in this study than in Oamaru in 2000, dive efficiency was similar (Chiaradia *et al.*, 2007b). Approximately 15% of a dive cycle (dive duration + post-dive interval) was spent in the bottom phase, compared to 14 ± 4% in 2000. A high proportion of time spent in the bottom phase is typically considered as an efficient form of diving, as individuals spend more time in the hunting phase of a dive, rather than in transit to and from hunting depths or resting on the surface (Ydenberg and Clark, 1989; Ropert-Coudert *et al.*, 2006b). However, a scenario where penguins capture prey relatively quickly once at the bottom could be less energetically demanding than one where prey was pursued throughout a long bottom phase. For example, king penguins had greater bottom durations during the winter, when prey density is lowest, compared to spring (Charrassin *et al.*, 2002). Dive duration was the same and the mean post-dive interval was shorter in winter, so dive efficiency was greater in winter than in spring. However, this could represent greater search effort during a period of low prey availability. At Phillip Island during the 2004 breeding season, little penguins with large dive loggers spent a greater proportion of time in the bottom phase of a dive compared to penguins with small loggers attached (Ropert-Coudert *et al.*, 2007). Birds with large loggers could have been less effective at hunting due to hydrodynamic drag, so spent longer in the bottom phase pursuing prey than birds with small

loggers. Measures of prey capture success from accelerometery data or video loggers could help clarify this index of efficiency.

There were approximately 1 000 dives per trip for penguins at Oamaru in 2016. This number was greater than the mean and median number of dives per trip previously reported at Oamaru (Mattern, 2001; Agnew, 2014). The number of dives can be highly variable between years, seasons and within seasons at a single colony. The mean number of dives reported in this study reflects only behaviour during the sampling period, rather than for each colony long term, and does not indicate diving behaviour throughout the breeding season. Agnew (2014) reported the number of dives per trip at the OBPC increased throughout the breeding season, particularly in 2010, and Pelletier *et al.* (2012) reported that the mean number of dives per trip during the guard stage changed over five weeks at Phillip Island.

The number of dives per trip negatively correlated with the mean dive duration for a trip. When penguins dived more often, they tended to dive for a short duration and to a shallow depth throughout the trip, relative to trips with very few dives. An increase in median dive depth was associated with decreased number of dives per trip during the 2005 breeding season at Phillip Island (Zimmer *et al.*, 2011b). Amélineau *et al.* (2021) reported that as the breeding season progressed, little penguins dived more frequently, but also for a shorter duration and to shallower depths, than earlier in the season. Similarly, in this study there was a negative correlation between date and mean dive duration and depth per trip, and a positive correlation with date and the number of dives per trip. Throughout the study, penguins tended to dive more frequently, but for a shorter duration and to shallower depths, compared to at the beginning of the sampling period. Foraging behaviour is inherently related to prey distribution. It is possible that changes in prey distribution throughout the study period

influenced a change in diving behaviour. If penguins are not diving deeply, they will be able to dive more often. Further study on prey distribution, and environmental variation, including changes in thermal stratification of the water column throughout the breeding season, could be valuable to determine the ecological processes that influence diving behaviour in Oamaru.

Total vertical distance travelled per trip was approximately 20 km at each colony (mean values OBPC 20.4 km and Creek 18.3 km). Mean total vertical distances of 15 to 18 km were reported for male or female little penguins at Phillip Island (Pelletier *et al.*, 2014). Hoskins *et al.* (2008) reported that vertical distance travelled per hour multiplied by the mean trip durations gave total distances of 13 to 15 km at Rabbit, Kanowna and Phillip Islands. While vertical travel distances were longer in Oamaru, previous measures have been calculated from dive depths and have not included all vertical movements that have occurred during the bottom phase. Total bottom phase movements ranged from 0.6 to 4.2 km (mean 2.3 km) in the current study, so total vertical distances in the current study were comparable to those reported in previous studies. In addition, this result highlights an often-overlooked aspect of the vertical distance travelled, the movements of bottom phase undulations, which may be substantial for some foraging trips.

4.4. Limitations of GPS loggers

GPS loggers were used to record the location data for this study. The use of GPS loggers has become widespread among seabird tracking studies. They provide precise estimates of location, and with technological developments and reduction in battery size and weight, these devices can be fitted to smaller species, such as little penguins. Furthermore, data loggers often provide additional information on foraging behaviour, such as diving activity, or

environmental data, such as temperature. However, data collected with GPS loggers can have limitations, particularly for diving animals. To record locations, GPS devices communicate with satellites. When signals are received from multiple satellites, a location can be triangulated. Penguin GPS devices do not receive satellite signals when the devices are under water, so fewer locations are obtained when penguins are diving frequently than when they are on the surface of the water. Failure to obtain satellite fixes means that GPS fix rates (how often a location is recorded) can occur less often than they are programmed for, and that often large gaps in data will occur with locations not recorded for prolonged periods. Multiple studies on little penguins have reported these problems with GPS data (Carroll *et al.*, 2016; Carroll *et al.*, 2018; Phillips *et al.*, 2019). While little penguins will repeatedly dive when searching for or pursuing prey during diving bouts, they also conduct shallow dives while commuting to and from their colony, and while travelling throughout the day. Therefore, much of a foraging trip is spent underwater, which can significantly reduce the effectiveness of GPS tracking devices. In this study, programmed fix rates varied from 1 to 5 minute intervals, and actual fix rates were often much less and large gaps between GPS fixes occurred occasionally. This can have implications for the analysis of foraging behaviour. For example, among little penguins tracked with GPS loggers from the St Kilda breakwater, the estimated size of the foraging area and the total distance travelled varied between samples with different GPS fix rates (Preston *et al.*, 2010). In addition, large gaps in location data could result in key foraging areas being overlooked, especially if these areas are associated with a high diving rate when GPS fixes were infrequent. Moreover, the importance of certain areas could be overestimated if a high proportion of total fixes are recorded at a specific location, but do not represent the proportion of actual time spent foraging there.

Programmable features on GPS devices can often help to reduce the incidence of gaps in GPS data. For example, the Axy-trek devices used in this study have an 'off time', which causes the device to stop searching for satellite signals if they failure to acquire a GPS fix in a given time frame. For diving animals, failure to obtain a fix is a common occurrence, and a long 'off time' will cause large gaps in the data to occur more frequently than a short 'off time'. However, such settings are a trade-off between battery consumption and more GPS fixes. In this study, GPS fix rate was set to continuous for 3 deployments. This recorded a GPS location once per second and resulted in fewer gaps in the data. However, it did not eliminate the problem. In addition, battery life was limited, with fewer tracks recorded for these deployments. Settings that could be adjusted to extend battery life included using a movement threshold, which prevents data from being recorded if the bird is not moving, such as when it is in a nest box. In addition, ensuring that the time between device attachment and the beginning of a foraging trip is minimised can help to reduce wasted battery consumption while the bird is not foraging. In this study, the beginning of a foraging trip could be predicted, as little penguins alternate daily between nest attendance and foraging during the guard stage. During all other times of the year, predicting the beginning of a foraging trip is not possible. Furthermore, device settings should be programmed to collect the type of data that is needed for the study. For example, it may be beneficial to obtain multiple days of location data, or to obtain high resolution location data for a single trip. This will vary depending upon the research questions.

After data is collected, GPS gaps are often minimised by interpolation. Interpolation is when locations are estimated along a linear path between two known locations. When the time between two points is known, the estimated locations can be plotted at any chosen rate to replicate the path an individual may have taken. In the current study, points were

interpolated at a rate of 1 per minute between known locations. This was the intended fix rate for most trips and matched the data from other sections of a track where gaps did not occur. Interpolation can be valuable for estimates of home range using kernel utilisation distribution, as was done in this study. The interpolated locations will reduce bias towards the observed locations. If there are many gaps in the data, the recorded locations will not reflect where penguins spent most of their time, but simply where most fixes occurred. Also, interpolated points between large gaps may not provide accurate locations, as it is unlikely that individuals travel in a linear path for extended periods. Instances where a gap was greater than 50 % of the total trip duration were not interpolated, and these tracks were excluded from analyses.

5. General discussion

This study is the first to compare the foraging behaviour of neighbouring little penguin colonies. Foraging behaviour has been reported to differ between little penguin colonies in New Zealand, with these differences attributed to local environmental conditions at each site. The current study investigated whether there are differences in foraging behaviour between nearby colonies at Oamaru. The Oamaru Blue Penguin Colony is run as a tourism operation, while the Oamaru Creek Penguin Refuge acts as a control site so potential impacts of tourism on the Oamaru Blue Penguin Colony can be assessed. While demographic parameters have been reported for each population (Agnew and Houston, 2020), this is the first time that the foraging behaviour has been compared at the two colonies.

In general, the foraging behaviour of little penguins did not differ between the OBPC and Creek colony during the 2016 guard stage. However, mean values of some foraging parameters differed between colonies. This included trip duration, the return time to the colony and the size of the trip foraging area. Trip return times can vary markedly between birds on a single night, and whether there was a true difference between colonies in arrival times was unclear due to the limited sample size. The relatively small sample at each colony, a small number of wide-ranging trips from the Creek colony increased the mean value of the foraging range, but wide-ranging trips were not characteristic of all birds at the Creek colony. The difference between colonies in mean range per trip may not reflect actual differences between colonies.

Neighbouring seabird populations of conspecifics often have independent foraging areas. This is thought to reduce intra-specific competition (Bolton *et al.*, 2019). While little penguin sub-colonies have been shown to have independent foraging areas at Phillip Island

(Sánchez *et al.*, 2018), this was not the case in the current study at Oamaru. When neighbouring seabird colonies have independent foraging areas, this is often attributed to high inter-colony competition. It is suggested that intra-specific competition was not high for penguins from the two Oamaru colonies during the 2016 guard stage. This is supported by the high adult survival rate, breeding success and heavy fledge weights reported for individuals at each colony (Agnew and Houston, 2020). As these populations continue to grow it is possible that intra-specific competition will increase, which may alter foraging patterns.

5.1 Major conclusions

The goal of this study was to determine whether there was a difference in foraging behaviour between OBPC and Creek colony individuals, and to determine whether individuals from each colony foraged within the same area during the 2016 guard stage. The major conclusions from this study are:

1. The mean maximum distance travelled away from the colony and mean total distance travelled per trip did not differ between the OBPC and Creek colony. Birds are limited by the constraints of chick rearing during the guard stage and cannot regularly travel further during single day trips than the mean distances at Oamaru.

2. All trips were day trips in which birds departed in the morning and returned in the evening. There was a difference between colonies in the mean trip duration, which was slightly longer for Creek colony birds than for OBPC individuals. The mean return time to the colony after a foraging trip was later for birds at the Creek colony. Time spent foraging did not however differ between colonies.

3. Two foraging patterns were observed; a short-range pattern where birds remained near their colony all day, and a wide-range pattern where birds travelled further from the colony in a large, looped pattern.

4. The mean foraging range per trip was greater for the Creek colony compared to the OBPC. The greater mean foraging range for the Creek colony arose from a small number of wide-ranging trips by Creek birds but almost no wide-ranging trips by OBPC birds. Wide-ranging trips are unlikely to be characteristic of individuals from the Creek colony, so the difference in mean values may not represent a true difference between colonies.

5. The foraging ranges of the colonies overlapped, with no distinct colony foraging areas. The absence of independent foraging areas suggests that competition between birds of the two colonies for food resources may have been low in Oamaru during the 2016 guard stage.

6. The mean values of all diving parameters did not differ between the OBPC and Creek colonies

7. Individual trips varied considerably in both distances travelled and in diving behaviour.

5.2 Future studies

While foraging behaviour during the 2016 guard stage did not differ between the two colonies in Oamaru, general conclusions about foraging behaviours for each colony cannot be

made from data from one stage of the annual cycle in a single year. Little penguins vary in foraging behaviour between years and between stages of the annual cycle. Studies of foraging behaviour at different times of the year for several years are needed for conclusions to be drawn about the presence or absence of differences between colonies in foraging behaviour.

While no difference was observed in travel distances, studies of both colonies at other stages of the breeding cycle and at other times of year, when little penguins are not constrained by the need to feed chicks daily, will be valuable.

While there were differences in the mean return time and trip duration between Creek colony and OBPC birds, arrival times can vary markedly on any given night, the small sample size used in this study may not provide a reliable estimate of mean arrival times at each colony. Previous studies of little penguin arrival times have had markedly larger sample sizes than those possible in the current study. The initial and peak arrival times for individuals at each colony should be studied further, to determine if there are differences between colonies in arrival time that are consistent across breeding stages and between years.

There was considerable individual variation in foraging trips, with variation between trips made by individual penguins and variation between penguins. For example, on some trips individuals travelled over twice as far or dived twice as often compared with other trips. Furthermore, two trip types were reported, short-range trips and wide-range trips. Individuals that encounter prey early in the trip are probably more likely to remain near the colony, compared to individuals that do not encounter prey early on. However, future studies could investigate whether there were relationships between individual differences in foraging

behaviour and individual differences in foraging success, whether behaviours are consistent within individuals, and relationships between behaviours and environmental variables.

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