Locating productive sea areas using seabird foraging aggregations
（海鳥採餌群を用いた高生産性海域の特定）

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Chapter 1 General Introduction

1.1 MARINE IMPORTANT AREA

Anthropogenic stresses in marine environment, i.e. fisheries (Tull & May 1972; Yatsu et al. 1993; Scheffer et al. 2005; Smith et al. 2011) and pollution (Piatt et al. 1990; Elliot et al. 2013; Gall et al. 2015) etc., are ubiquitous over coastal, shelf and high seas (Halpern et al. 2007), and impact the diversity of top predators (Tittensor et al. 2010). Marine top predators, such as seabird and sea turtles that breed on land, are also affected by harvesting (mostly historical), introduced predators and land development (Duffy 2010; Hume 2012). Management of these anthropogenic stresses is in progress on land but not in the high sea because of a lack of information and practical techniques (Weaver & Johnson 2012). To provide sufficient information to national and international organizations and enable these organizations to conserve marine biodiversity, Convention on Biological Diversity (CBD) and National Biodiversity Strategic Action Plans (NBSAPs) recommend establishing Ecologically or Biologically Significant Areas (EBSAs). EBSAs, being identified by seven criteria (**Table 1-1**), are used to support and encourage the use of area-based management tools, such as marine protected areas (MPAs) or activity-specific management zones including areas to be avoided, particularly sensitive areas, fishing gear restriction zones, or closed areas. (Johnson et al. 2018)

Biological productivity and diversity are key to EBSAs. Although chlorophyll *a* concentration and Particulate Organic Carbon (POC) flux have been used to identify EBSAs as the productive areas (Lavoie et al. 2008; Clark et al. 2014), the important information related to trophic energy flow still remains scarce. For an example, the seamounts in the region where POC flux is high could be a candidate for an EBSA (Clark et al. 2014), but the information on consumers is not available at the scale of each seamount (Kitchingman et al. 2008). Satellite- based surface chlorophyll *a* concentration is helpful to identify productive areas globally but the maximum values of chlorophyll *a* concentration often occur in subsurface that can't be detected directly by satellite (Furuya et al. 1990; Barlow et al. 2002). Key components of marine food web, such as copepods and myctophid, are mainly distributed in deeper layers (Hunt et al. 2013; Pitcher et al. 2007) and hence can't be detected by remote sensing. The areas of high primary production in the surface layer do not always correspond with those of abundant consumers (Grémillet et al. 2008). Furthermore, although the marine biological productivity is associated with the biomass of forage fish (Grados et al.

2014), schools of forage fish are ephemeral (Clua et al. 2001). Because of these reasons, identifying productive marine areas is challenging especially in the high seas. Only three (11%) out of 32 EBSAs were identified following the criteria of biological productivity (Johnson et al. 2018).

Information on biological diversity is not sufficient in the high seas. Data on top predators are collected through fisheries activities: harvest (Christensen et al. 1996) and by catch (Tittensor et al. 2010). These fishery-based data are highly biased towards potential target species and areas of high fishing efforts (Chrysafi et al. 2016). Scientific censuses of whales, sea-turtles and seabirds have been carried out intensively but the areas covered have been limited (Bovery et al. 2015; Nowacek et al. 2016). To identify the areas of special importance for various life-history stages of different species and to connect these areas, the network system requires development based on a larger data base of migration routes of different groups of marine organisms (Johnson et al. 2018; Dunn. et al. 2019). However, most of the candidates were not evaluated as EBSAs due to a lack of information (Johnson et al. 2018). Affordable and convenient methods need to be developed for global and long-term data collection.

Table 1-1 Criteria and definition of each criterion of Ecologically or Biologically Significant Marine Areas (EBSA) (http://gobi.org/ebsas/).

NO.	Criteria	Definition
1	Uniqueness or rarity	Area contains: (i) unique, rare or endemic species, populations or communities and/or (ii) unique, rare or distinct habitats or ecosystems and/or (iii) unique or unusual geomorphological or oceanographic features
2	Special importance for life-history stages of species	Area that is required for a population to survive and thrive
3	Importance for threatened, endangered, or declining species and/or habitats	Area containing habitat for the survival and recovery of endangered, threatened, declining species, or areas with significant assemblages of such species
4	Vulnerability, fragility, sensitivity, or slow recovery	Area that contains a relatively high proportion of sensitive habitats, biotopes or species that are functionally fragile (i.e., highly susceptible to degradation or depletion by human activity or by natural events) or with slow recovery
5	Biological productivity	Area containing species, populations, or communities with comparatively higher natural biological productivity
6	Biological diversity	Area contains comparatively higher diversity of ecosystems, habitats, communities, or species, or has higher genetic diversity
7	Naturalness	Area with a comparatively higher degree of naturalness as a result of the lack of or low level of human-induced disturbance or degradation

1.2 SEABIRDS AS INDICATORS

The areas of high density of seabirds can represent high energy flow through the food-web because they consume more energy per unit of body mass than fish, and they search productive areas efficiently (Sydeman et al. 2006; Watanuki et al. 2018), thus meeting the requirements of EBSA criterion 5, i.e. biological productivity. Since seabirds can detect small prey patches over large areas, they are well associated with the areas where the density of prey is increased at a 10 km scale (Hunt et al. 1990; Burger et al. 2004; Mehlum et al. 1999; Fauchald et al. 2000; Erikstad et al. 1990). The usage of these areas can be highly stable over a long period of time (Davoren et al. 2003; Sigler et al. 2012; Davoren 2013).

As the areas of high density of seabirds represent the presence of other marine top predators (Thiers et al. 2014), seabirds are also considered an indicator of high biodiversity (criterion 6). In fact, the areas highly used by seabirds have shown to be also used by whales, dolphins, sea-turtles, sharks and tunas (Croxall et al. 2002; Carman et al. 2016; Miller et al. 2018; Thiers et al. 2014; Raymond et al. 2014). Those areas included various seascapes: seamount, continental slope, and upwelling and front regiones (Kaschner 2007; Thompson 2007; Lascelles et al. 2012; Santos et al. 2008; Stocks et al. 2008; Duffy et al. 1983; Scales et al. 2014, Bost et al. 2009). Furthermore, surface-feeding seabirds depend on sub-surface feeding divers including such as penguins, whales and tunas that chase and collect prey to the surface (Clua et al. 2001; Au et al. 1986; Camphuysen et al. 1999; Hodges et al. 1994). Therefore, foraging aggregations of surface-feeding seabirds should indicate the existence of subsurface predators and also are indicative of areas of high biological diversity. In addition, 43% of seabird species are categorized as endangered on the Red List (Dias et al. 2019; Phillips et al. 2023), so the information on these species helps for establishing critical habitats (criterion 4). Most of seabirds migrate between breeding areas and non-breeding areas often 100-6000 km apart, which cover large oceanic areas (McDuie et al. 2016; van Bemmelen et al. 2017; Kentie et al. 2023). Thus, these breeding and non-breeding areas connected by migration routes, are expected to reveal information of special importance for the life-history stages of species (criterion 2), providing connectivity access for all sea areas and forming the EBSAs network (Johnson et al. 2018).

Seabirds are easily observed above the surface from the boats. Because they breed on land, it is easy to deploy biologging devices to measure the activity during foraging trips

in the breeding season and migration in the non-breeding season. They live and breed for multiple years, thus they may increase the ability to search, find and exploit prey patches that are persistent at some extents through experience (Irons 1998, Davoren et al. 2003). They can also be easily accessed during breeding seasons. Therefore, their diets and breeding success are easy to monitor and help understanding the changes in ecosystems (Cairns et al. 1987; Frederiksen et al.2007; Parsons et al. 2008). Databases of seabirds are usually more extensive than other taxa and is more stable and easier to update, so that they can provide data for longer periods (Lascelles et al. 2012). Among seabirds, surface-feeding species are observed easily above the sea, hence suitable as an indicator of EBSA.

1.3 TECHINICAL DIFFICULTIES

Information on the at-sea density of seabirds is mainly collected through boat/aerial surveys and tracking surveys. However, there are problems with these approaches, sometimes making it difficult to apply for the identification of EBSA. First, there are inevitable errors or biases in boats/aerial surveys (Ronconi et al. 2009; Spear et al. 2004). Visibility is affected by bad weather (Hyrenbach et al 2007) and low illumination conditions (Camphuysen et al. 2004). Some bird species are attracted to boats while others avoid them (Spear et al. 2004). Most studies can cover only a small part of the ocean (Mott et al. 2018). Direct observations of highly mobile seabirds are usually limited in terms of space and time coverage, so may be carried out on subset of the larger population. In the boats/aerial censuses, sex, age, breeding colonies and reproductive status of individual birds remain mostly unknown. These different sections of the population of a species are affected differently by environmental factors (Fay et al. 2015; Kazama et al. 2018). This intra-species variation in responses to environmental change causes the bias in the prediction of the habitat model. Yamamoto (2015) combined tracking and boat surveys to alleviate this problem; however, the data from the ship survey is relatively small, which may still cause bias. Due to the high cost and various policies, however, boat surveys are difficult to carry out periodically and globally (Johnson et al. 2018)

Density of seabirds and prey correlate with each other at some scales in some regions but not at other scales in other regiones (Benoit-Bird et al. 2013; Decker et al. 1996; Veit et al. 1993; Logerwell & Hargreaves 1996; Swartzman & Hunt 2000). Intensity of these associations depends on the time of day, season, region, seabird species, prey types, prey density, etc., and in some cases seabird density does not correlate with

productivity (Safina et al. 1985; Decker et al. 1996; Becker et al. 2003; Ainley et al. 2009; Kurasawa et al. 2011). When seabirds are in the staging phase during the transit to and from the foraging area, the migration, or the roosting/resting phase, the density of aggregation can be high (Camphuysen et al. 2012; Dean et al. 2013). Therefore, those areas with high seabird density can be misidentified as EBSAs (Camphuysen et al. 2012). Boat census and GPS tracking give the information on the density of seabirds but not always the intensity of foraging activity. Thus, the evaluation of energy flow through seabirds using these techniques is not accurate enough. Locations of foraging areas are more critical and provide direct information for identifying EBSAs. Furthermore, GPS tracking does not give information on the numbers of conspecifics members and other species along the tracks. To estimate density, track lines of sample individuals are assumed to represent that of the population.

1.4 IMPORTANCE OF FEEDING AGGREGATION

The density of seabirds does not always match with prey density (Grémillet et al. 2008). In addition, seabird density may indicate the spatial pattern of prey consumption, although the accuracy is not high (Barrett et al. 2006). The fine scale spatial pattern of the amount of prey consumed by seabird should give direct information on the productivity, and can provide robust data for identifying EBSA. To explore the spatial pattern of the prey consumption, a study of feeding aggregations will be a key, because prey consumption per individual can be much higher in individuals feeding in aggregation than those feeding solitary as below. A “feeding aggregation” is an aggregation of individuals including one or more species that feed over a prey patch. Feeding aggregation of seabird sometimes include the subsurface top predators such as whales, dolphins, tunas and sharks.

Rate of encounter with individual prey or prey patch can be greater when seabirds forage in aggregation. In order to form foraging aggregation, surface feeding seabirds fly or stay on the sea at the positions where they can exchange information with other members, which can enhance the efficiency of searching prey patch. In general, larger aggregations of seabirds are formed over larger fish schools (Manisicalco et al. 1998). The number of feeding attempt and the feeding success (amount of prey capture per unit time) of individuals are higher when seabirds feed in aggregations than solitary and higher when larger number of birds are in aggregation (**Table 1-2**). Feeding success reached a ceiling and decreased in aggregations larger than the optimal size due to interference among individuals and disturbance to the fish school (**Table 1-2**). For

example, the feeding efficiency of little egrets (*Egretta garzetta*) and intermediate egrets (*Egretta intermedia*) decreased when the size of aggregations increased to greater than 10 (Huang et al. 2021). Seasonal changes in species composition (Anguita et al. 2015) also affect the feeding success (**Table 1-2**). Porter (1981) found that juvenile seabirds had lower feeding success than adults and did not initiate feeding aggregations but tended to join.

Studies on terrestrial birds have shown that birds are more likely to form aggregations when resource availability is low, and prey are dispersed (Hino 2009; Hobson et al. 2006). When the average density of prey species (krill or fish) is high, the schooling behavior of prey species increases visibility to their predators, seabirds, over the sea surface. When the average density is low, schooling behavior may reduce the likelihood of being detected by seabirds. In the latter case, seabirds may be able to find the schools of krill or fish by joining other seabirds already making a feeding aggregation over the schools of prey. Surface-feeding seabirds are attracted to visual cues such as brightness (Kushlan 1977) and specific behaviors such as flying in circles (Hoffman et al. 1981) and hovering of conspecifics, which is known as local enhancement (Harrison et al. 1991; Hoffman et al. 1981; Buckley 1997). Local enhancement (coloniality concentrates foragers in space, which leads to more rapid discovery of food patches; Buckley 1997; Camphuysen & Webb 1999; Garthe 2004) is a mechanism to increase the feeding rate (Thiebault et al. 2014; Seal 1973; Buckley 1997; Grünbaum et al. 2003; Götmark et al. 1986; Manisicalco et al. 2001; Sutton et al. 2020), it is considered as adaptive response to feed fish or krill school (Grünbaum & Veit 2003). The increase of the rates of prey encounter, feeding attempts or feeding success in feeding aggregations are generated by the local enhancement and the cooperation of multiple species. The durations of foraging bouts, aggressive foraging behaviors, and hovering time usually increase with aggregation size (Grünbaum et al. 2003; Bayer 1983). Diving seabirds force fish schools to the surface and form a high-density aggregation in the shape of a ball, and forage these schools of fish (Clua et al. 2001), so they forage efficiently in aggregations than in solitary conditions (Sutton et al. 2020). Competing behaviors are seldom observed in these foraging aggregations with diving seabird, indicating that stabilization effect of diving seabird outcompetes the negative effects of interference among individuals and disturbance to fish school, prey is abundant to satisfy all members (Sealy 1973) or available for too short period to induce aggressive interactions (Hoffman et al. 1981).

Dark-colored small diving species such as alcids and penguins maintain fish schools intact while light-colored and medium sized surface-feeding seabirds including gulls, terns, and shearwaters, trigger the formation of aggregations and increase their size (Hoffman et al. 1981; Camphuysen & Webb 1999). The divers and surface-feeders are likely to benefit each other by feeding in aggregations as divers force prey schools to the surface while surface-feeders track the movement of prey patches and can prevent the prey from escaping out of the water (Schneide et al. 1990; Grover et al.1983; Mills 1998). In addition, kleptoparasites such as parasitic jaegers (*Stercorarius parasiticus*) steal prey from other birds and suppressors such as cormorants decrease prey availability quickly (Hoffman et al. 1981, Manisicalco et al. 2001). Generally, divers come to the fish school first, then surface-feeders join the aggregation, then kleptoparasites or suppressors come (Hoffman et al. 1981; Camphuysen & Webb 1999). The rate of feeding attempts of catalysts decreases when kleptoparasites and suppressors join the aggregations (Hoffman et al. 1981; Camphuysen & Webb 1999).

Seabirds usually forage in feeding aggregations (Camphuysen et al. 1999; Chilton et al. 1987; Hoffman et al. 1981; Veit et al. 1993; Assali et al. 2017; Evans et al. 1982). For instance, 76% percentage of Parkinson's petrel feed in aggregations (Manisicalco et al. 2001). The most seabird species fed in large multi-species aggregations around Réunion Island, especially when they fed with sub-surface predatory fish (Jaquemet et al. 2004). During at sea census onboard Oshoro-maru around Aleutian Islands in the Bering and Chukchi Seas in June-July 2018, seabirds were counted in 300m x 300m grid (Hayashi et al. Unpublished). Top 5 of mostly seen foraging species were used for their analysis, fork-tailed storm-petrel (*Oceanodroma furcata*), Northern fulmar (*Fulmarus glacialis*), red phalarope (*Phalaropus fulicarius*), sooty (*Puffinus griseus*) and short-tailed (*Puffinus tenuirostris*) shearwaters. While 197 foraging aggregation comprised single species, 68 comprised multiple species. As to individuals, 88% (526/599) of fork-tailed storm-petrel, 90% (1173/1310) of Northern fulmar, 99% (155/156) of red phalarope, 97% (110/113) of sooty shearwater, 75% (40/53) of short-tailed shearwater were foraging in aggregation. Fork-tailed storm-petrel and Northern fulmar foraged together in most of the mix-specific foraging aggregation, while in 7 aggregations, they also foraged with red phalarope (*Phalaropus fulicarius*) or short-tailed shearwater. Sizes of single -specific foraging aggregation were shown in **Fig. 1-1**. More than 80% of the on-water seabirds were defined as aggregation (more than 2 birds foraging within a 300 m block). Thus, feeding aggregation appears to be the main feeding strategy for seabirds.

Table 1-2 Foraging behaviors of seabirds and marine mammals in foraging aggregations and factors facilitating foraging aggregations that increase the prey encounter rate and feeding attempt/ success rate of individual birds.

Predator species	Prey species	Sea area	Period	Feeding behaviours and characteristics of foraging aggregations	Reference
Cape Gannets *Morus capensis*	Sardines *Sardinops melanostictus*/Anchovies *Engraulidae*	South coast of South African	December to January, 2010-2011	Dive rate increased together with the number of birds but decreased in large flock (>200 individuals)	Thiebault et al. 2014
Cape gannets *Morus capensis*, long-beaked common dolphins *Delphinus capensis*	South American pilchard *Sardinops sagax*	East coast of South Africa	June - July, 2005	The success rate was increased with the number of birds in the flock. The occurrence of attack before diving increase success rate. Fish school was disorganized by successive attacks. The success rate was higher in plunging than pursuiting. Success rate was not affected by the number of fishes in school.	Thiebault et al. 2015
Black-headed Gull *Larus ridibundus*	Common bleak *Alburnus alburnu*	Pool	/	If the flock size was <10 individuals, plunging rate and success rate increased with flock size. Larger predator flock size increases success rate.	Götmark et al. 1986
Black-browed Albatross *Diomedea melanophris*	Antarctic krill *Euphausia antarctica*	South Atlantic	Summer of 1986	Flock size was mostly smaller than 20 individuals. The proportion of birds feeding increased with flock size. Allee-type density dependence was observed in feeding success rate	Grünbaum et al. 2003
African penguin *Diomedea demersal*	Anchovy/Sardine/Red-eye round herring *Etrumeus teres*/Pipe fish *Syngnathinae*	East coast of South Africa	April-June, 2017	The presence of other seabirds increased individual feeding success rate, while the other predatory fish reduced it.	Sutton et al. 2020

African penguin *Diomedea demersal*	Anchovy *Engraulidae*	Southern Cape, South Africa	Breeding season of African penguin, 2015-2016	Higher attack rate in flock. The presence of conspecies increased catch-per-unit-effort. Higher catch-per-unit-effort rate in fish school than single fish	Mcinnes et al. 2017
Black-legged Kittiwakes *Larus tridactylus*, Glaucous-winged Gulls *Larus glaucescens*	Pacific herring *Clupea pallasii*, caplin *Mallotus villosus*, Pacific sand lance *Ammodytes hexapterus*, walleye pollock, eulachon *Gadus chalcogrammus*	South coast of Alaska	Summers of 1995 and 1996	Tightly aggregated flock with size from 3 to 194 individuals of Black-legged Kittiwakes without piracy. Black-legged Kittiwakes perform less plunging when more Glaucous-winged Gulls were in the flock. Feeding success rate was not affected by species composition	Manisicalco et al. 2001
Roseate Terns *Sterna dougallii*, Brown Noddies *Sterna stolida*	Silversided fish *Menidia menidia*	Isla Culebra, Puerto Rico	May-July 1990	Flock size was < 40 individuals. Roseate Terns conducted more dipping in mixed species flocks but aborted further dives because of the interference in mixed species flocks. Feeding attempts rate in Roseate Terns decreased with increasing size of mixed-species flocks. In monospecific Roseate Tern flocks, the size of flocks had no effect on foraging attempt frequency	Shealer et al. 1993

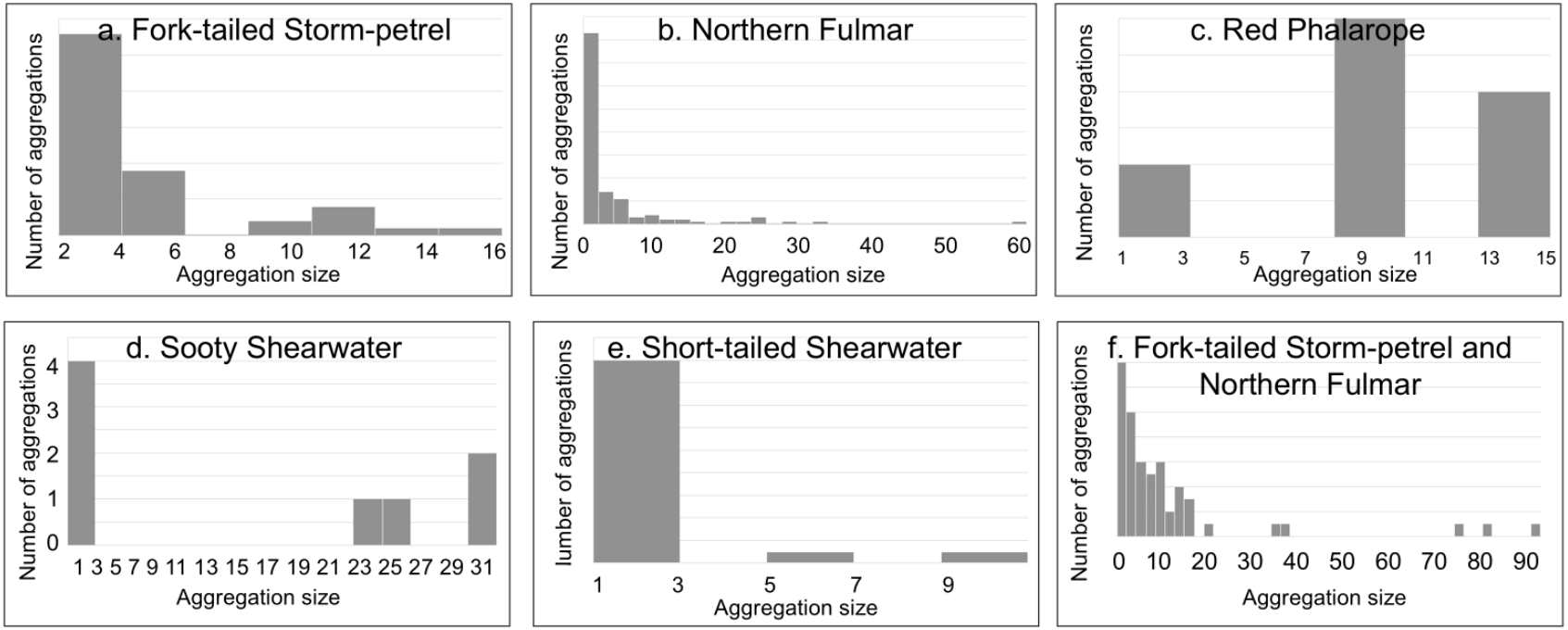


Fig. 1-1 Size (number of birds) of foraging aggregations of different species (a-e), and size of aggregations containing multiple species, observed during the boat census during the Oshoro-maru 56th cruise in 2018 (Hayashi, unpublished).

1.5 AIM OF THE STUDY

Individual seabirds may behave differently when they are feeding solitarily and when they are feeding in large aggregations. The rate of feeding attempt by individual seabirds showed Allee-type density dependence in aggregations of lower density: low in solitary feeding or small aggregations and large in large aggregations (Grünbaum et al. 2003; Thiebault et al. 2014; Maynard et al .2019). In aggregations of higher density, the rate of feeding attempt of divers and surface-feeders decreases as the number of kleptoparasites/suppressors, such as parasitic jaegers and cormorants and competitors, mainly of the same species, increases (Camphuysen et al. 1999; Hoffman et al. 1981). The duration of the aggregations and the time individuals stay in these aggregations increases with the size of the aggregations (Bayer 1983; Hoffman et al. 1981). Therefore, I expected that the behavior of individuals recorded by biologging techniques could be used to determine whether they were foraging in aggregations or solitarily. The aim of this study is to develop techniques for identifying areas of high density of feeding aggregations by using bio-logging (**Fig. 1-2**) with black-tailed gulls *Larus crassirostris* (see below). Firstly, I identified the types of behaviors of individuals that indicate foraging aggregations (Chapter 2). Secondly, I developed the technique to identify behavior using the body acceleration of individuals (Chapter 3). Thirdly, I checked if GPS tracks only inform about foraging aggregation with the aid of machine learning technique (Chapter 4). Finally, I made the map of foraging aggregations using GPS tracks, checked if these were different from the map based on the conventional GPS kernel density, and then developed the models explaining the density of foraging aggregations (Chapter 5).

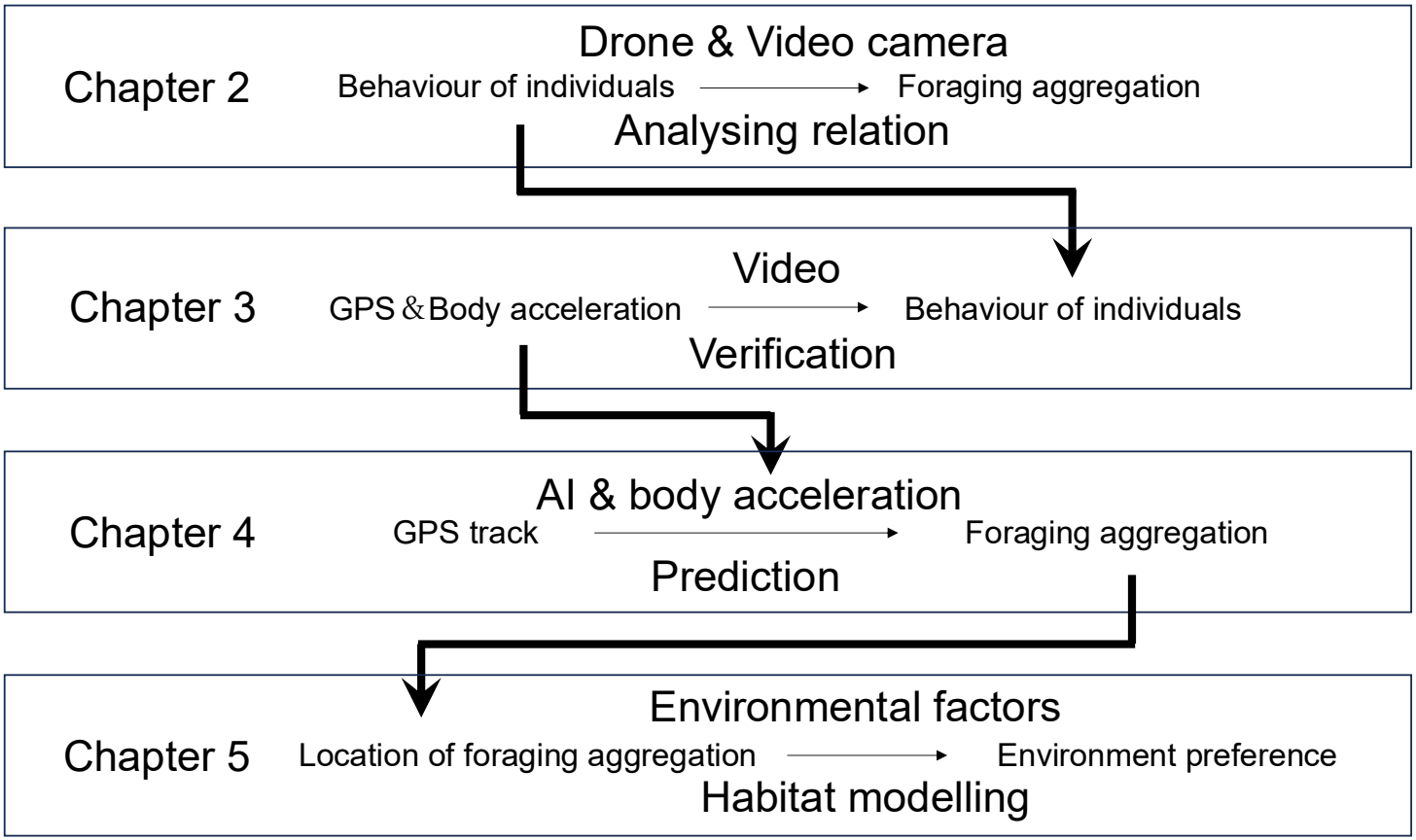


Fig. 1-2 Flow chart of this study. Arrows between squares show the same factors that have been used between chapters. Inside squares, methods are shown above the arrows, aims of methods are shown under the arrows, data for analysis are shown on the left of the arrow, the aims results factors are shown on the left of the arrows.

1.6 STUDY SPECIES: BLACK-TAILED GULLS

Diving seabirds have higher wing loading than surface feeding seabirds, thus resulting in a smaller foraging range restricted to near the colony (Thaxter et al 2010). High predation pressure near the colony can lead to decreased prey availability (Forero et al. 2002, Ainley et al. 2003), although diving seabirds can still manage to maintain the capture by extending their diving duration (Thaxter et al 2010). Surface feeding seabirds, on the other hand can search for wider area, being less affected by the spatial handicaps, and can search for fish patch or productive areas more efficiently. The medium sized surface feeding seabirds with bright body color play a role of catalyst which attracts the conspecifics and other seabird species (Chilton et al. 1987; Ballance et al. 1997) and could be more appropriate to detect areas of high productivity and biodiversity. These surface feeding seabirds tend to feed in aggregations with other subsurface predators generating the feeding aggregations (Haynes 2011) often including divers (Clua et al. 2001). Subsurface predators may force prey to stay in the euphotic zone and make those areas more productive (Willis 2007). Small seabird species avoid highly productive areas to reduce competition with larger seabird species, while the latter are more likely to stay in areas of high productivity (Ballance et al. 1997). If birds stay within areas such as the area around the breeding colonies, prey may descend to deeper depths to avoid the birds (Ainley et al. 2003, Lewis et al. 2001). In such cases, the ability to search a larger range should become more important. However, as body size increases, the flight efficiency, hence the ability to search over wider area, decreases among species flying by wing-propelling (Ballance et al. 1997). Thus, the medium-sized seabirds flying by wing-propelling and feeding on the surface may be more preferable as the material of present study because they can cover larger range, usually attract large birds to form aggregations, and can outcompete small seabird species.

Black-tailed Gull *Larus crassirostris*, is a medium body sized (400-700 g) and bright-colored surface feeder, that explores a larger area efficiently by flying with flapping flight. This species is one of the most abundant breeding seabird species (c. 10,000-100,000 breeding pairs) in Japan (Brazil 2009) and often acts as a main component in feeding aggregations (direct observation at Rishiri and Teuri coasts as well as onboard the ferry boats toward the islands). This species feed on forage fish including sardine *Sardinops melanostictus*, anchovy *Engraulis japonicus* and sand lance *Ammodytes spp.* and also fish discards from the fishing boats (Kazama et al. 2018). During the breeding season, this species feed within the highly productive areas 1-140 km distant from the colonies (Kazama et al. 2018; Kumagai et al. 2023). Such surface feeders will take different

behaviors when feed in different stages of feeding aggregation; in preparatory phase they mostly sit on water with a few keeps watching in flight, gather rapidly once a feeding event take place; in intensification and mature phase, they make surface plunging or attack prey on surface, in dispersion phase they fly away (Clua et al. 2001). According to my observations on the feeding aggregations (Chapter 2 and 3), black-tailed gulls behave differently in different feeding aggregation and in different development stages of aggregations. Therefore, the behaviors of individual black-tailed gulls may inform if they were feeding in aggregations or not. Thus, this species is an appropriate for detecting areas of high productivity and biodiversity.

1.7 OUTLIINE OF THE THESIS

In Chapter 2, I examined whether the behaviors of individual birds reflect the characters of feeding aggregation. I observed individual birds in feeding aggregations using a telescope, video recorder and drone at Teuri Island. Additional observation was carried out along the west coast of Rishiri Island. Dynamics of species composition, horizontal extent, density, duration and location aggregations will be recorded. Frequency and proportion of time spent on each behavior of individual birds were also recorded. To estimate characteristics of the aggregation, a model was constructed using the characteristics of behaviors of individual birds. In Chapter 3, I investigated whether the body acceleration reflects individual behaviors, following my previous study (Ma et al. 2022). A camera and an accelerometer were attached to the black-tailed gulls to record body acceleration and behaviors of individual birds simultaneously. Then, the relationships between the pattern of body acceleration and behaviors of individual birds were examined. In Chapter 4, I examined whether the GPS track only indicates foraging behavior. Firstly, to identify behaviors (true value), I used a GPS and an accelerometer. Then, the characteristics of GPS tracks in locations where birds showed foraging behaviors associated within the foraging aggregations were modeled using machine learning. Accuracy was checked by calculating the precision recall rate. As these worked well, I finally mapped the density of aggregation foraging using GPS tracks of black-tailed gulls in Chapter 5. Marine environmental factors (SST, topology, front structure, primary production) that facilitate aggregation foraging and solitary foraging were modeled (**Fig. 1-2**). Finally, I will discuss its applications. First, I will apply the procedures for sensitivity map of seabirds to wind farms in Chapter 6, then I will discuss how the result help finding the Ecologically and Biologically Significant Areas in Chapter 7.

Chapter 2 Behaviors informing foraging aggregations

2.1 INTRODUCTION

As feeding in aggregation is a main foraging mode in seabirds (Pitman et al. 1992, Jaquemet et al. 2004), it can be a good indicator of a marine important area (Chapter 1). The size and duration of such aggregations are known to vary with the prey species and the subsurface predators (Hoffman et al. 1981; Harrison et al. 1991). Small and short-lived aggregations are likely formed over dense prey schools, while larger and longer-lasting aggregations are likely formed over non-cohesive prey (Fauchald et al.2009; Hoffman et al. 1981; Camphuysen & Webb 1999). Aggregations tend to become larger when small-sized surface feeding species are included (Clua et al. 2001; Camphuysen & Webb 1999), whereas they disappear when large-sized seabirds come to join (Camphuysen & Webb 1999, Haynes 2011). Thus, it is expected that the behaviors of individual birds in different types of aggregations also varies.

The frequency of plunging (a shallow dive close to sea surface) in surface-feeding seabirds usually increases as the aggregations become larger. Aggregation size in this case is usually under ca. 10 birds, disturbance on prey school is not strong (Götmark et al. 1986; Huang et al. 2021). In mix-species aggregations, the rate of feeding attempts (number of attacks at an interval) decreases when other bird species exist (**Table 1-2**). The rates of these feeding attempts may depend directly on the characteristics of a *local group* (small group around individuals within an aggregation) rather than those of a whole aggregation (more than 2 birds within a 10 m radius), it may relate to uneven distribution in prey school, also showing interaction between different species, when larger birds can reduce the prey availability for other birds around. Small and tight *local groups* may be generated by diving seabirds around an individual, to accumulate prey close to the surface, and they last for short periods. Plunging rate with short hovering may be higher in high-density *local groups*, because landing, taking off and hovering usually demand high energy consumption, prey availability and accessibility in hovering areas should be high and outweigh the cost, thus attracting more birds. An excessive number of birds sitting on the surface may block the light and affect the preferred light intensity for fish (Inoue 1972), and may cause fish to move away from the area. Thus, birds may hover to avoid such a situation. As long-lasting aggregations can be generated over spatially non-homogeneous prey, individuals of the surface feeding species tend to feed for a short period at each location and switch locations frequently (Hoffman et al. 1981). In this case, the longer flights to the next foraging

locations (*local groups*) inside an aggregation may be frequent. Further as they were attracted by conspecifics flying in circle (Hoffman et al. 1981) and hovering (flying without significant horizontal movement) (Camphuysen & Webb 1999; Garthe 2004), the frequency of the area-restricted short flight or hovering may increase in larger aggregations because birds are highly attracted by these behaviors thus gathering large aggregation (Hoffman et al. 1981). The change of rate and duration of plunging, hovering, long-flight of individual seabirds, therefore, may change according to these characteristics of the aggregations and the *local groups*. Thus, the analyses of these relationships should help the understanding of causes and consequences of formation of seabirds' feeding aggregations at the sea.

Studies of individual behavior in these aggregations have been conducted based on opportunistic onboard observations (Camphuysen et al. 1999, Haynes et al. 2011). In these observations, it was difficult to track a specific individual and a whole aggregation. Recently, video-loggers or camera-loggers mounted to birds made it possible to record at sea behaviors of individual seabird continuously for a prolonged period (Yoda et al. 2012, Sakamoto et al. 2009, see chapter 3 as well) as well as the behaviors of other members in the feeding aggregations (Watanuki et al. 2008). However, it has still remained difficult to identify the types of the whole aggregations because of the small angle of view of the loggers. Collecting behavioral data on individual seabirds and the types of aggregations simultaneously by means of bio-logging still remains a challenge.

To develop the technique to detect seabirds' aggregation at sea using GPS tracking, I observed the foraging and moving behaviors of individual birds in aggregations and those foraging solitarily. In this study, I used a drone to record the behaviors of individual black-tailed gulls *Larus crassirostris*, and recorded the characteristics (the number of members and the species of subsurface predators) of *local groups* and foraging aggregations. I also used a land-based video camera to record whole aggregations in the purpose of collecting additional information.

I hypothesized that 1) the rate of plunging increases with aggregation size, but a ceiling should occur at certain a size, limiting its usefulness for predicting aggregation types, 2) hovering occurs in foraging aggregation*s* as this behavior usually indicates highly stable small prey schools and required an addition altitude before attack. The rate of surface

seizing should also vary across different types of feeding aggregations. However, because I could not accurately record all surface seizing by the drone, it was impossible to make predictions on the surface seizing. It was also hypothesized that 3) birds conduct shorter flight in less concentrated feeding aggregations. When more subsurface predators exist to chase the prey up to the sea surface, the birds do not need to conduct a short flight and switch to plunging or surface seizing. I also hypothesized that 4) when the birds made longer flights within a feeding aggregation, there should be less dense and fewer subsurface predators thus less prey should be accumulated. I finally hypothesized that 5) birds conduct turning flights in larger feeding aggregations because turning flights usually attract other birds but less so when more subsurface predators are already present. Individuals were expected to conduct a very long flight to leave the feeding aggregation when prey is not accessible.

2.2 MATERIALS AND METHODS

Fieldwork

Fieldwork was carried out along the Kurosaki coast, where more than 2,000 pair of black-tailed gulls were breeding, at Teuri Island (44°N, 141°E), Hokkaido, Japan, from April to July in 2019, 2021 and 2022 (**Fig. 2-1a**). An additional work was carried out along the southeast coasts, where more than 20,000 pair of black-tailed gulls were breeding, at Rishiri Island (45°N, 141°E), Hokkaido, Japan, from May to July in 2018 (**Fig. 2-1b**). I used a drone (DJI, Phantom 4 PRO V2.0) furnished with a 4k/60fps video camera and the land-based video camera (Panasonic, HC-V480MS) mounted on a tripod at Kurosaki coast. I took the video footage of individual black-tailed gulls foraging over feeding aggregations or those foraging solitarily within 500 m of the coast using the drone (Kurosaki coast) or the video camera set on the edge of the land (15 m altitude; Kurosaki coast and southwest coasts of Rishiri Island).

The drone was operated at 15 m to 40 m altitude over aggregations. Before collecting data, I tested the disturbance cause by the drone. Japanese cormorants *Phalacrocorax capillatus* and non-foraging individuals of black-tailed gulls flew away when the drone descended to ca. 20 m over the birds. Foraging individuals of black-tailed gulls flew away when the drone descended to the <10 m altitude. Therefore, the drone approached the aggregations, keeping the >30 m altitude, and took the images covering the entire aggregation. It was then descended above the foraging individuals of black-tailed gulls not to induce them to fly away. Newly formed aggregations of black-tailed gulls were recorded preferentially. I took the video images of the whole foraging *aggregations* first

to know the number and species of seabirds involved in the aggregation, and the species of subsurface predators (**Fig. 2-2a**), then to focus on the members of each aggregation for 30 s - 30 min. I defined "foraging aggregation" as more than 3 individuals of black-tailed gulls foraging. While focusing on an aggregation, I recorded behaviors (flight, foraging and etc.) of individual Black-tailed Gulls.

Analysis

In the analysis of a video image of an aggregation, the numbers of individuals of different species comprising the aggregation were recorded initially: black-tailed gulls, slaty-backed gulls, and small subsurface predators (rhinoceros auklets (RA), *Cerorhinca monocerata*) and large subsurface predators (Japanese cormorants (JC) *Phalacrocorax capillatus* and pinnipeds including Steller sea lion *Eumetopias jubatus* and spotted seal *Phoca largha*). When the aggregation was too large to cover by the drone or land-based video camera, I categorized the size as ">1000 individuals" and recorded species composition of subsamples (generally ~200 individuals) of the aggregations.

Black-tailed gulls in the aggregation spent majority of time drifting or swimming when they were waiting for the chance to feed. Individual black-tailed gulls usually conducted foraging after flight. I defined the birds foraging/searching as they flew for longer than 2 s, as the flights <2 s could be maintenance behaviors (Ma et al. 2022). To analyze the foraging behavior of individuals, I arbitrarily sampled a single target individual of black-tailed gull foraging/searching prey in each video footage and followed this individual for 30 s, and treated the record of the individual as a sample. Then, I switched to another foraging/searching individual.

The distribution of birds and prey could be uneven in the foraging aggregation. Thus, I introduced a new variable "size of *local group*", i.e. the maximum number of black-tailed gulls and slaty-backed gulls within a radius of 3.8 m (8 times the body length of black-tailed gull) of the targeted individual (**Fig. 2-2b**). I use the radius of 3.8 m because this range can cover most of the active feeding birds in each higher density group in an aggregation. In the land-based video footage, it was difficult to determine the distance of the birds' positioning along the direction of the video camera. To set these sizes of radius in the land-based video, I first used footage where aggregation looks like nearly a horizon and front-back distance can be ignored. For other images, I then estimated the front-back distance referring to the time of individual black-tailed

gulls swimming in this direction and assuming their swimming speed to be 0.36±0.06 m/s based on our drone data (n=20).

For a 30-s sample of each bird, I recorded the sum of the duration of each behavior. Behaviors were categorized as *surface plunging* (birds took short flight and immersed its head in the water), *hop plunging* (birds sit on the water and immersed its head in the water), and *others* (birds conducted drifting, swimming, surface seizing) following Ma et al. (2022). In addition to the categories, flying behaviors were further classified as: *hovering* (birds conducted flapping flight without horizontal movement that lasted for more than 2.5 s), *short flight* (birds conducted flapping flight less than 5 s), *long flight* (birds conducted flapping flight for 5－10 s), and *turning flight* (birds stayed in the air for more than 10 s within a radius of 25 m), *leaving flight* (birds left from the area of a radius of 25 m and conducted flapping flight for more than 10 s) in this study. I put surface seizing into *others*, because it was difficult to identify this behavior from the upper view. I sampled ten 30-s video footage at maximum to define the characteristics of each feeding aggregation to reduce the bias of the size of the aggregation, except when the aggregation size was >1000 and multiple video-footages were taken from different parts of the aggregation. *Hop plunging* (birds sit on the water and immersed its head in the water) was excluded because my sample individuals rarely conducted this behavior.

Statistical analyses

I use a generalized additive model (GAM) to examine how local group size and the characteristics of aggregation affected the sum of the duration of each behavior of individual black-tailed gulls in a 30-s sample. Aggregation size, the number of black-tailed gulls, slaty-backed gulls and cormorants correlated with each other (**Table 2-1**). The number of cormorants maximized the average R^2 value in all models; therefore, it was used as an explanatory variable. The effect of aggregation size was considered similar to the number of cormorants as JC number/ aggregation size. *Local group* size (number of black-tailed gulls within a 3.8 m radius of target individuals), the number of RA (number of the auklets in aggregation) were included as the potential explanatory variables. The number of large subsurface predators (whales and pinnipeds) was another explanatory variable. I selected the model that minimized the Akaike information criterion (AIC) value and those with delta AIC <2. When multiple models with the delta AIC <2 were constructed, the model with the fewer number of explanatory variables was chosen (Burnham et al. 2003). All statistical analyses were performed using R

version 4.4.1 (R Core team 2024). I conducted GAM analyses using the mgcv package (Wood 2023) and AIC analyses using the MuMIn package (Bartoń 2024) operated in R. Type of dependent variable was set as negative-binomial, log link function was used. F-test was conducted to test the regression significance of the model. All samples were considered independent.

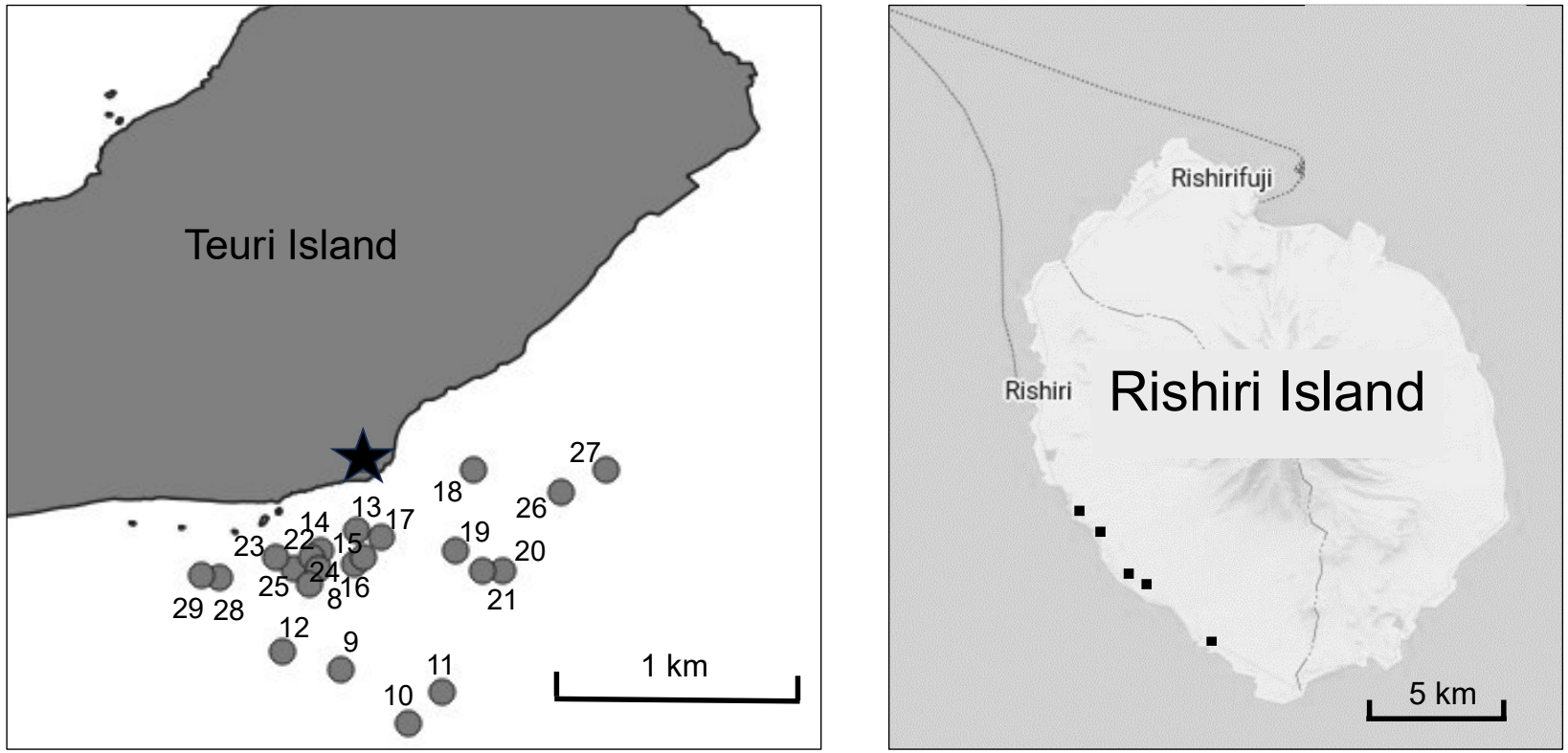


Fig. 2-1 a) Map of Teuri Island. The star indicates the location of the Kurosaki area, at-sea circles mark the location of foraging aggregation locations of Black-tailed Gulls observed by drone. IDs were also shown. b) Map of Rishiri Island. The rectangle indicates the approximate location of the video observation.

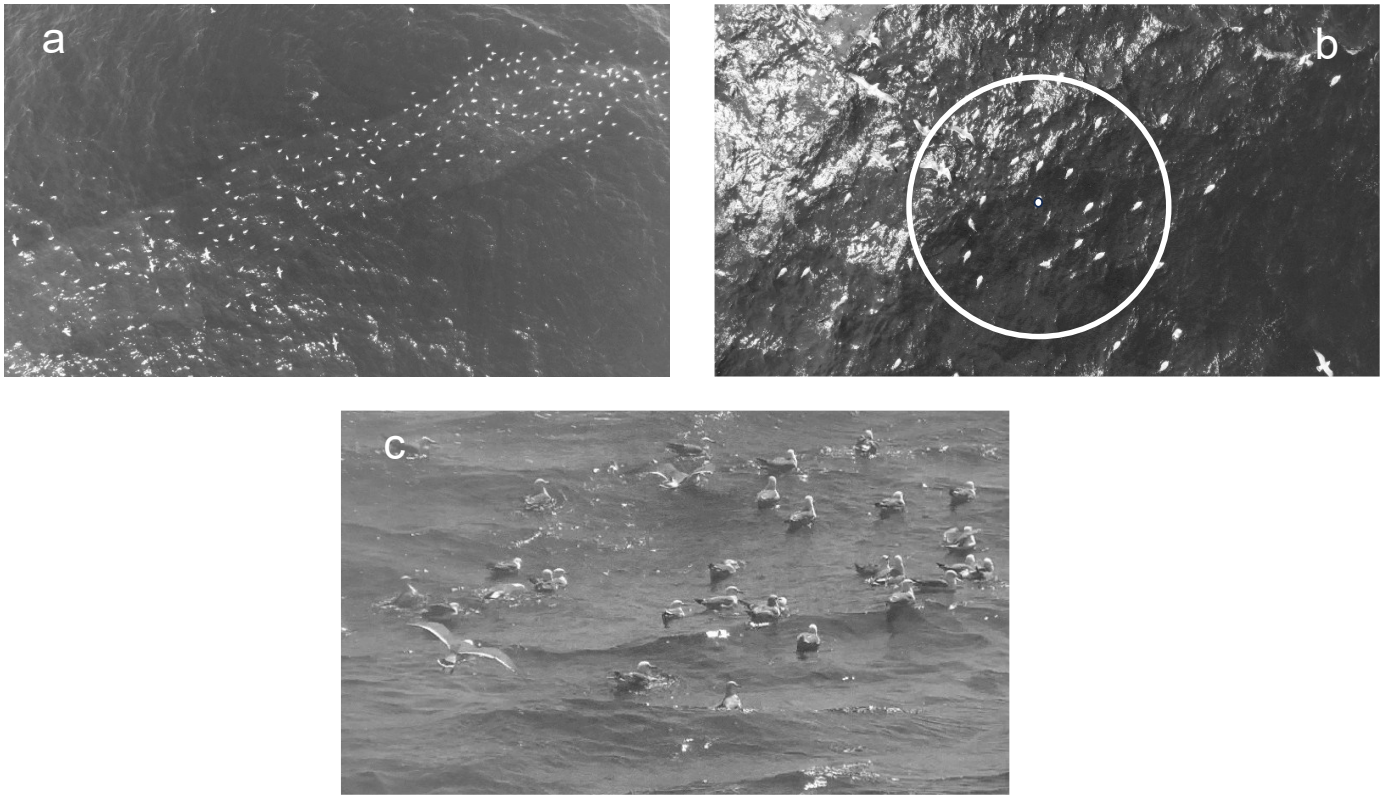


Fig. 2-2 a) The whole foraging aggregation (ID 8) off Kurosaki area taken by the onboard camera of the drone in April 2021, the shadow under the birds is probably a school of krill. b) Enlarged picture of a part of the feeding aggregation (ID 8). The local group within a radius of 3.8 m. c) Photo of a part of the feeding aggregation (ID 32) taken from 100 m away from the land by the video camera.

Table 2-1 Variance inflation factor between each explanatory variable; BTG: Black-tailed Gull, SBG: Slaty-backed Gull, RA: Rhinoceros Auklet. *: Low level of multicollinearity, **: medium level of multicollinearity, ***: high level of multicollinearity.

	Local group size	*Aggregation* size	BTG	SBG	RA	Cormorant	Pinniped
Local group size	1	0	-0.01	0.23	0.11	-0.03	-0.11
Aggregation size	0	1	1	0.75	0.27	0.86	-0.11
BTG	*	1	1	0.73	0.25	0.86	-0.12
SBG	*	***	***	1	0.35	0.82	-0.09
RA	*	*	*	*	1	0.53	0.18
Cormorant	*	***	***	***	**	1	-0.06
Pinniped	*	*	*	*	*	*	1

2.3 RESULTS

In total, 25 and 20 video footages were recorded by drone (**Fig. 2-2a**) and land-based video (**Fig. 2-2c**), respectively, over 37 feeding aggregations (one aggregation can include >2 videos) of black-tailed gulls and on 5 solitarily feeding black-tailed gulls (**Table 2-2)**. Location of aggregation ID 1-7 and 31-37 were within 500 m from the Kurosaki colony and the coast of Rishiri and the others within 2 km, respectively (**Fig. 2-1)**. I did not record location of the aggregations in Rishiri thus I only showed the location of observation. The size of aggregations ranged between 3 and >1000 birds, comprising mostly Black-tailed Gulls while 18 aggregations included rhinoceros auklets, 18 and 1 aggregations included Japanese cormorants and pinniped, respectively (**Table 2-2**).

I collected a total of 189 30-second samples of foraging black-tailed gulls over the aggregations and five over individual foraging birds (**Table 2-2**). Three commonly observed behavioral series among different aggregations are shown in **Fig. 2-3**; birds repeated *hovering* and *surface plunging* in dense aggregations, conduct *short flight* in spare aggregations that have more space, attack and then leave immediately when foraging solitarily. Among 37 aggregations, 36 (95%) of aggregations recorded birds conducting *others*, i.e. on the water without significant change in body angles, next followed by *short flight* (70%), and *surface plunging* (62%). Among 5 samples of single, 100% was *leaving flight*, next dominant was *surface plunging* (60%) then *others* (40%) (**Table 2-3**).

In all 30 s samples, except *turning flight* and *leaving flight*, most of behaviors were conducted together with *others* (> 90%). Among birds that conducted *hovering*, most of them also conducted *surface plunging* (88%) which was often conducted accompanied by *hovering* (30%) or *short flight* (28%). The birds conducted *turning flight* tended to conducted *short flight* (58%) and *surface plunging* (38%) as well (**Table 2-4)**.

The effects included in the models and the result of model selection are shown in **Fig. 2-4** and **Table 2-5**, respectively. As expected**,** surface plunging was conducted more when JC number/ aggregation size was the median value (Prediction 1), hovering was conducted more with larger *local group* size and with a larger number of rhinoceros auklets but was not affected by JC number/ aggregation size (Prediction 2). *Short flight* was conducted more with lower *local group* size but less when the number of rhinoceros auklets was more than 30 as prediction 3. *Others* were conducted more when

there were greater number of rhinoceros auklets (Prediction 3) and long-flight was conducted more when *local group* size and the number of rhinoceros auklets was below 40 and 15, respectively (Prediction 4). Turning flight was conducted more with larger JC number/ aggregation size but less when the number of rhinoceros auklets was more than 20, following my prediction 5. The time of leaving-flight was not significantly affected by any aggregation/local group characteristic.

Table 2-2 Size and species composition of 37 foraging aggregations observed by the drone or video camera.

ID	Area	Type	Drone/Land	Time/date	Aggregation size	Black-tailed Gull	Slaty-backed Gull	Rhinoceros Auklet	Cormorant	Pinniped	Number of samples	Color of prey
1	Rishiri	Aggregation	Land	6/2018	42	36	0	6	0	0	5	NA
2	Rishiri	Aggregation	Land	6/2018	79	72	1	5	1	0	4	NA
3	Rishiri	Aggregation	Land	6/2018	113	103	1	8	1	0	9	NA
4	Rishiri	Aggregation	Land	6/2018	65	52	2	5	6	0	3	NA
5	Rishiri	Aggregation	Land	6/2018	47	45	0	2	0	0	3	NA
6	Teuri	Aggregation	Land	6/2018	3	1	0	1	1	0	1	NA
7	Teuri	Aggregation	Land	6/2018	84	11	35	25	13	0	4	NA
8	Teuri	Aggregation	Drone	11:35 14/4/2021	>1000	>1000	20 (estimated)	0 (estimated)	20 (estimated)	0	14	Dark pinkish
9	Teuri	Aggregation	Drone	16:30 22/4/2021	200	199	0	0	1	0	4	NA
10	Teuri	Aggregation	Drone	16:58 22/4/2021	50	49	0	0	1	0	6	NA
11	Teuri	Aggregation	Drone	17:22 22/4/2021	31	31	0	0	0	0	5	NA
12	Teuri	Aggregation	Drone	15:39 1/5/2021	100	100	0	0	2	0	3	NA
13	Teuri	Aggregation	Drone	17:45 14/6/2021	152	142	0	10	0	0	3	NA
14	Teuri	Aggregation	Drone	17:57 14/6/2021	45	43	0	2	0	0	5	NA
15	Teuri	Aggregation	Drone	18:29 14/6/2021	101	86	0	13	2	0	10	NA

16	Teuri	Aggregation	Drone	18:36 14/6/2021	333	282	0	50 (estimated)	1	0	5	NA
17	Teuri	Aggregation	Drone	12:48 16/4/2022	24	24	0	0	0	0	1	NA
18	Teuri	Aggregation	Drone	12:49 16/4/2022	31	31	0	0	0	0	3	NA
19	Teuri	Aggregation	Drone	12:55 16/4/2022	199	199	0	0	0	0	4	NA
20	Teuri	Aggregation	Drone	13:00 16/4/2022	90	90	0	0	0	0	1	NA
21	Teuri	Aggregation	Drone	13:08 16/4/2022	80	80	0	0	0	0	3	NA
22	Teuri	Aggregation	Drone	12:07 19/4/2022	>1000	>1000	20 (estimated)	40 (estimated)	40 (estimated)	0	4	Dark pinkish
23	Teuri	Aggregation	Drone	12:13 19/4/2022	>1000	>1000	20 (estimated)	40 (estimated)	40 (estimated)	0	5	Dark pinkish
24	Teuri	Aggregation	Drone	12:23 19/4/2022	150	150	0	0	0	0	4	NA
25	Teuri	Aggregation	Drone	12:30 19/4/2022	178	178	0	0	0	0	5	NA
26	Teuri	Aggregation	Drone	17:12 10/5/2022	240	240	0	0	0	0	7	NA
27	Teuri	Aggregation	Drone	17:21 10/5/2022	300	300	0	0	0	0	3	NA
28	Teuri	Aggregation	Drone	17:30 10/5/2022	260	260	0	0	0	0	3	NA
29	Teuri	Aggregation	Drone	17:35 10/5/2022	80	80	0	0	0	0	6	NA

30	Teuri	Aggregation	Land	16:35 27/4/2021	16	16	0	0	0	2	6	NA
31	Teuri	Aggregation	Land	17:41 14/6/2021	152	140	0	20	2	0	8	NA
32	Teuri	Aggregation	Land	17:51 14/6/2021	65	40	0	20	5	0	6	NA
33	Teuri	Aggregation	Land	18:31 14/6/2021	114 (estimated)	80	0	30 (estimated)	4 (estimated)	0	6	NA
34	Teuri	Aggregation	Land	14:50 25/6/2021	50	45	0	5	0	0	6	NA
35	Teuri	Aggregation	Land	17:51 10/5/2022	150	130	0	20	0	0	9	NA
36	Teuri	Aggregation	Land	16:53 7/6/2022	26	22	0	0	4	0	9	NA
37	Teuri	Aggregation	Land	18:18 7/6/2022	34	30	0	0	4	0	6	NA

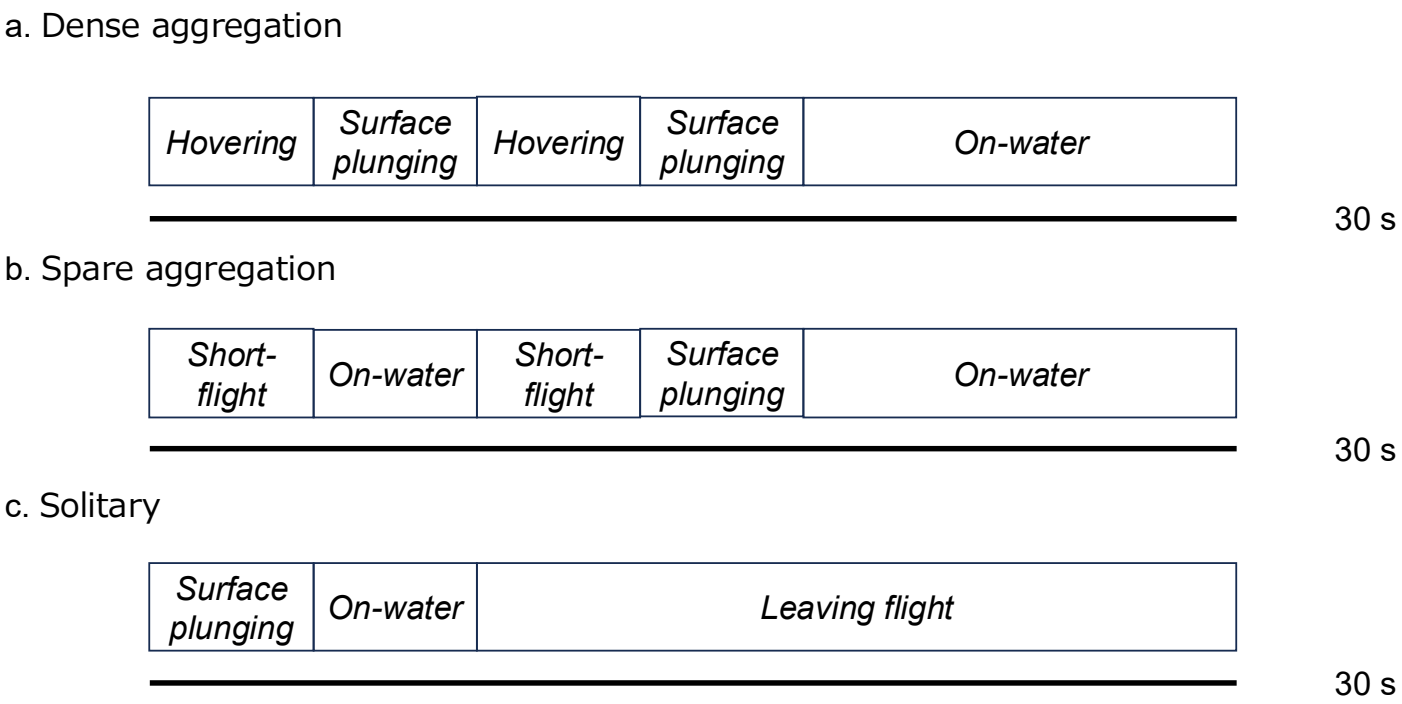


Fig. 2-3 a) Commonly seen behavioral pattern in a) dense aggregation, b) sparse aggregation c) solitary foraging.

Table 2-3 Frequency of occurrence of foraging behaviors in feeding aggregations (Flock feeding; N=37) and solitary feeding occasions (Single; N=5).

	Hovering	*Short flight*	*Long flight*	*Surface plunging*	*Hop plunging*	*Turning flight*	*Leaving flight*	*Others*
Flock feeding	16%	70%	32%	62%	5%	19%	30%	95%
Single	0	0	0	60%	0	0	100%	40%

Table 2-4 Frequency of occurrence of flying behaviors that represented ≥2 kinds of behaviors. For example, among birds representing hovering, 8% conducted short flights, and 13% conducted long flights.

	Hovering	*Short flight*	*Long flight*	*Surface plunging*	*Hop plunging*	*Turning flight*	*Leaving flight*	*Others*
Hovering	/	8%	13%	88%	4%	8%	0%	100%
Short flight	2%	/	4%	27%	1%	8%	0%	100%
Long flight	10%	14%	/	21%	0%	3%	0%	97%
Surface plunging	30%	38%	9%	/	4%	12%	0%	94%
Hop plunging	25%	25%	0%	75%	/	0%	0%	100%
Turning flight	10%	40%	5%	40%	0%	/	15%	1%
Leaving flight	0%	0%	0%	0%	0%	11%	/	26%
Others	14%	58%	16%	38%	0%	8%	4%	/

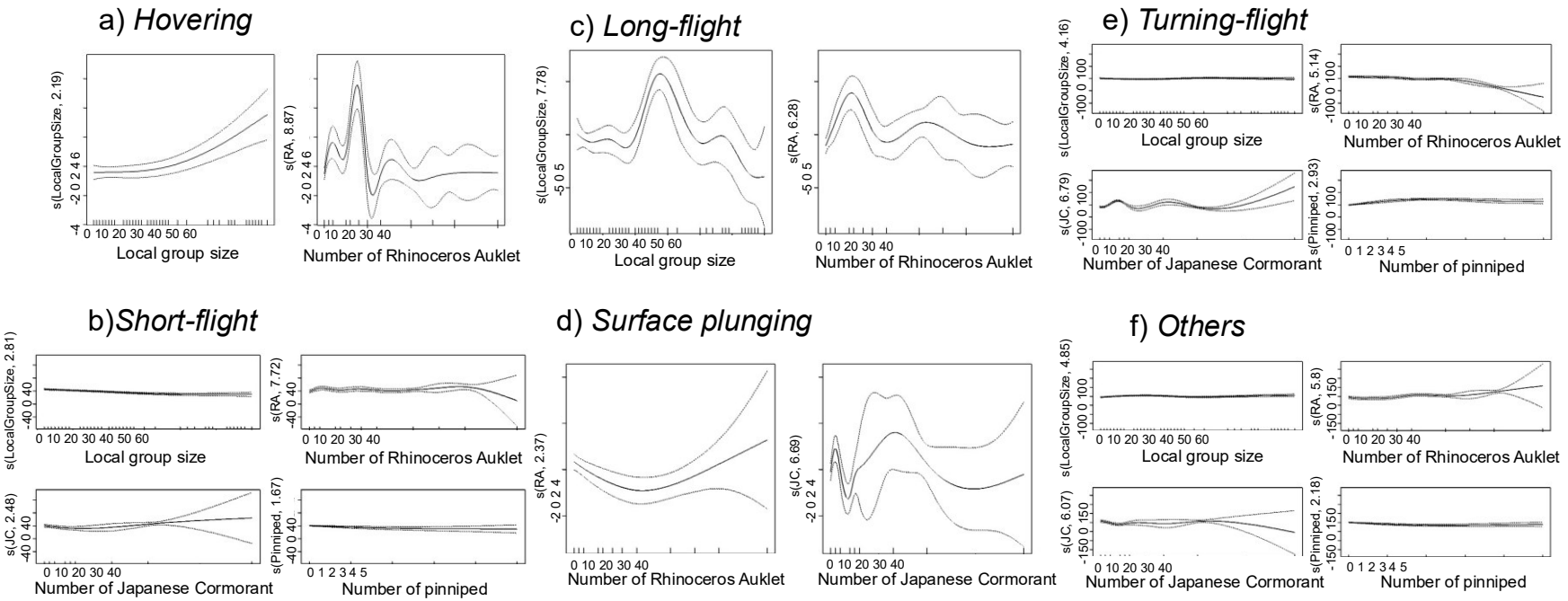


Fig. 2-4 Response curves for the generalized additive model explaining the sum of time for a) hovering, b) short-flight, c) long-flight, d) surface plunging, e) turning-flight and f) others in a 30 s window by local group size, number of auklets, pinnipeds, and the number of cormorants. The areas between dashed lines indicate 95% confidence intervals.

Table 2-5 Selection of top 3 adequate models (multiple regression models) explaining the foraging behavior of black-tailed gulls. Adequate models (delta AIC <2) are shown in bold, and the best models are underlined; RA: number of rhinoceros auklet.

Behaviour	Model	AIC	delta AIC	R^2 of the best model
Hovering	**LocalGroupSize + RA**	**761.3**	**0**	0.59
	LocalGroupSize + RA + Cormorant	**763.1**	**1.85**	
	LocalGroupSize + Cormorant + Pinniped	**763.3**	**1.99**	
Short Flight	**LocalGroupSize + RA + Cormorant + Pinniped**	**1000.5**	**0**	0.34
	LocalGroupSize + Cormorant + Pinniped	1008.8	8.27	
	LocalGroupSize + Cormorant	1023.9	23.42	
Long Flight	**LocalGroupSize + RA**	**982.6**	**0**	0.38
	LocalGroupSize + RA + Cormorant	**983.4**	**0.84**	
	LocalGroupSize + RA + Pinniped	**984.4**	**1.84**	
Surface Plunging	**RA + Cormorant**	**688.3**	**0**	0.18
	RA + Cormorant + LocalGroupSize	**689.5**	**1.14**	
	RA + LocalGroupSize + Pinniped	700.4	12.08	
Turning	**Cormorant + RA + Pinniped + LocalGroupSize**	**1106.4**	**0**	0.82
	Cormorant + RA + Pinniped	1114.5	8.11	
	Cormorant +RA + LocalGroupSize	1239.3	132.92	
Others	**LocalGroupSize+ Pinniped + RA + Cormorant**	**1242.7**	**0**	0.60
	Pinniped + RA + Cormorant	1272.3	29.65	
	LocalGroupSize + RA + Cormorant	1278.1	35.54	

2.4 DISCUSSION

Previous studies have shown that fewer than 10% of individual diving seabirds exhibit escape behavior in response to a drone, and the gull species are also unaffected by the drone's approach (Brisson-Curadeau et al. 2017). I observed similar reactions. When the drone took off from the coast and approached the aggregation, I observed several black-tailed gulls following the drone. Thus, it seemed that the black-tailed gulls did not consider the drone as threat. Aggregation size did not affect the reaction of Anatidae to the drone (Takahashi et al. 2024), I also found that birds responses did not vary across aggregation sizes, but were more likely to avoid a drone once feeding event had ended. Benefit of feeding can let them ignore drone. Gulls seem less willing to avoid drone (Takahashi et al. 2024), the negative effect of using drone on gulls' feeding aggregation may be minor.

Surface seizing among *others* is probably the most used foraging behavior. *Short flight* is frequently used, usually paired with *surface plunging* and probably surface seizing to catch prey. Before conducting *surface plunging*, birds usually conducted *short flight* or *hovering*. *Hovering* requires more power compared to other flight modes as it shows higher frequency and amplitude. The high probability of *surface plunging* after it suggests that hovering might have a high catch rate on prey. *Hop plunging* was recorded only slightly in this study, although Ma et al. (2022) reported that it was a feeding mode used frequently. This inconsistency is likely due to the confusion in Ma et al. (2022) between hop plunging and drastic surface seizing, both of which exhibit similar patterns in body acceleration.

In this chapter, all 5 predictions I made have been supported. The behaviors of individual black-tailed gulls were different across *local group* sizes as well as aggregation sizes, indicating that individuals behave differently even within a feeding aggregation. Individuals changed the duration of flight within a feeding aggregation. *Turning flight* increased when the aggregation size was greater, but decreased when the number of rhinoceros auklets in aggregation was greater. *Turning flight* is used to attract other birds to form larger flocks. The individual black-tailed gulls increased the duration of flight to chase prey when fewer subsurface predators were present, but stayed on water when more subsurface predators were present. When the local group size was greater, the duration of *short flight* was shorter, while that of hovering was longer. They switched from *short flight* to *hovering*, which may be related to the less available surface space when the local groups included larger number of black-tailed gulls.

In addition to the number of black-tailed gulls in aggregations or local groups, prey type may affect the foraging behavior of individuals. In spring, black-tailed gulls at Teuri Island feed mainly on krill (Deguchi et al. 2004; Ito et al. 2009; Tomita et al. 2009). Slowly moving dark pinkish prey aggregations were observed below three large feeding aggregations (**Fig. 2-2**). The duration of *short flights* increased when the aggregation size was greater but decreased when the local group size increased. Both the durations of hovering and long flights were shorter when the local group size was smaller than 30 individuals. Over these large patches of prey, presumably krill, exhibiting rather constant density across a large area, black-tailed gulls might not need to make *long flights* to chase prey patches or use hovering in the high-density area, and so they might keep space between each other and can locate prey patches using *short flights*.

The presence of other seabird species affected behavior of individual Black-tailed Gulls. The number of rhinoceros auklets in a local group has affected types of behavior of black-tailed gulls in feeding aggregations. The durations of *hovering* and *long flight* were longer when the number of rhinoceros auklets was smaller than 10. When the number of rhinoceros auklets was greater than 10, the durations of the turning flight and *short flight* were shorter, but the time of surface plunging and others was longer. Surface plunging and *short flight* were conducted when Black-tailed Gulls were foraging, but the turning flight was conducted just before the foraging and during foraging. Diving seabirds chase and form stable prey schools close to the surface (Hoffman et al. 1981; Balance et al. 1997). Gulls used more time to attack prey patches when the number of rhinoceros auklets was greater. Rhinoceros auklets should be important for gulls' foraging because they improve the accessibility to prey for gulls. Without the presence of diving seabirds, prey can avoid predation by simply diving to deeper water.

With the aids of a drone and a land-based video, I found that back-tailed gulls change feeding behavior and duration of flights according to the local density and the presence of subsurface predators in relation to the types of prey. Thus, the results of this study indicate that the approximate size and type of aggregations can be estimated using the behavior of black-tailed gulls, which can be measured by an accelerometer and GPS (Berlincourt et al. 2015, Cianchetti et al. 2018, Ma et al. 2022).

Chapter 3 Body-acceleration informs behavior

3.1 INTRODUCTION

The development and miniaturization of data-loggers have rapidly advanced the studies of behavior of highly mobile animals (e.g., Fort et al. 2012, Thiebault et al. 2016, Lescroël et al. 2016). Among these devices, the accelerometers are small (<3 g) and can be deployed on small seabirds (<500 g) with minimum negative effect (Berlincourt et al. 2015, Cianchetti et al. 2018). The high sampling rate (>24 Hz) of body-acceleration allows for measuring changes of the angle of body axis, movements of head and body trunk, and strokes of wings of birds in the wild (<1 s, Watanuki et al. 2004, Ropert-Coudert et al. 2006, Kokubun et al. 2011).

Classification of behavior using body-acceleration aids in the study of the behavior of seabirds at sea (e.g., Fehlmann et al. 2017, Shamoun-Baranes et al. 2012, Sur et al. 2017). To verify the accuracy of identifications of behaviors using body-acceleration, simultaneous direct observations are essential. Direct observation was conducted simultaneously in caged songbird (Alarcón-Nieto et al. 2018) and griffon vulture *Gyps fulvus* in the field (Nathan et al. 2012). However, this direct method is difficult to apply to wide-ranging seabirds in the high seas. Therefore, video loggers have been attached long with the acceleration loggers on the same individuals to verify the identification of behavior by body acceleration in black-tailed gulls (Yoda 2019), streaked shearwaters (Garrod et al. 2021), black-footed albatross (Tsukamoto et al. 2019) and Adelie penguins (Watanabe & Takahashi 2013).

In previous study, I identified specific activities of black-tailed gulls *Larus crassirostris* by recording body acceleration at 25 Hz using the video images of this species taken from the land (Ma et al. 2022). However, the accuracy of classifying behaviors during foraging trips remains to be verified. In the present study, video loggers were attached simultaneously with accelerometers to this species breeding at Teuri Island, Hokkaido, Japan. To test the accuracy, I identified behaviors using the cycle and amplitude of body acceleration as was done in the previous study, and confirmed the behavior using video-images as well. Then, the sensitivity test was conducted using the confusion matrix, where the behavior determined using the video was a true value.

3.2 MATERIALS AND METHODS

Fieldwork

I conducted fieldwork in Kurosaki area (**Fig. 3-1a**) at Teuri Island (44°N, 141°E), Hokkaido, Japan, during the incubation period (from May to June) in 2021 and 2022. Using snare trap, I captured 4 and 9 incubating birds on the nests in 2021 and 2022, respectively (**Table 3-1**). I weighed and measured these birds and then attached video-logger (DVL400M, Little Leonardo, Japan, 52 × 20 × 11 mm, 15 g including battery) and accelerometer (Axy 5 XS, TechnoSmart, Italy, 15 × 10 × 4 mm, 2 g including battery) on the back feathers using Tesa tape (**Fig. 3-1b**). The total mass of these two data loggers and tape was 20 g, which equates to 2.9% and 3.4% of body mass for male (680 g) and female (580 g) black-tailed gulls, respectively (Chochi et al. 2002). These proportional masses of loggers were close to or exceeding the critical logger–body mass ratio (3%) that may reduce flight efficiency of albatross (Phillips et al. 2003). Video loggers were programmed to take 2.5 hours of images in 1280×960 resolution at 30 fps from 12:00 am. Birds were recaptured using cage traps 2–3 days later, and the devices were retrieved. I recaptured three birds and eight birds in 2021 and 2022, respectively **(Table 3-1**).

The acceleration along the 3-axis, sway (X, left to right), surge (Y, tail to head), and heave (Z, ventral to dorsal) were recorded at 25 Hz. This sampling rate of the accelerations enables the identification of the behaviors, including high-frequency body movements such as wing flapping and ruffling (Ma et al. 2022). The sampling rate of video in 2020 and 2021 was 30 fps.

Analyses of acceleration

Due to the lack of speed data from GPS location, by using only acceleration data, I classified 5 groups of behaviors according to the specific body angles, cycles and amplitude of body movement as *Flapping* (Flapping flight, hovering), *Bathing* (head bathing, wings shaking), *Plunging* (shallow-angle surface plunging, steep-angle surface plunging, hop plunging, rapid landing), *Low-amplitude* (gliding, swimming, surface seizing), and *Passive state* (gliding, drifting). The same behavior was allowed to show in different groups because one behavior can include multiple types of acceleration style, for example, gliding can be conducted in low amplitude due to wind (*Low-amplitude*) or almost no fluctuation (*Passive state*). The definition of behaviors within each group followed Ma et al. (2022) (**Table 3-2**). Each behavior was identified in a 1-second windows with exceptions of "head bathing" which was defined as a large angular change (>20 degree) at ~1 Hz lasing for >3 s, and "hop plunging" which was defined as a bird made large angular change (>20 degree) at ~1 Hz with a duration <3 s (Ma et al. 2022).

Video-images

The video-loggers recorded the head, back and wing of individuals that carried devices as well as the sea, sky and objects such as boats, land, and the birds accompanying them. Using these pictures and the cycle of vertical movement of their body, I identified behaviors every second, and analyzed the pictures taken during flight or at sea, excluding those taken in the colony (grass environment) or on land. Behaviors were classified into the five groups: *flapping* (body fluctuate largely at around 4 Hz), *bathing* (dive into water at 1 Hz for more than 3 times), *plunging* (dive into water), *low-amplitude* (head up, significant change in body movement without diving into water), *and passive state* (head up, no significant change in body movement). Whole analysing process is shown in **Fig. 3-2**.

Accuracy of identification

The accuracy of identifying behavior based on body-acceleration was judged by video for each one-second window. In this analysis, I made a confusion matrix for each bird, as accuracy may vary among individuals (Tsukamoto et al. 2019).

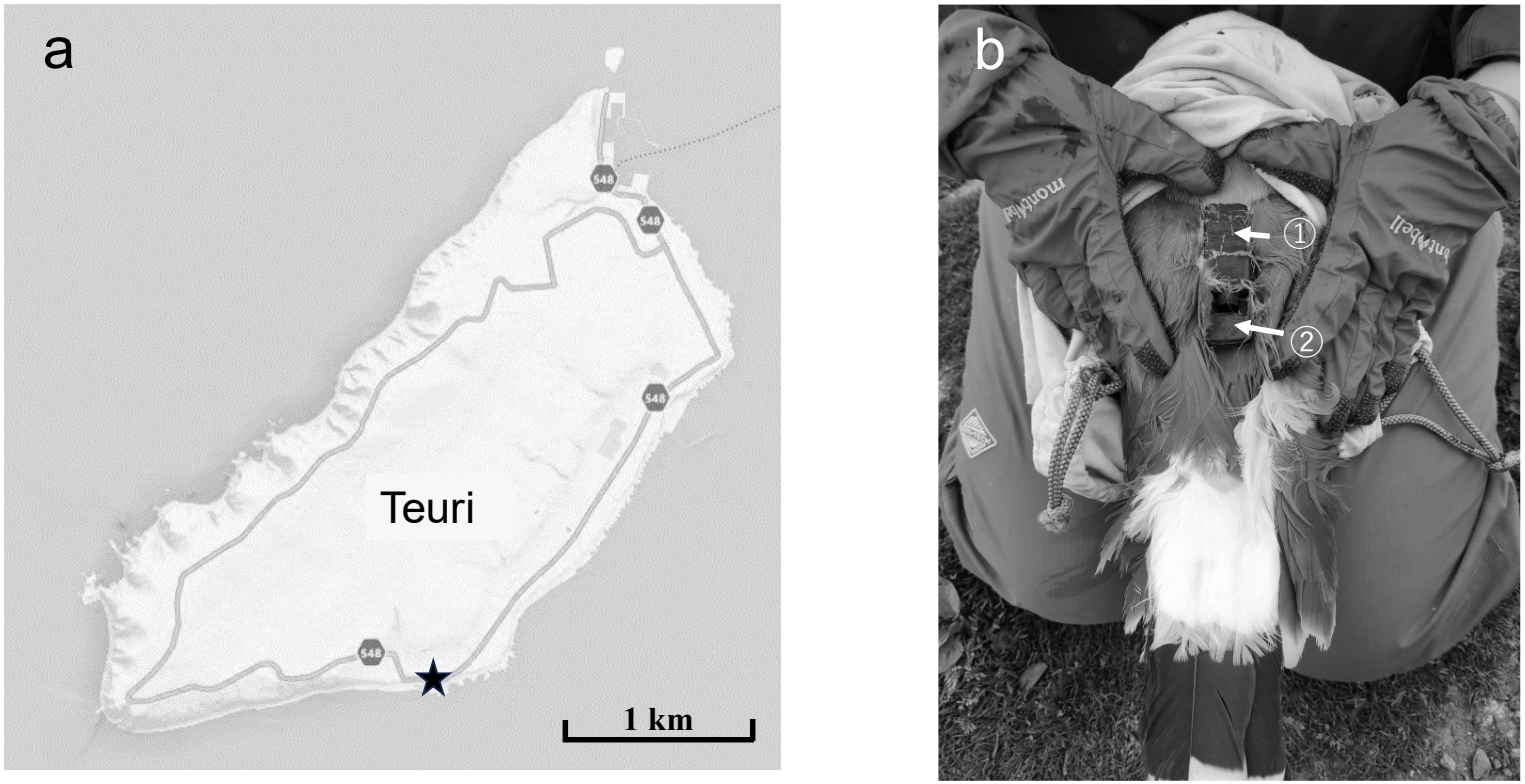


Fig. 3-1 a) Teuri Island. The star indicates the location of the study site (Kurosaki area). b) Video logger (①) and accelerometer (②) attached to the back feather of a black-tailed gull.

Table 3-1 List of birds attached with video and acceleration data logger; -: no video data available.

Bird ID	Date of capture	Mass at capture (g)	Sex	Date recapture	Mass at recapture (g)	Acceleration data	Video record start	Video record end
1	2021/5/18	650	M	2021/5/19	640	Yes	2021/5/18/12:56	2022/5/18/16:11
2	2021/5/18	595	M	2021/5/19	610	Yes	2021/5/18/13:02	2022/5/18/15:14
3	2021/5/22	625	M	2021/5/22	635	Yes	2021/5/22/12:50	2021/5/22/16:14
4	2021/5/22	730	M	2021/5/22	740	Yes	-	-
5	2022/5/22	585	F	2022/5/22	555	Yes	-	-
6	2022/5/22	630	F	2022/5/23	595	Yes	-	-
7	2022/5/22	615	M	2022/5/22	600	Yes	-	-
8	2022/5/23	520	F	2022/5/23	505	Yes	-	-
9	2022/5/23	710	M	2022/5/24	685	Yes	2022/5/23/13:31	2022/5/23/16:41
10	2022/5/24	570	F	2022/5/26	545	Yes	2022/5/24/13:26	2022/5/24/16:50
11	2022/5/24	600	F	2022/5/25	550	Yes	-	-
12	2022/5/26	725	M	2022/5/27	715	Yes	2022/5/26/13:11	2022/5/26/16:23
13	2022/5/17	670	M	2022/5/21	670	No data	No data	No data

Table 3-2 Characteristics of different behaviours. The maximum and minimum values of the grand average of cycle of body movement is shown. When birds feed underwater, their body angle decreases and becomes negative. Thus, the maximum and minimum values of the grand average of the minimum body angle are used to identify shallow-angle surface plunging, steep-angle surface plunging, and hop plunging (at intervals of 5º). Range of the average difference between the minimum and maximum instantaneous body angle is shown as the change of body angle (at intervals of 5º). Moving speeds are shown as body lengths per second. NA: not applicable. Classification of foraging behavior was based on Ashmole (1971) and Hoffman et al. (1981).

Behavior	No. footages	Cycle (s)	Min angle (º)	Change of angle (º)	Duration (s)	Moving speed (by body length)
Flapping flight	20	0.26~ 0.31	/	NA	>0.2	>10
Hovering	20	0.15~ 0.25	0~50	0~40	>0.3	<10
Gliding	10	-	-10~0	-	0.3~40	>10
Shallow-angle surface plunging	10	-	-20 ~0	0~20	0.5~1.3	>10 (start) / <5 (end)
Steep-angle surface plunging	10	-	-90 ~ -30	60~150	0.5~1.3	<5
Hop plunging	10	-	-60~ -30	40~120	0.5~2.1	<5
Surface seizing	10	-	-15~ 0	0~15	0.2~2.2	<5
Swimming	10	0.22~0.40	-15~ 0	0~15	>1	<5
Head bathing	10	0.75~1.15	-30~ -20	40~60	2.5~12.5	<5
Wings shaking	10	0.18~0.23	-15~ 0	NA	0.4~1.4	<5
Drifting	10	-	/	-	>1	<5

Ruffling	5	0.09~ 0.18	NA	NA	0.4~2.3	<5 (water) / >10 (air)
Scratching	5	0.12~0.16	-10~ 0	NA	1.8~5.8	<5 (water) / >10 (air)
Preening	5	-	-10~ 0	NA	0.7~1.5	<5

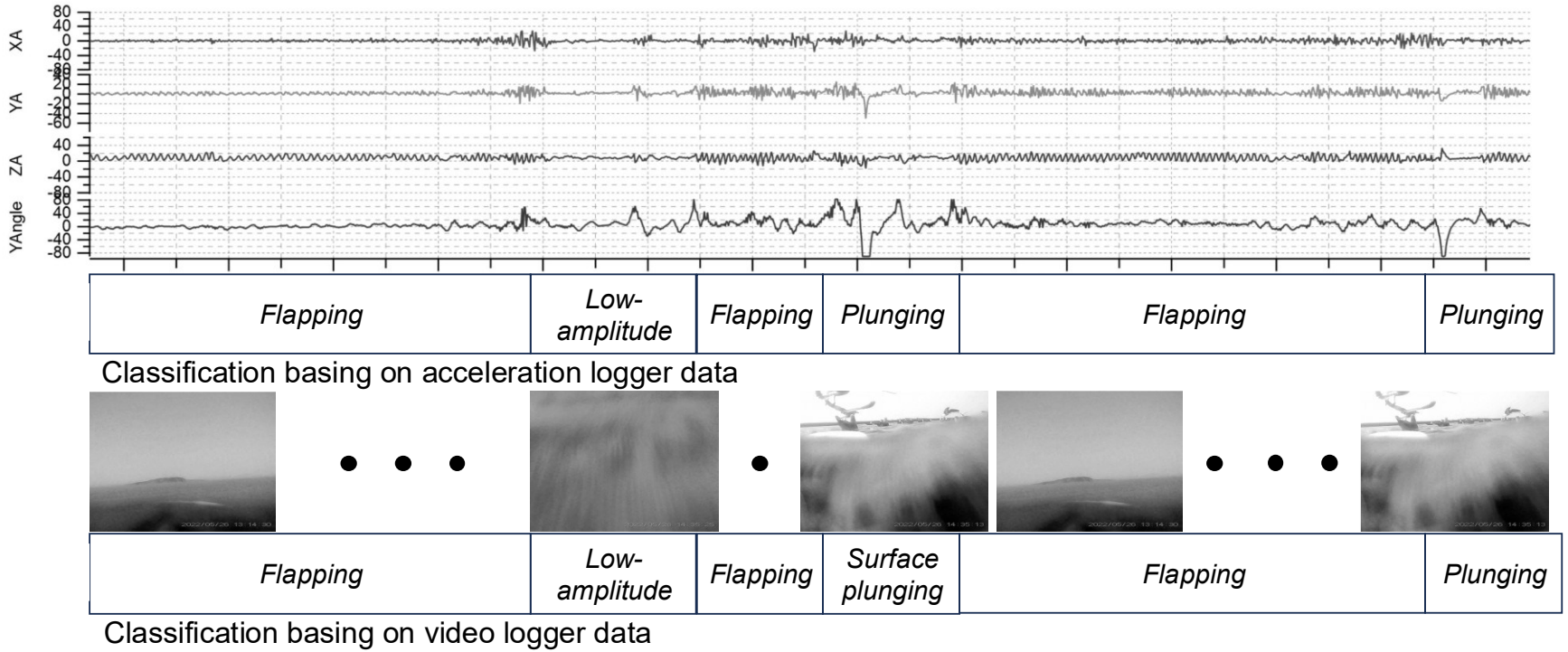


Fig. 3-2 An example of classification for different parts of a foraging event using acceleration logger data and video logger data (ID 1).

3.3 RESULTS & DISCUSSION

Effects of device

Change in body weight in birds with AxyTrek mini (10g, recapture in around 4 days, next chapter) was -17±31 g when birds with video logger and accelerometer (20g, recapture in around 1 days) is-22±14 g, not showing a significant difference between 2 groups (T-test, p=0.5), although, the weight of device approximated or exceeded 3% of body weight of the birds. Lida et al. (2024) also showed a similar result in rhinoceros auklets that have a similar body mass to black-tailed gulls. Rhinoceros auklets can carry a heavy load in long flights (Okada & Watanuki 2023). Increase in weight of the logger may be within the range of change in prey weights, thus not significantly affected their health.

Identification of behaviors

Video-images showed the birds making flights (*flapping*, **Fig. 3-3a**), head-bathing (*bathing*, **Fig. 3-3b**), surface plunging (*plunging*, mainly around the fishing boats, **Fig. 3-3c**), and swimming (*low-amplitude*, **Fig. 3-3d**). In one bird (ID: 9), back feathers covered the lens, and no effective footage was obtained (**Table 3-1**). Excluding the data from this bird, I used the data from other five birds for the analysis. From the 12.5 hours of footage, a total of 19098 one-second windows of *flapping*, 3374 of *bathing*, 64 of *plunging* and 9170 of *low-amplitude* were identified (**Table 3-3**). Basing on video-images, the birds rarely exhibited *plunging*. Instead, they foraged mainly by surface seizing near the fishing boats (**Fig. 3-3e-h, Table 3-3**).

Of the five birds whose footage was available, three often stayed close to fishing boats. It was sometimes difficult to classify the birds' behavior base on the footage. Because the bodies shook so frequently, it was impossible to determine if the birds were hovering or making an attack. Acceleration usually showed a huge change in body angle; these behaviors may indicate foraging. Birds conducted a turning flight when getting close to the fishing boat. Because a large number of black-tailed gulls gathered around the boat, when flying, they needed to adjust their body angles frequently to avoid collision. They only spent a short time getting very close to the boat. Mostly flying or swimming occurred at a certain distance away from the boat. According to the acceleration data, next to flapping flight, birds spent most of the time swimming, followed by bathing, which is similar to our previous study (Ma et al. 2022). According to the acceleration data, the birds rarely spent more time for swimming than flying in short trip. Ma et al. (2022) concluded that, most individuals chose to travel more and

spent less time on water, which is consistent with this study, perhaps reflecting a higher foraging efficiency by doing so. The footage of long swimming sessions of birds that could last for more than an hour, before and after these sessions, from the air, the camera recorded that no aggregation of birds was existed, perhaps reflecting the fact that the bird swam solitarily during these long sessions. Although the beak was not recorded in these sessions due to the camera angle, the shaking of the body, that is different from swimming or bathing, suggests that the birds were probably making a lot of surface seizing in these sessions. Yoda et al. (2012) also recorded black-tailed gulls, which fed close to human houses, and concluded that some part of food resource of them were related to human.

Accuracy of behavior detection

Behaviors determined based on the footage almost coincided with those identified using body acceleration (**Fig. 3-2e-h**), except for drifting, which has not been recorded in the footage. The fraction of 1-second windows identified as *Passive state* behaviors by body acceleration was 0.3%. Using the data from the five individuals, the true-positive rate and true-negative rate summed up for more than 90% in *flapping*, *bathing*, *plunging*, and *low-amplitude* (**Table 3-4**). In this study, therefore, the classification of four groups of behaviors, determined using body acceleration, showed high precision (82%-99%) and recall (91%-99%). As no difference across individuals were detected neither, my method is useful for studying multiple individuals (**Table 3-5**). Classification accuracy in this study was comparable to that for streaked shearwaters *Calonectris leucomelas*, carrying video and acceleration loggers on their chest (Garrod et al. 2021); they also used acceleration data to classify flight, foraging and resting.

In the footage of the five individuals, the birds frequently attacked the loggers when they were flying or on the water. I did not classify this behavior by acceleration into any group of behaviors. Using video images, however, the cycles (0.1 - 0.5 s) of accelerations recorded during the attacks fell within the range of *Low-amplitude* (0.2 - 0.4 s); the angle change can be large and would have exceeded the threshold of *Plunging* (20 degree). Therefore, when using body-acceleration, those attacks would have been misclassified as *Low-amplitude* or *Plunging*. Actually, nine (12.5%) out of the attacks identified by video images were misclassified as *Plunging* according to body-acceleration. During the hop plunging, Y-axis acceleration changed probably at higher amplitude whereas it probably changed along Y- and X-axes during the surface seizing. Detailed analyses of body

acceleration along these axes would enable the identification of a logger attack from surface seizing or hop plunging.

Drifting was not recorded in the video images. In the video-images of bird ID: 9 that was excluded from the analyses because the head was not observed as the feathers covered the video lens, the feathers showed no fluctuation for 2 minutes (**Fig. 3-4a**). During this period, the standard deviation of the X and Y axis angles, the criteria of Drifting (Ma et al. 2022), was small (**Fig. 3-4b**). Thus, the bird ID: 9 could be drifting during these 2 minutes. Based on body acceleration, the bird ID: 1 and ID: 2 conducted rapid downward movements with the change of body angle with large amplitude when it was on the water (**Fig. 3-5b),** and the video image showed water splash possibly generated by the beak (**Fig. 3-5a**). Therefore, it would be concluded that body acceleration may be able to detect surface seizing correctly.

Comparison with previous studies

Acceleration and video logger attached to the black-tailed gulls showed that the birds were feeding on insects at sea (Mizutani et al. 2021). In this study, I observed that gulls spent most of their on-water time swimming, but rarely just drifting, spent long time swimming alone, and conducted surface seizing less intensively than in aggregation. This may relate to insect foraging. In streaked shearwaters, loggers attached to the chest were also attacked by them frequently (Garrod et al. 2021). The method they used to identify each behavior was similar to the present study, and the accuracy of classification was also at the same level. They also record short flights and surface plunging made by birds in aggregations with large fish or marine mammals. Thus, these behaviors can properly act as an indicator of foraging aggregations. Tsukamoto et al. 2018 classified surface seizing of black-footed albatross *Diomedea nigripes* attached with an accelerometer, and showed that approximately half of this behavior was accompanied by significant changes in body angle. The intensity of attacks on surface seizing may vary a lot. Therefore, it has been concluded that the accelerometer should be attached to the neck or head to accurately record this behavior.

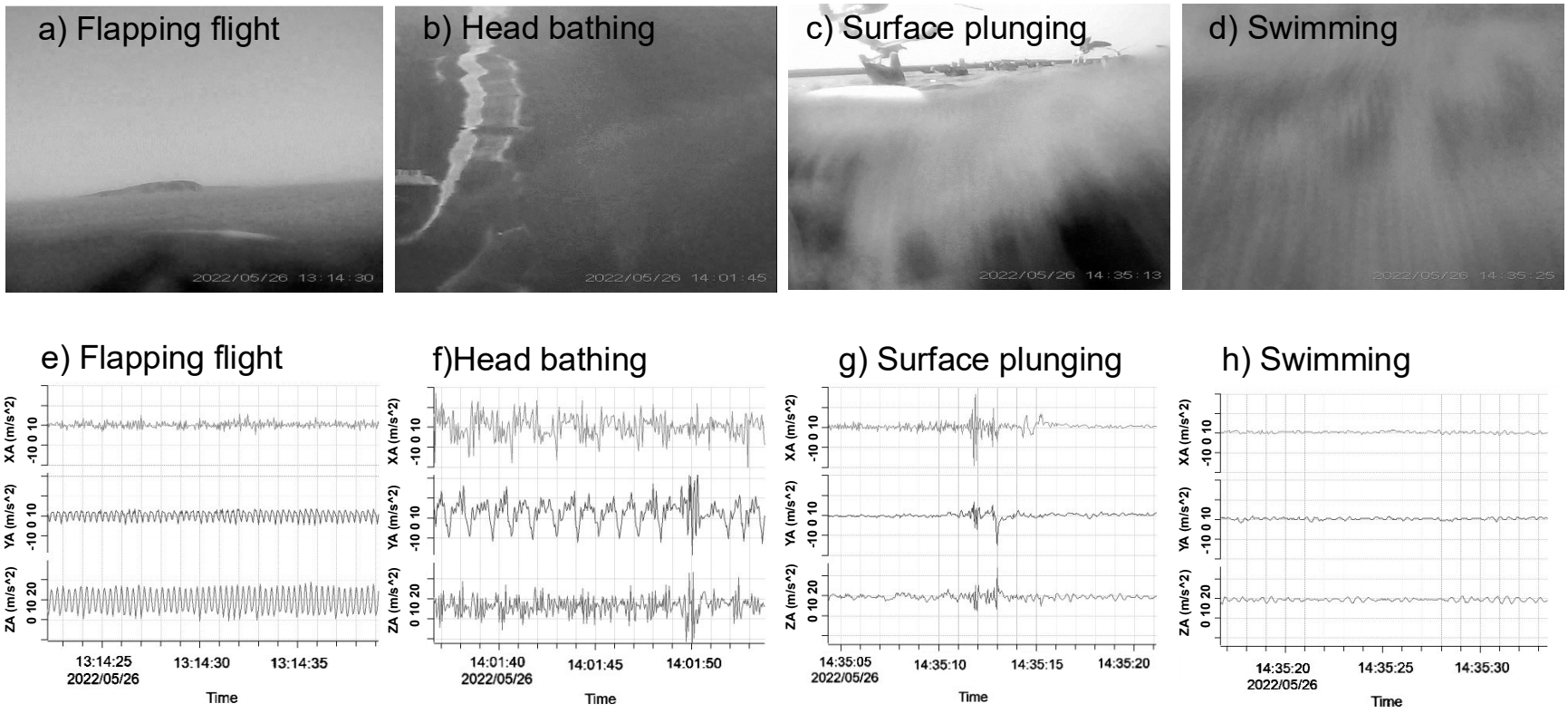


Fig. 3-3 Pictures taken by video-logger on the back of the black-tailed gulls conducting different behaviors (upper) with accelerometry data simultaneously taken (bottom) (a), head bathing (distortion in picture showing head submerging in water when bathing) (b), surface plunging (c), and swimming (head was up and blocked the view of the camera, swimming was identified by the shaking frequency of the body) (d) and the acceleration XA (head-tail), YA(dorso-ventral), ZA (left-right) sampling at 25 Hz, recorded during the corresponding period below (e-h).

Table 3-3 Total duration of each behavior cluster classified by acceleration and video.

Bird ID	*Flapping flight* in video *(s)*	*Flapping flight* in acceleration (s)	*Bathing* in video *(s)*	*Bathing* in acceleration (s)	*Plunging* in video (s)	*Plunging* in acceleration (s)	*Swimming* in video (s)	*Swimming* in acceleration (s)
1	3917	3881	1319	1290	25	23	3962	4030
2	1989	1988	817	940	19	25	3389	3218
3	5075	5063	372	413	11	13	1235	1197
8	4785	4780	384	336	8	9	470	484
11	3332	3319	482	494	1	1	114	109

Table 3-4 Confusion matrices showing the accuracy in distinguishing different behaviors against those based on video observations; left upper: Flapping, right upper: Bathing, left bottom: Plunging, and right bottom: Low-amplitude.

Flapping		Predicted	
		Positive	Negative
Actual	Positive	18839 (true positive)	259 (false negative)
	Negative	191 (false positive)	12380 (true negative)

Bathing		Predicted	
		Positive	Negative
Actual	Positive	3183	191
	Negative	290	27948

Plunging		Predicted	
		Positive	Negative
Actual	Positive	58	6
	Negative	13	31535

Low-amplitude		Predicted	
		Positive	Negative
Actual	Positive	8737	396
	Negative	301	22178

Table 3-5 Confusion matrices showing the accuracy in distinguishing different behaviors for each individual against those based on video observations.

Flapping (ID. 1)		Predicted	
		Positive	Negative
Actual	Positive	3819 (true positive)	98 (false negative)
	Negative	61 (false positive)	5245 (true negative)

Bathing (ID. 1)		Predicted	
		Positive	Negative
Actual	Positive	1190	129
	Negative	100	7804

Plunging (ID. 1)		Predicted	
		Positive	Negative
Actual	Positive	22	4
	Negative	2	9196

Low-amplitude (ID. 1)		Predicted	
		Positive	Negative
Actual	Positive	3829	133
	Negative	201	5060

Flapping (ID. 2)		Predicted	
		Positive	Negative
Actual	Positive	1908	81
	Negative	80	4145

Bathing (ID. 2)		Predicted	
		Positive	Negative
Actual	Positive	817	0
	Negative	123	5274

Plunging (ID. 2)		Predicted	
		Positive	Negative
Actual	Positive	18	1
	Negative	7	6188

Low-amplitude (ID. 2)		Predicted	
		Positive	Negative
Actual	Positive	3201	188
	Negative	17	2808

Flapping (ID. 3)		Predicted	
		Positive	Negative
Actual	Positive	5057	18
	Negative	6	1612

Bathing (ID. 3)		Predicted	
		Positive	Negative
Actual	Positive	372	0
	Negative	41	6280

Plunging (ID. 3)		Predicted	
		Positive	Negative
Actual	Positive	11	0
	Negative	2	6680

Low-amplitude (ID. 3)		Predicted	
		Positive	Negative
Actual	Positive	1187	48
	Negative	10	5448

Flapping (ID. 8)		Predicted	
		Positive	Negative
Actual	Positive	4749	36
	Negative	31	831

Bathing (ID. 8)		Predicted	
		Positive	Negative
Actual	Positive	323	61
	Negative	13	5250

Plunging (ID. 8)		Predicted	
		Positive	Negative
Actual	Positive	7	1
	Negative	2	5637

Low-amplitude (ID. 8)		Predicted	
		Positive	Negative
Actual	Positive	419	51
	Negative	65	5112

Flapping (ID. 11)		Predicted	
		Positive	Negative
Actual	Positive	3306	26
	Negative	13	584

Bathing (ID. 11)		Predicted	
		Positive	Negative
Actual	Positive	481	1
	Negative	13	3434

Plunging (ID. 11)		Predicted	
		Positive	Negative
Actual	Positive	1	0
	Negative	0	3928

Low-amplitude (ID. 11)		Predicted	
		Positive	Negative
Actual	Positive	101	13
	Negative	8	3807

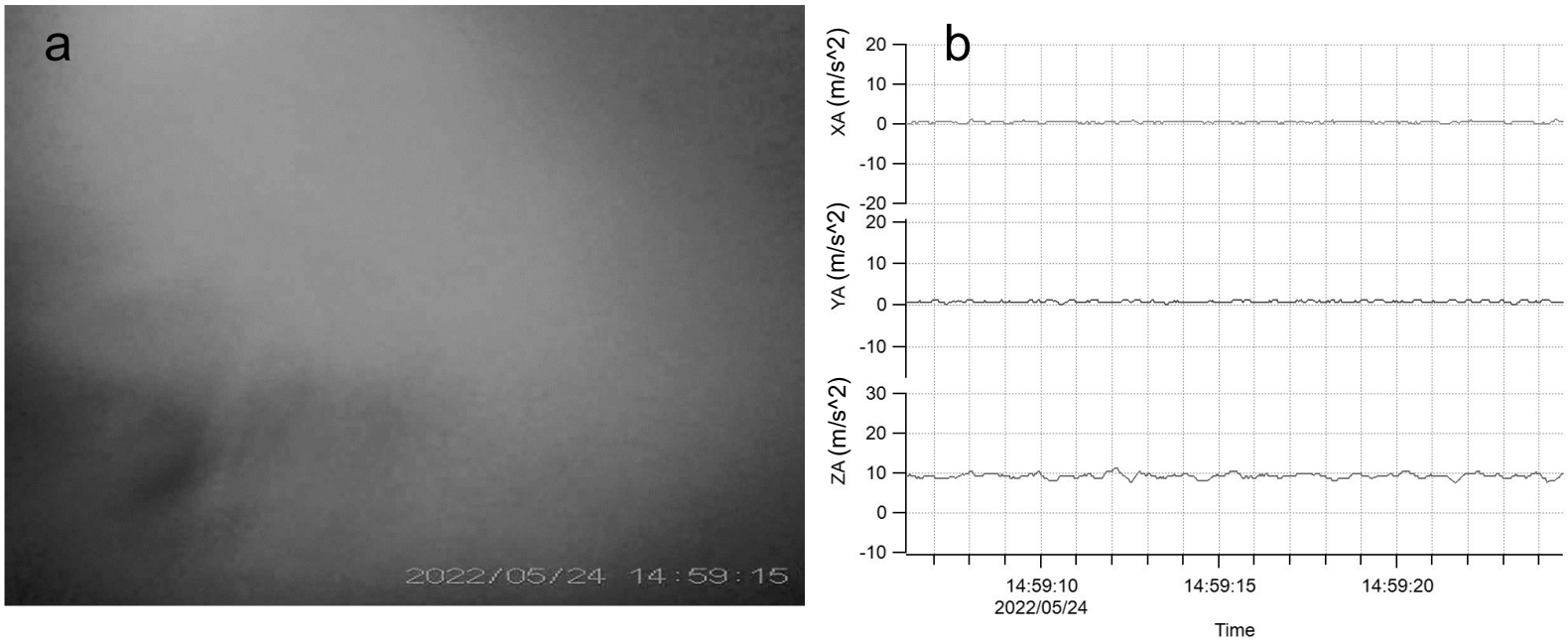


Fig. 3-4 a) A picture taken by the video-logger mounted on the back of bird (ID 9) conducting drifting behavior (different from swimming, video showing almost no movement in the feathers). b) Records of body acceleration (XA, head-tail; YA, dorso-ventral; ZA, left-right) recorded in the corresponding time.

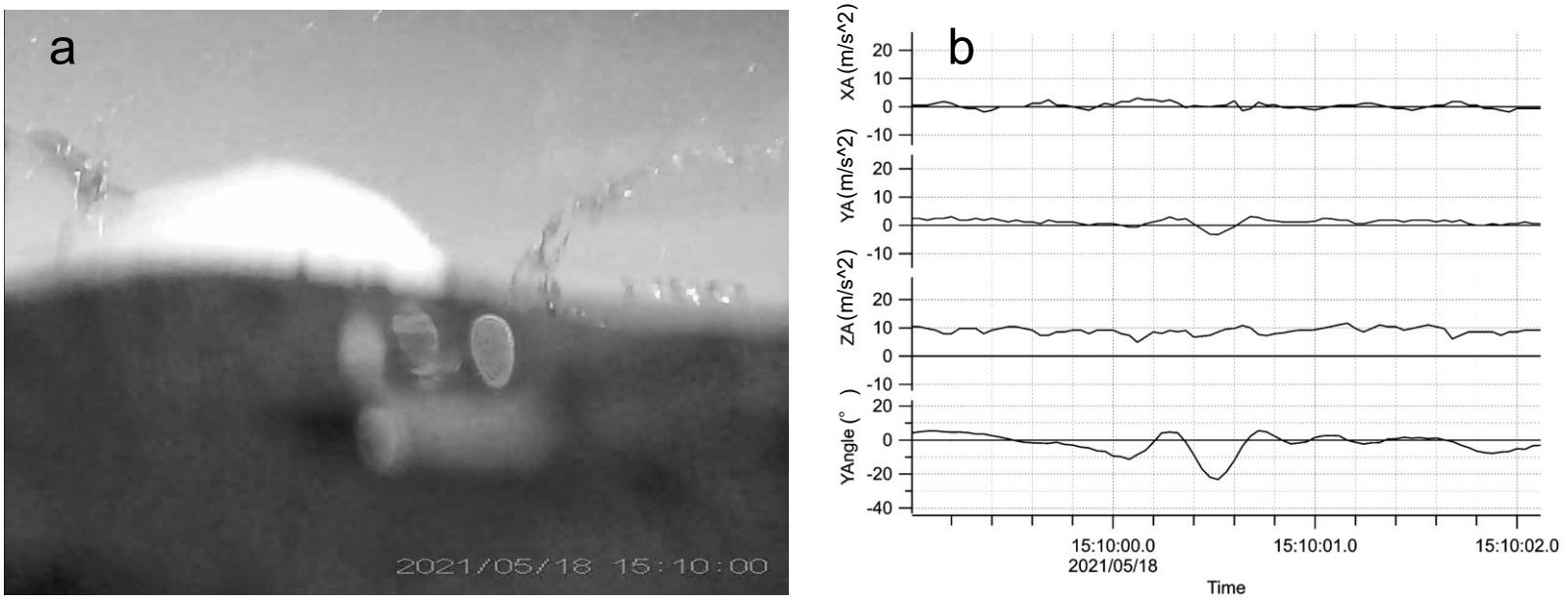


Fig. 3-5 a) A picture taken by a video logger attached to a bird (ID 1) conducting surface seizing (water splashes generated by beak attack). b) Records of body acceleration (XA, head-tail; YA, dorso-ventral; ZA, left-right) and the body angle (YAngle) in the corresponding time.

Chapter 4 Modeling hovering

4.1 INTRODUCTION

Thanks to the development of biologging technology, GPS logger is now miniaturized and can be applied to even small birds (Campion et al. 2020, Soanes et al. 2015). GPS tracking data of seabirds have been accumulating and used for identifying important marine areas (mIBAs; BirdLife International 2010, EBSAs; Lascelles et al. 2016, Sydeman et al. 2012; Wong et al. 2018, see Chapter 1, and MPA; Hays et al. 2019). Recently, a combination of GPS and accelerometer, camera or time-depth recorder enabled identifying the intensively used foraging areas (Hussey et al. 2015, Kays et al. 2015, Ma et al. 2022). These combinations, however, increase the loads due to loggers and may cause adverse effects on birds (Chivers et al. 2016, Evans et al. 2020). Thus, the technique of estimating the intensively used area by GPS track is essential.

The foraging behaviors in diving seabirds can be determined solely by GPS data. As GPS signals disappear when birds are in the water, with shape of GPS track and the percentage of location of GPS signal, dive can be estimated accurately using models constructed by machine learning (deep learning) (Browning et al. 2017, Roy et al. 2022). However, in the surface-feeding or shallow-diving seabirds, the GPS coverage ratio is unusable to detect foraging (Cianchetti et al. 2017). The movement speed of surface-feeding species based on GPS locations can be categorized into stationary or traveling modes (Weimerskirch et al. 2005). The area-restricted searching (ARS) is believed to indicate foraging behaviors and has been confirmed in diving seabirds (Sommerfeld et al. 2013). However, if the ARS indicates that the foraging behaviors of surface-feeding and shallow-diving seabirds have not been examined yet, as surface-feeding species are more likely to use ARS to adapt to environmental conditions, prey are sometimes captured opportunistically (Weimerskirch et al. 2007). Although ARS areas across large spatial-temporal scales may be related to foraging (Regular et al. 2013, Ma et al. 2022), small-scale foraging can be overlooked at the same spatial-temporal scale. As these small spots are often used by a large number of foraging seabirds (Viswanathan et al. 2000, Fritz et al. 2003), detecting these small spots by GPS locations should provide direct evidence of intense use of areas, although it is challenging.

In Chapter 2, it has been shown that black tailed gulls *Larus crassirostris* change their flight mode with size and type of feeding aggregations; the gulls are likely to take

hovering when they are foraging in high density aggregation but take short flight when they are foraging in lower density aggregation. Plunging was not related to the size and type of aggregations. Short flight can be distinguished easily by flights (> 4.7 m/s, Ma et al. 2002) of short duration (< 5 s, Chapter 2) that is determined solely by GPS data. However, acceleration data was essential to distinguish hovering. If it is able to be detected only by GPS tracks, feeding aggregations can be easily located using hovering and short flight that is modeled and observed by means of only GPS tracks. Unfortunately, surface seizing, an important foraging behavior, was not distinguished with high accuracy (Ma et al.2022), in Chapter 3, I also recorded birds foraging solitarily using surface seizing for long duration. Thus, surface seizing is not used to predict foraging aggregation in this study.

In this chapter, I endeavored to identify hovering of black-tailed gulls using solely GPS tracks. I deployed GPS loggers and accelerometers simultaneously and then identified hovering (observed) using speed and wing flapping following Ma et al. (2022). Using 80% of individuals (train group), I constructed a model distinguishing hovering (modeled) through the recurrent neural network (RNN) using hovering determined by GPS-acceleration data as train data. RNN is considered to be a robust method for time series data and has been used in determining animal behaviors (Nunes et al.2021, Weerd et al. 2015). Accuracy of result was tested by comparing with other 20% of individuals (test group).

4.2 MATERIALS AND METHODS

Fieldwork

I conducted fieldwork in Kurosaki colony at Teuri Island (44°N, 141°E) where over 2000 pairs of black-tailed gulls bred (Teuri Seabird Research Institute Unpublished), Hokkaido, Japan, during the incubation period (from May to June) in and 2022. Using a snare trap, I captured 26 birds incubating on the nests (**Table 4-1**). I weighed and measured them and then attached a GPS and 3-axis accelerometer (AxyTrek Mini, Techno SmArt, Italy, 34 × 13 × 6 mm, 5 g including battery) to the back feathers using Tesa tape (**Fig. 4-1**). The total mass of these two data loggers and tape was 10 g, which equates to 1.4% and 1.7% of body mass for male (680 g) and female (580 g) black-tailed gulls (Chochi et al. 2002), respectively. These proportional masses of loggers were below the critical logger–body mass ratio (3%) that may reduce flight efficiency in albatrosses and petrels (Phillips et al. 2003). All 26 birds were recaptured using box traps 3–5 days later, and the devices were retrieved from 24 birds while two of them

were lost. The data was downloaded from 24 birds but one malfunctioned because of water leakage and one was dropped, giving 125 foraging trips (**Table 4-1**) from 23 birds.

The GPS loggers were set to record GPS location at 1Hz from 3:00 to 20:00. The acceleration along 3-axis [sway (X, left to right), surge (Y, tail to head), and heave (Z, ventral to dorsal)] were recorded at 25 Hz. Acceleration recorded at G, and I calibrated 1 G = 9.8 m/s^2. This sampling rate of acceleration allowed to identify behaviors involving high-frequency body movements such as wing flapping and ruffling (Ma et al. 2022).

Determination of behavioral state

At-sea behaviors within 1 s window were classified into 8 categories using body acceleration and speed: flapping flight, gliding, hovering, ruffling, surface plunging, hop plunging, surface seizing/swimming and drifting (**Figs. 4-2** and **4-3**). Body acceleration was analyzed as in Chapter 3 and Ma et al. (2022). Hovering (observed) was classified when cycle of heave acceleration was inside the cycle range of flapping behavior and amplitude was above the threshold (**Table 3-2**, Chapter 3). Then, as the aim of this study was to distinguish hovering (flapping flight in low moving speed) using GPS data only, I classified other behaviors including high-speed flapping flight/gliding, surface plunging/hop plunging, surface seizing/swimming and ruffling/drifting into a single type, others.

Train and test

Data from randomly selected 20 individuals (ca. 80% of the entire data, **Table 4-1**) were used for training, and data from remaining 4 individuals were used for testing the prediction accuracy. Behavioral state (hovering vs others) determined using acceleration and GPS locations as above was objective variable in the model construction. Longitude and latitude of GPS data were transferred to Universal Transverse Mercator (UTM) coordinates, comprising coordinate X and Y. Then difference of X and Y between each point were calculated. X-difference and Y-difference of X and Y coordinates per second within a window of 10, 30, 60 s, were explanatory variables (**Fig. 4-4**). Long Short-Term Memory (LSTM), a type of recurrent neural network (RNN), was used to model the behavioral states. I used the TensorFlow package in R (Allaire & Tang Y 2024), that have been widely used for conducting machine learning and deep neural networks research. Model included a sequential input layer to input explanatory variables (X-

difference, Y-difference), followed by three hidden layers (a series of artificial neurons that processes the inputs received from the input layers before passing them to the output layer) that used for testing the relation between the characteristics of different scales of track data and behavioral state, each of which includes a certain number of artificial neurons (a function that receives one or more inputs, applies weights to these inputs, and sums them to produce an output), and a dense output layer (a layer feeds all outputs from the previous layer to all its neurons, each neuron providing one output to the next layer, **Fig. 4-5**). The model was trained 10 times before final output that used to model hovering. Then, I calculated the presence/absence of Hovering in each 1 to 30 s sampling size both from modeled data and test data as I consider bird performed a hovering (presence) in each sample. First, Youden's index analysis was used to find the best size of sample in separating the status into hovering and others by giving the best match with the observed state of test data. Then using these thresholds, I calculated a confusion matrix of observed hovering vs modeled hovering for each size of window.

Table 4-1 Data for 26 individuals attached with loggers, of which 24 retrieved data, 20 of them were used for training, and four were used for testing. Note that the proportion of hovering was within the range of 1-10%, except for ID-1.

Bird ID	Date of capture	Logger start	Time capture	Mass at capture	Date of recapture	Time of recapture	Mass at recapture	Sex	No. of trip	Note	*Hovering*	*Others*	Train / Test
1	2022-05-09	6:39	6:54	540	2022-05-12	10:09	545	F	6		10386	63974	Train
2	2022-05-09	7:35	8:07	530	2022-05-12	15:50	535	F	9		6858	77168	Train
3	2022-05-09	8:37	8:50	645	2022-05-12	9:15	690	M	–	Leakage	–	–	–
4	2022-05-09	9:18	9:40	550	2022-05-12	14:02	580	F	3		1795	61263	Train
5	2022-05-10	6:50	7:10	635	2022-05-15	9:47	620	M	5		3787	73048	Train
6	2022-05-10	7:35	7:53	600	2022-05-12	16:31	560	F	3		850	24932	Train
7	2022-05-10	8:37	8:50	510	2022-05-13	13:57	520	F	3		3694	55851	Test
8	2022-05-10	9:13	9:25	660	2022-05-12	14:48	685	M	3		1539	39908	Train
9	2022-05-13	15:21	15:40	580	2022-05-16	9:16	570	F	4		7031	62876	Train
10	2022-05-13	16:13	16:29	700	–	–	–	–	–	Dropped	–	–	–
11	2022-05-13	17:10	17:57	580	2022-05-16	14:48	530	F	2		3863	41652	Test
12	2022-05-15	10:25	10:41	725	2022-05-19	19:13	695	M	7		5746	79129	Train
13	2022-05-15	11:07	11:17	530	2022-05-19	17:35	520	F	7		6144	111826	Train
14	2022-05-15	11:40	12:05	550	2022-05-19	13:34	520	F	4		464	41521	Train

15	2022-05-16	9:51	10:06	690	2022-05-20	16:25	665	M	4	3936	126959	Train
16	2022-05-17	12:43	12:56	650	2022-05-21	16:50	640	M	4	1494	49452	Train
17	2022-05-21	9:57	10:16	535	2022-05-25	11:09	530	F	6	3756	79153	Train
18	2022-05-21	10:39	10:45	810	2022-05-25	10:45	765	M	6	922	45061	Train
19	2022-05-21	11:12	11:26	785	2022-05-25	16:40	725	M	13	2545	100066	Test
20	2022-05-21	11:42	11:58	690	2022-05-26	8:05	625	M	8	1673	71329	Train
21	2022-05-22	11:05	11:21	620	2022-05-25	17:17	580	F	3	450	38992	Train
22	2022-05-31	8:59	9:36	565	2022-06-03	17:52	580	F	7	4322	41829	Train
23	2022-05-31	9:53	10:48	705	2022-06-05	13:55	665	M	10	11035	109521	Train
24	2022-05-31	11:13	11:37	600	2022-06-04	15:00	615	F	3	3218	38079	Train
25	2022-05-31	12:03	12:36	800	2022-06-03	17:01	785	M	4	1388	28917	Test
26	2022-06-01	8:45	8:59	735	2022-06-04	14:05	650	F	1	1632	14273	Train

Fig. 4-1 Picture showing AxyTrek mini attached to the back feathers of a black-tailed gull.

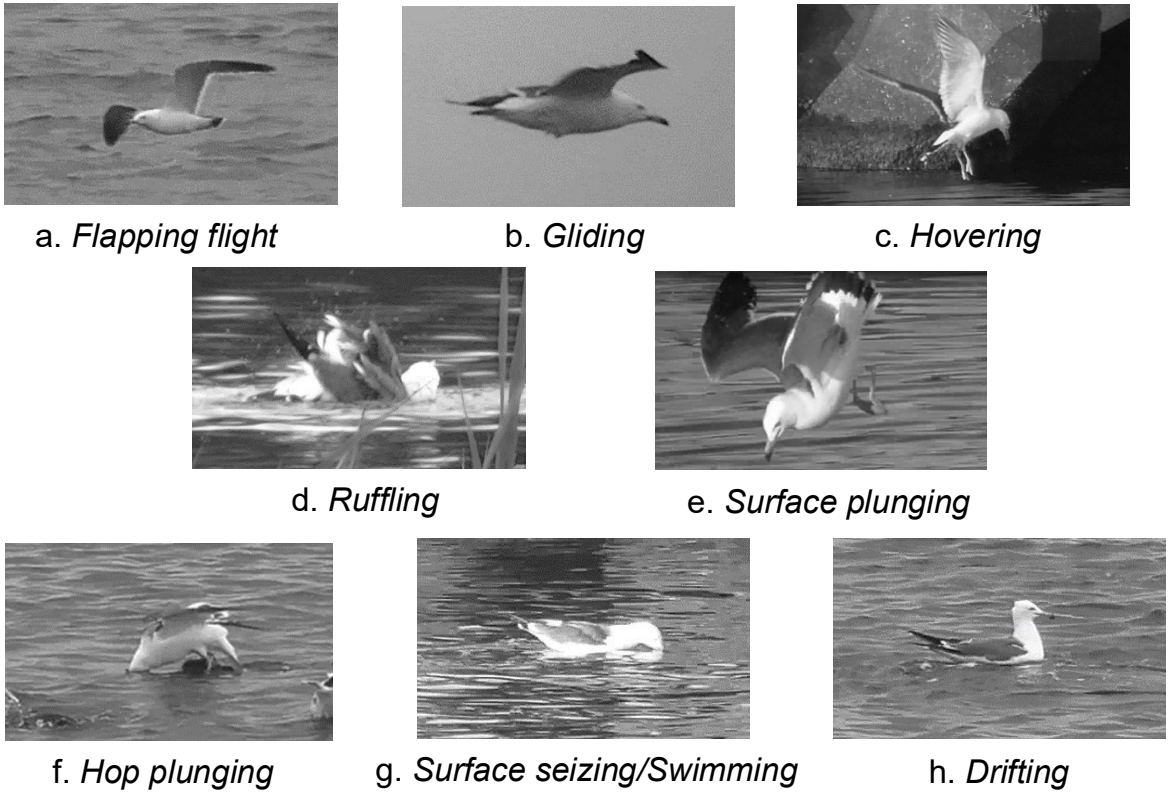
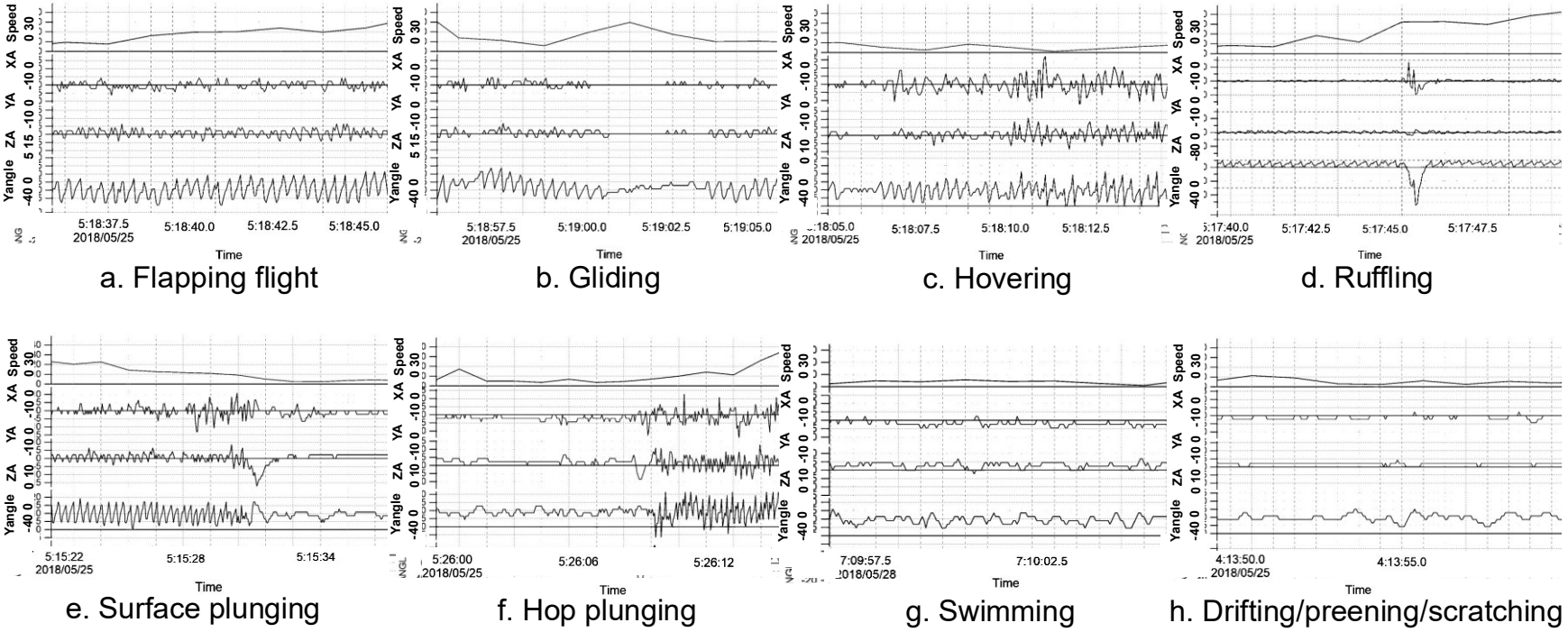


Figure. 4-2 Pictures of flight (a. Flapping flight; b. Gliding; c. Hovering), maintenance (d. Ruffling; h. Drifting) and foraging behaviors (e. Surface plunging; f. Hop plunging, g. Surface seizing) of black-tailed gulls.



a. Flapping flight b. Gliding c. Hovering d. Ruffling

e. Surface plunging f. Hop plunging g. Swimming h. Drifting/preening/scratching

Fig. 4-3 Body acceleration (XA (head-tail, measured in m/s^2), YA(dorso-ventral, measured in m/s^2), ZA (left-right, measured in m/s^2)), and Yangle (upside-down, measured in °) determined by accelerometers and speed (measured in km/h) determined by GPS locations of birds conducting of flight (a, flapping; b, gliding; c, hovering), maintenance (d, ruffling; h, drifting) and foraging behaviors (e, surface plunging; f. hop plunging, g, surface seizing). See corresponding pictures in Figure 4-2.

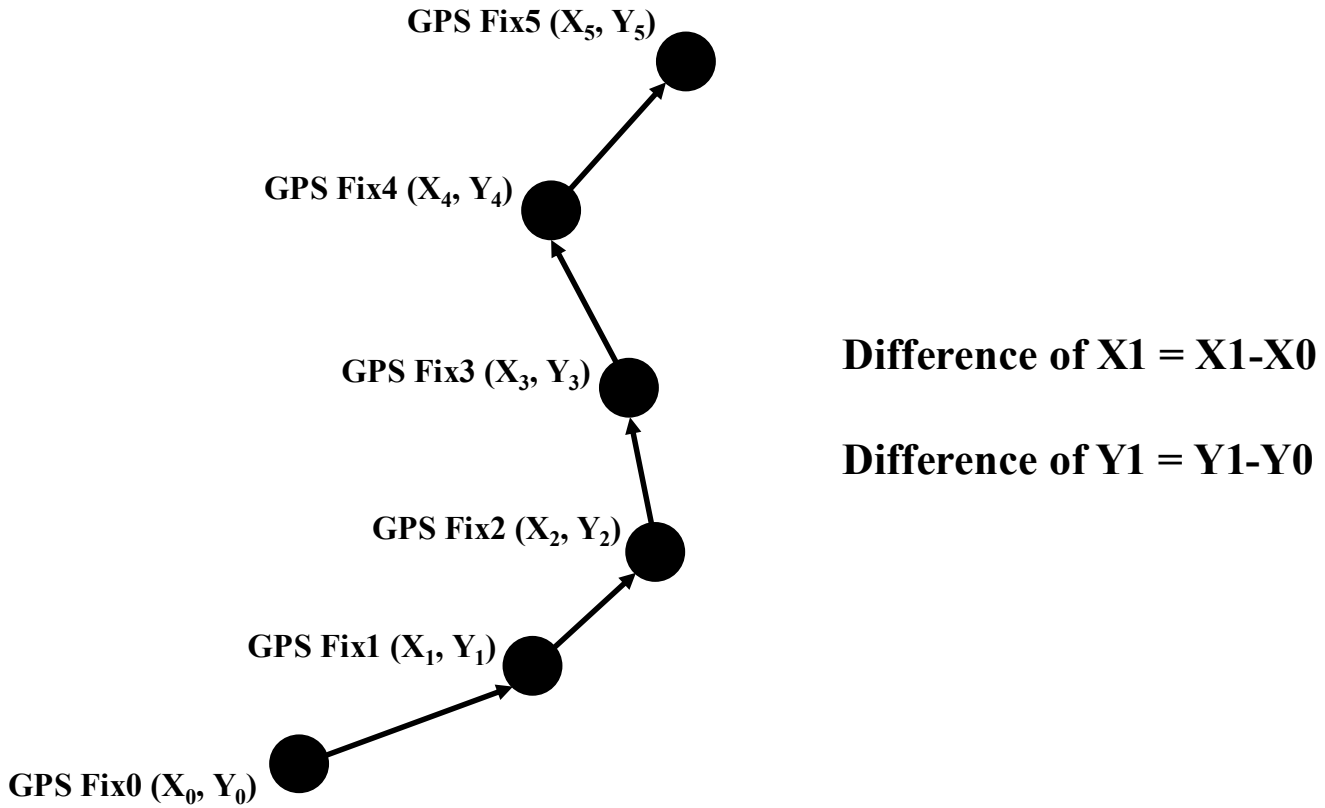


Fig. 4-4 X-difference and Y-difference between each GPS location. We used difference between each point to exclude the effect of actual longitude and latitude when training the model, we used these 2 factors to figure out if there is specific spatial pattern recorded when hovering.

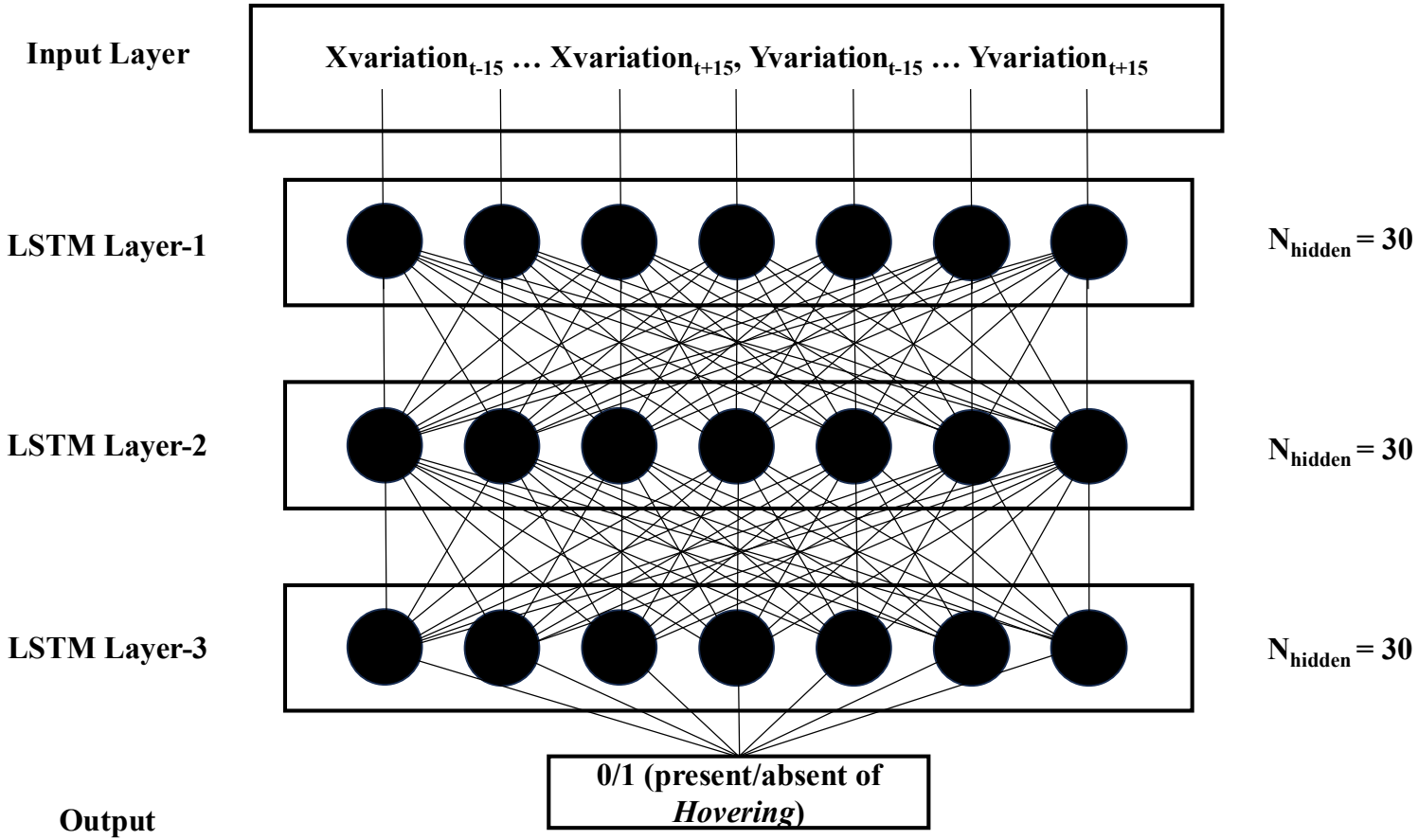


Fig. 4-5 Structure of the LSTM network, which includes one input layer (track data), 3 hidden layers (data training) and 1 output layer (prediction). I used three types of layers to figure out the relation between track data and the presence/absence of hovering, and tried to predict based on the track data only.

4.3 RESULTS

The proportional time of observed hovering was averaged 0.056±0.033, and varied among individuals (0.01-0.14). However, there was no difference between train and test groups (t test. P=0.44, **Table 4-1**).

All window sizes show no or only slight differences in prediction accuracy (**Table 4-2**), where the 30 s window showed slightly larger in accuracy. Therefore, I used this size of window for training. Youden's index (sensitivity + specificity - 1) reached its maximum value when using the sampling sizes 15-20 s (**Fig. 4-6**.). I therefore used 15 s as sampling threshold for identifying presence/absence of hovering. A sample of the modeling result was shown in **Fig. 4-7**.

Using an optimal threshold, I separated modeled hovering and others for each size of window. Modeled values matched true values well for all four individuals (**Fig.4-8, Table 4-3)**. The precision (true positive/predicted positive) of modeled hovering (presence of hovering) was 51%, 72%, 67% and 79%, whereas recall (true positive/actual positive) was 91%, 86%, 78% and 83% for Bird 7, 11, 19, and 25, respectively (**Table 4-2**). Using all four test individuals, the precision was 64% (1118/3136) and recall was 86% (2018/2360). Accuracy: (True negative + True negative)/Total, was 91% (13647/15107; **Table 4-3**).

I also tried to use GPS data in lower resolution at 2 s and 10 s interval, I used the sampling size of 20 s considering 1 s interval data showed highest Youden's index between 15-20 s and 20 s size would match the 10 s interval data better. Using GPS data re-sampled at 2 s interval, the ability to predict hovering was similar compared to that derived from 1-s data; using similar sample size, precision and recall was 71% and 79%, respectively and accuracy was 91% (**Table 4-4**), using 10 s re-sampled data, in 20 s sampling size the precision and recall decreased to 50% and 100%, respectively, whereas accuracy was 91% (**Table 4-4**). When compared with 1 s interval data, which showed precision and recall of 63% and 88%, and accuracy of 89%, a decrease in recall and increase in precision were attained.

Table 4-2 Confusion matrices showing the precision of predicting hovering used for testing, for different durations of time window. Data from four birds were combined

Hovering (10 s window, 15 s block)	Predicted positive	Predicted negative
Actual positive	2031 (True positive)	329 (False negative)
Actual negative	1265 (False positive)	11473 (True negative)

Hovering (30 s window, 15 s block)	Predicted positive	Predicted negative
Actual positive	2018	342
Actual negative	1118	11629

Hovering (60 s window, 15 s block)	Predicted positive	Predicted negative
Actual positive	2063	297
Actual negative	1362	11376

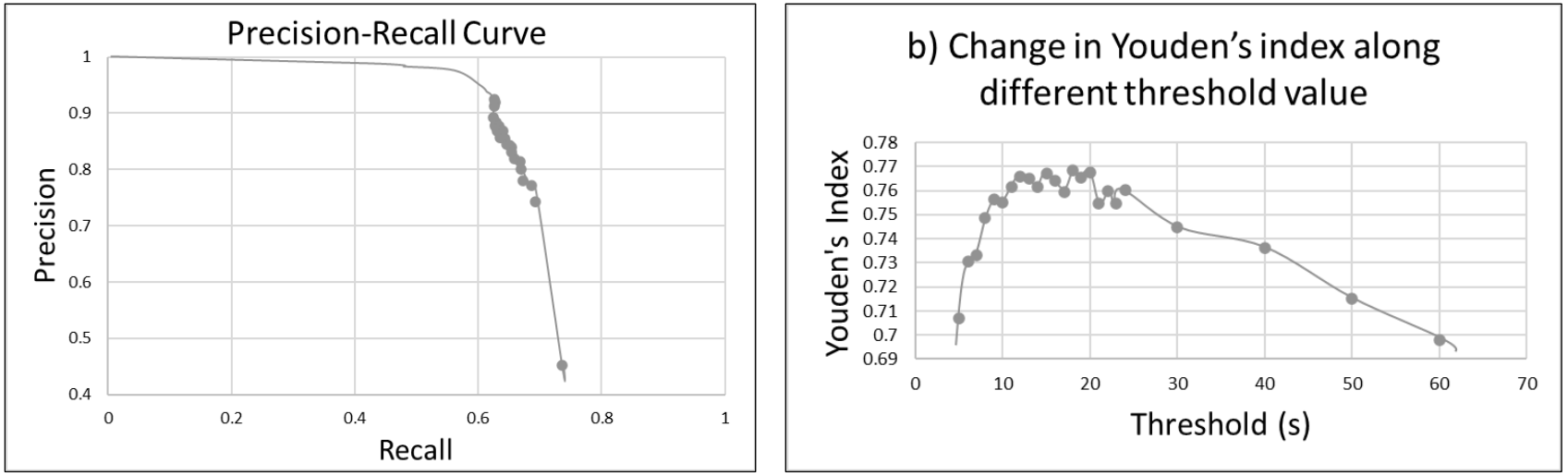
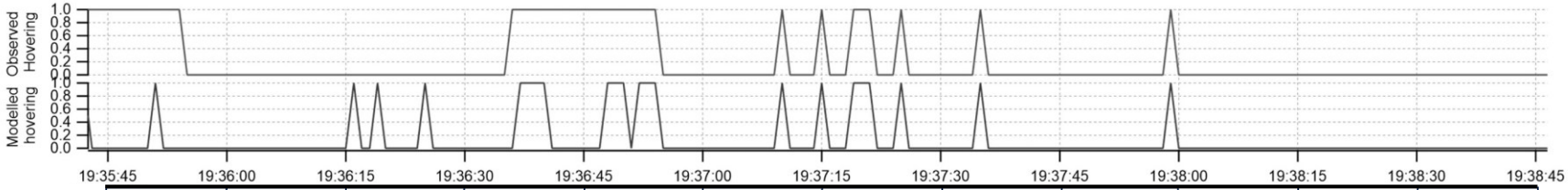


Fig. 4-6 a) Precision-Recall curve to find the threshold to separate each 30 s window as presence/absence of modelled Hovering behaviour. The star indicates the threshold to optimize true/positive and false/positive is around 15-20 s. b) Youden's index showing optimized threshold to be around 15-20 s.



Observed Hovering	presence	absence	absence	presence	presence	presence	presence	presence	presence	absence	absence	absence
Modelled hovering	presence	absence	presence	presence	presence	presence	presence	presence	presence	absence	absence	absence

Fig. 4-7 An example of results from deep learning. In each 15s window, the presence/absence of observed hovering and modelled hovering was calculated. The result was used to analyse the accuracy of the prediction.

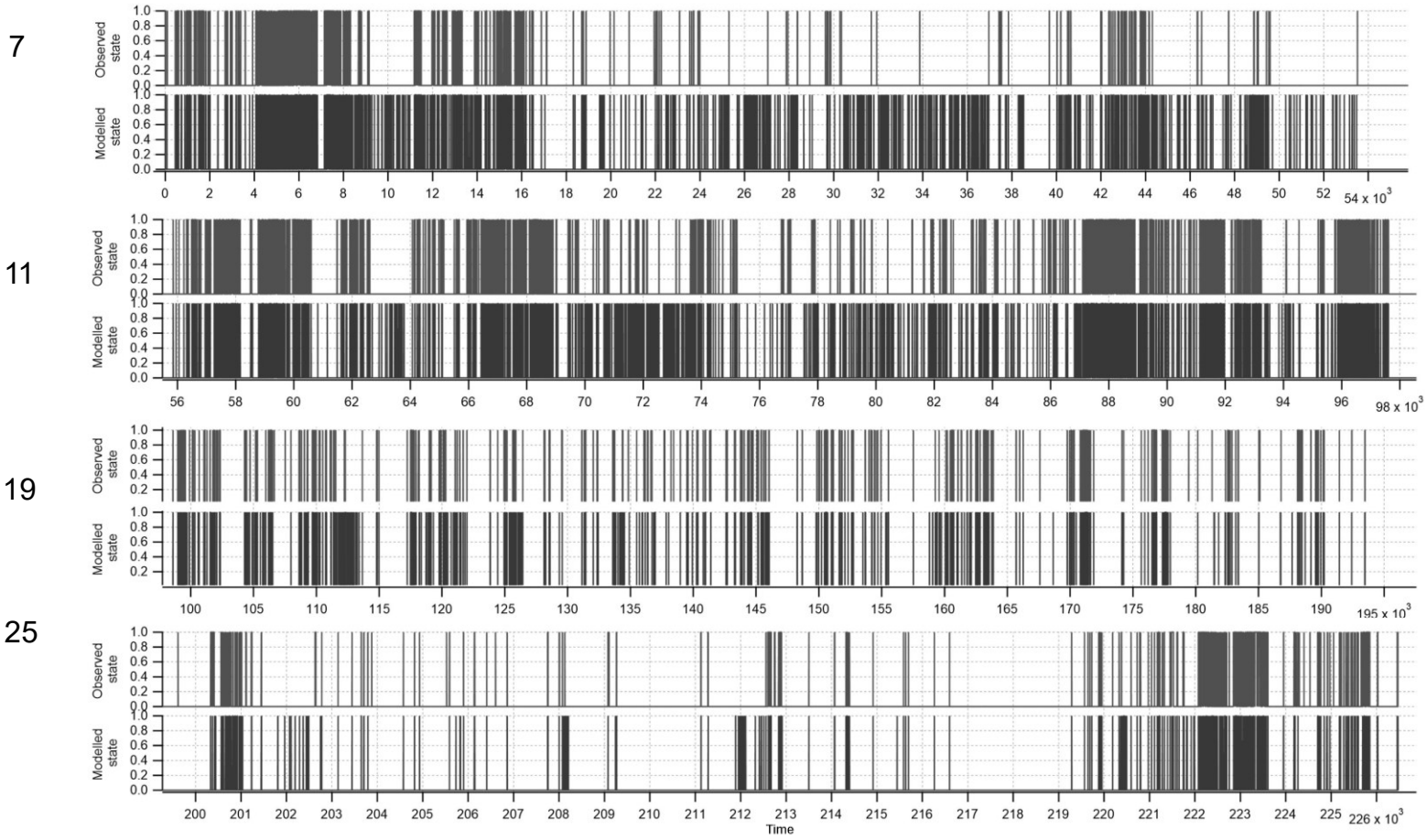


Fig. 4-8 Observed and modelled behavioral status (0/1 means present/absent of *Hovering*) of four birds. Numbers on the left side of the graph show bird IDs.

Table 4-3 Confusion matrices showing the precision of predicting hovering for each individual used for testing.

Hovering (Birds NO. 7)	Predicted positive	Predicted negative
Actual positive	544 (True positive)	55 (False negative)
Actual negative	526 (False positive)	2598 (True negative)

Hovering (Birds NO. 11)	Predicted positive	Predicted negative
Actual positive	787	128
Actual negative	308	1553

Hovering (Birds NO. 19)	Predicted positive	Predicted negative
Actual positive	442	125
Actual negative	221	5883

Hovering (Birds NO. 25)	Predicted positive	Predicted negative
Actual positive	233	48
Actual negative	63	1583

Table 4-4 Confusion matrices showing the precision of predicting hovering for different time interval of GPS data.

Hovering (1 s interval GPS data, 30 s window, sampling size 20 s)	Predicted positive	Predicted negative
Actual positive	1765 (True positive)	248 (False negative)
Actual negative	1018 (False positive)	8293 (True negative)

Hovering (2 s interval GPS data, 30 s window, sampling size 20 s)	Predicted positive	Predicted negative
Actual positive	1582	431
Actual negative	641	8670

Hovering (10 s interval GPS data, 30 second window, sampling size 20 s)	Predicted positive	Predicted negative
Actual positive	1020	997
Actual negative	41	9265

4.4 DISCUSSION

By combining data from GPS and acceleration, foraging behavior was determined (Ma et al. 2022, Chapter 3). I trained the artificial neural networks to model the hovering using GPS locations collected at 1 s interval from 20 individuals. Using the remaining 4 individuals, I examined the accuracy of the model and found the accuracy to be 91%. This study, therefore, suggests that GPS alone can provide useful information on hovering in black-tailed gulls; the suitable indicator of high-density foraging aggregations.

LSTM is a suitable learning model to handling fine-scale time series data and was recommended over other machine learning models (Ruvinga et al. 2021; Williams 2024). A model similar to LSTM was used by Roy et al. (2022) to predict behavioral state in diving seabirds based on tracks. Their model outperformed the fixed-scale model and conventional methods including hidden Markov models. Thus, I used LSTM to find tracks, showing different lengths and tortuosity that corresponded to hovering. Unlike other normal RNN models, LSTM can handle extended time series data (Sherstinsky 2020). Seabird performed multiple scale area restricted searching behavior ARS (Fauchald 2009), that usually correlates to different spatial and temporal scale, thus I considered LSTM more useful in the discrimination of foraging behaviors in seabirds.

The accuracy of estimating behavior by using GPS data depends on the individuals, type of behavior, and the sampling rate of the GPS. There were some inconsistencies between modeled and true values in Bird 7. According to speed and acceleration data, the bird's swimming behavior may be attributed to its high speed (> 1 m/s, **Fig. 3-2h**, Chapter 3). The bird seemed to conducted surface seizing during this period, because this bird increased swimming speed perhaps to chase prey, the moving speed and track changed thus causing misclassification as hovering. Bird 19 shows low recall. According to the speed, it flew at a speed close to the threshold level (4.7 m/s) that was used in Chapter 3 to distinguish flapping flight from hovering. The decrease of speed which likely to be due to the wind, caused the misclassification of flapping flight as hovering. Thus, the model output needs verification to deal with misclassifications, and still wants a modification especially for short-time behavior in future.

My model for classifying hovering using GPS location obtained similar precision (64%) and recall (86%) compared to Browning et al. (2017) (precision: 51-62%; recall: 67-

73%) who modeled diving species using GPS location employing the leave-one-out cross validation method. I used LSTM to make better use of the information contained in the high-resolution GPS tracks. Browning et al. (2017) may not benefit from the same method because of the low fix rate of their GPS data (1 fix/ 100 s). Although my model for the surface-feeding species achieved the same level of accuracy as the model for diving species did, the lower resolution in GPS tracks may have caused unreliable results in my model. Roy et al. (2022) also showed a decrease in accuracy of their model for predicting foraging in diving seabird species, although the decrease was insignificant. The dive durations of the diving seabird species in their study (ca. 1.2 min for European shag, ca. 1 min for Common guillemot, ca. 0.6 min for Razorbill) were longer than hovering in surface feeding seabird. Thus, high sampling rate was required to cover the short in hovering time. I recommend using GPS data with an interval below 10 s in order to predict hovering accurately. Using different window sizes do not make significant change in precision and recall, mostly under 1%, means no increase in the ability to predict hovering.

As hovering was successfully modeled using GPS data solely, I can predict the location of feeding aggregations only by GPS data. Short (2-5 s) and long flight (5-10 s) (see Chapter 2), which are indicators of lower local-group-density foraging aggregations, can be identified directly from their speed (> 4.7 m/s) and durations. Thus, using GPS locations only, I can analyse the relation between the feeding aggregation and the bird's searching behaviors. In conclusion, this study provided a novel tool to locate feeding aggregation in surface-feeding seabirds only by GPS location that is easily applicable even for small seabirds.

Chapter 5 Locations of foraging aggregation

5.1 INTRODUCTION

As seabirds mainly forage in feeding aggregations, the locations of foraging aggregations are robust indicator of areas of high energy flow from prey to seabirds, i.e. important marine areas (Sydeman et al. 2006). Foraging aggregations, however, have been determined only by boat census (Camphuysen et al. 2012; Goyert et al. 2014; Goyert et al. 2018; Michael et al. 2025). New techniques to find foraging aggregations using bio-logging should help study the marine important areas. The foraging areas of surface feeding seabirds, where they may forage in aggregation, or may be associated with the areas where they are probably carried by current and move slowly (< 4.7 m/s), which is easily detected using GPS locations (Yoda et al. 2012; Kazama et al. 2018). If there is a high correlation between areas of foraging aggregations and areas where birds move slowly or show exhibit specific behaviors, the existing GPS location data should give useful information. The aim of this chapter is to find out if the areas with slow-moving speed are associated with the foraging aggregations, and to determine the environmental factors that enhance the formation of foraging aggregations.

Seabirds increase their foraging efficiency by making an aggregation over a prey patch to restrict movement of prey (Thiebault et al. 2015) and by searching a large area to find a prey patch (Fauchald 1999; Veit 1999). As seabirds' foraging aggregations and formation of prey patch occur at various time and spatial scales (Fauchald et al. 2002; Fauchald et al. 2011), the correlation between bird density and prey density should vary across scales (Schneider et al. 1986; Decker et al. 1996; Logerwell et al. 1996; Mehlum et al. 1999; Fauchald et al. 2000; Burger et al. 2004; Ainley et al. 2009; Bertrand et al. 2014). Thus, analyses of foraging aggregations and areas where birds move slowly are needed at various spatial scales.

Determining a spatial scale at which the landscape affects the habitat selection of birds is a very complex question (Lima et al. 1996). Birds probably search landscapes with highly productive using large-scale ARS or sit and wait on water. With this strategy, individual seabirds locate intact prey patches (Lima et al. 1996; Fauchald et al. 2009). Sit-and-wait on water strategy seems to be more preferable for small-sized birds like black-tailed gull in this study, because the cost to land and take off is smaller than large-sized bird (Weimerskirch et al. 2000; Weimerskirch et al. 2007). I considered that on-water areas defined in the previous chapter, was the area where birds used large-scale landscape. The

areas where foraging aggregation are observed indicate the local enhancement over prey patches whose scale should be below 1 km (Kurasawa et al. 2011). I predicted that the correlation between the areas of on-water determined by speed and those of foraging aggregation areas determined by speed and acceleration will diminish in smaller scales.

I found that the behaviors of individual black-tailed gull (*Larus crassirostris*) inform the type of foraging; aggregation or solitarily (Chapter 2); they conducted hovering and short-flight in different foraging aggregations but not during the solitary foraging. In this chapter, I firstly categorized the behavior at 1 s using acceleration and GPS locations as: hovering (observed), short flight (first speed >4.7 m/s, short duration of each flight < 5 s), and on-water using the slow-moving speed (< 4.7 m/s) (Chapter 2).

I then calculated the sum of the time of each behavior in each cell with variable size (100 m to 10 km) to look at the effects of spatial scale. Then 1) I checked if the spatial pattern of the time of modeled hovering was reliable using Spearmen's correlation coefficient with the time of observed hovering across these spatial scales. Also, I checked the correlation between the time modeled hovering and the on-water. To examine if the behavioral correlation depends on the spatial scale, I calculated 2) the correlations between time on-water, observed hovering and short flight were tested. I expected that these correlations might disappear in small scale. As on-water includes non-foraging behaviors, locations of foraging aggregation where birds conducted hovering or short flight might not match with locations of on-water at small scale. Finally, 3) I explored the environmental factors affecting each of time on-water, observed hovering and short flight by habitat modelling.

5.2 MATERIALS AND METHODS

Fieldwork

I conducted fieldwork in Kurosaki colony at Teuri Island (44°N, 141°E), Hokkaido, Japan, during the incubation period (from May to June) in and 2022. More than 2000 pairs of black-tailed gulls breed in this island (Environmental Agency 2023). Using a snare trap, I captured 26 incubating birds on the nests, the same individuals as in Chapter 4. I weighed and measured these birds and then attached a GPS and 3-axis accelerometer (AxyTrek Mini, Techno SmArt, Italy, 34 × 13 × 6 mm, 5 g including battery) on the back feathers using Tesa tape. The total mass of these two data loggers and tape was 10 g, which equates to 1.4% and 1.7% of body mass for male (680 g) and female (580 g) black-tailed gulls, respectively (Chochi et al. 2002). These proportional

masses of loggers were below the critical logger–body mass ratio (3%) that may reduce flight efficiency in albatrosses and petrels (Phillips et al. 2003). The data was downloaded from 24 birds except for one with malfunction due to water leakage and one dropped, giving 125 foraging trips. Among these 24 birds carrying acceleration sensors, the combination of GPS and acceleration were used to distinguish their behavior more precisely as was shown in chapter 3.

The GPS loggers were set to record location at 1Hz from 3:00 to 20:00. The acceleration along 3-axis; sway (X, left to right), surge (Y, tail to head), and heave (Z, ventral to dorsal) were recorded at 25 Hz. They were recorded at G, with calibrated 1G=9.8 m/s2. This sampling rate of acceleration allowed to identify behaviors involving high-frequency body movements such as wing flapping and ruffling (Ma et al. 2022).

Determination of areas of *On-water*, *Hovering* and *Short flight*

Hovering was determined by using body acceleration and GPS locations (flapping at 3-5 Hz) with low moving speed (< 4.7 m/s); Ma et al 2022), *Short-flight* was determined using GSP locations with high speed of moving and short duration of flight (2-5 second duration of moving speed > 4.7 m/s, Chapter 3), respectively, at 1-s intervals. *On-water* (<4.7 m/s) was determined using speed (Chapter 4). Further *Hovering* was modeled using AI and GPS locations (*Modeled hovering*) (Chapter 4).

To compare the relationship among the number of locations with different behaviors in each cell, I calculated Spearman's rank correlation coefficients (r_s). Cell sizes were 100 m × 100 m, 200 m × 200 m, 400 m × 400 m, 1 km × 1 km, 4 km × 4 km and 10 km × 10 km for analysing correlation of total duration of *on-water* and other.

Habitat model

I explored the environmental factors affecting each behavior applying a generalized additive model (GAM) using the mgcv package (Wood 2023); MuMIn package (Bartoń 2024) was also used for model selection. I selected the model that minimized the Akaike information criterion (AIC) value and the delta AIC >2. When multiple models with the delta AIC <2 were constructed, the model with the smaller number of explanatory variables was selected (Burnham et al. 2003). The response variable is the sum of time spend for the hovering, short flight or on-water. Considering the foraging efficiency and prey distribution affected by flight distance (Krebs et al. 2009), sea bottom topography (Freeman et al. 2010), current (Tanaka et al. 2008), and artificial facilities (Kazama et

al. 2018) were considered, while other explanatory factors included colony distance (distance to the middle of colony in Teuri Island), fishing port distance (distance to the closest fishing port), depth of the sea, slope of the depth, sea surface temperature (SST, https://coastwatch.pfeg.noaa.gov/erddap/griddap), and the gradient of SST as an index of the front. Data of depth is provided by NOAA's National Geospatial Data Center (https://www.ncei.noaa.gov/maps/grid-extract/), slope of the depth is calculated using slope function package in QGIS. Data of SST is also provided by NOAA's National Geospatial Data Center (https://coastwatch.pfeg.noaa.gov/erddap/griddap/). I found no significant correlation among the explanatory factors.

5.3 RESULTS

Spatial pattern

Birds performed on-water (36% of whole trips), observed hovering (0.6% of whole trip) and short flight (0.6% of whole trip) extensively in the areas around the colony and at the sea 1-20 km west of the colony, and moderately in the coastal areas near Haboro-city along the mainland of Hokkaido (**Fig. 5-1 abc**).

The Spearman's rank correlation coefficient (rs) between the density of modeled hovering and observed hovering was high at all scales ranging between 0.4 and 0.9, and showed a small peak at 100 m (**Fig. 5-2**), which were significant (T-test, $P<0.01$).

The Spearman's rank correlation coefficients (rs) between the time of on-water and those of hovering, short-flight or modeled hovering in each cell showed relatively low value (0.05-0.5), even at 10 km scale and lower in finer scales, except modeled hovering (**Fig. 5-3a**). Correlations coefficient between on-water and hovering, short-flight and modeled hovering were 0.4, 0.5 and 0.3at 10 km scale, respectively (**Fig. 5-3b**), which were significant (T-test, $P<0.01$).

Environmental factors

Considering prey patches scale which is below 1 km, also the limitation in the availability of environmental factors, habitat modelling (GAM) was carried out only at 1 km scale (**Fig. 5-4**). All adequate models (delta AIC<2) explaining the spatial pattern of the density of locations of on-water included colony distance, fishing port distance, depth slope and SST gradient, whereas that of observed hovering included colony distance, fishing port distance, depth and its slope, and that of short-flight included fishing port distance, depth and depth slope, although the coefficient of determination (R^2) remained low (0.07-0.15)

(**Table 5-1**). The birds tended to exhibit on-water along the coast and areas near the colony, preferred steep depth slope (ca. 3-4 deg) and larger SST gradient; hovering occurred in the areas near the coast and colony, bottom depths ca. 200 m and <50 m and steep depth slope (ca. 3-4 deg); birds conducted short-flight in the area near the coast, depth ca. 200 m and <50 m and steep depth slope (ca. 3－4 deg) (**Fig. 5-4**).

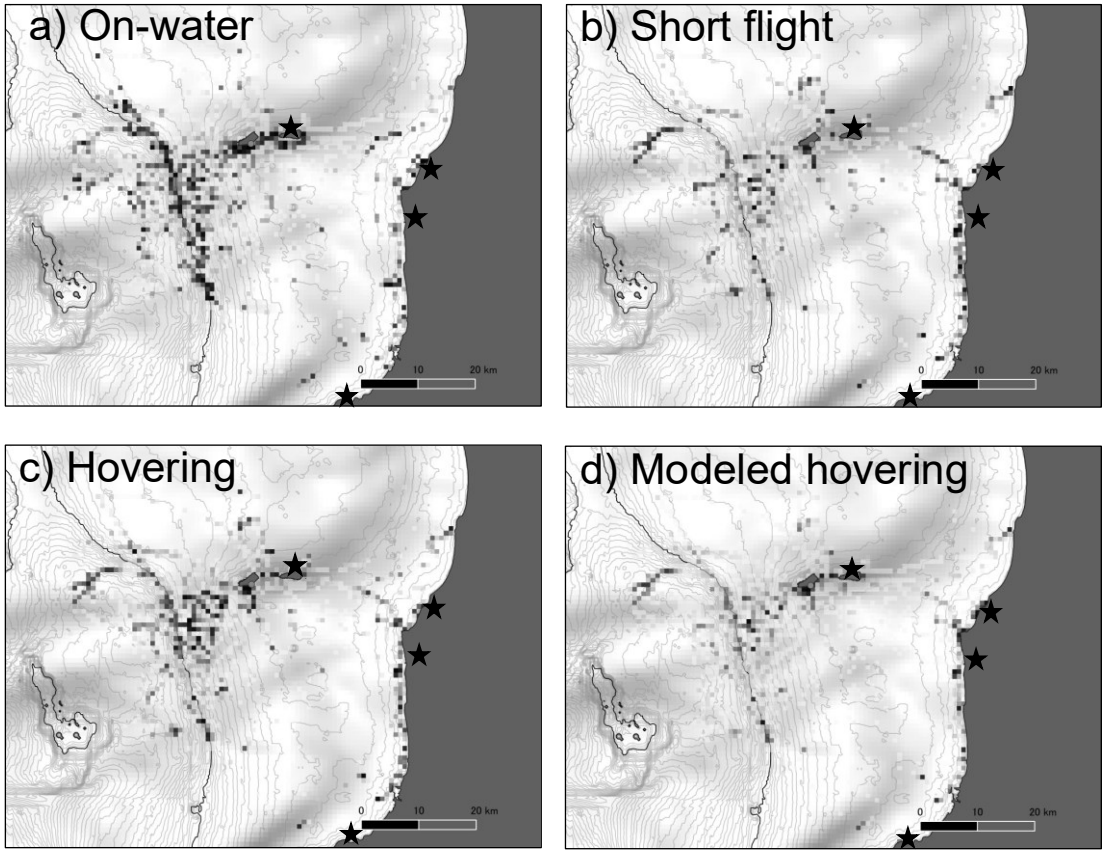


Fig. 5-1 Maps showing the standardized occurrence of different behaviors determined by GPS-acceleration: a) on-water, b) short-flight, and c) hovering, and d) the number of 15-s windows of modeled hovering by deep-learning GPS location shown on the 1 x 1 km grid. Black grid shows highest frequency of occurrence. The grey circle shows the colony in Teuri Island. Stars show fishing ports. Black line highlights 200 m isobath. Shadows show the areas of high SST gradient.

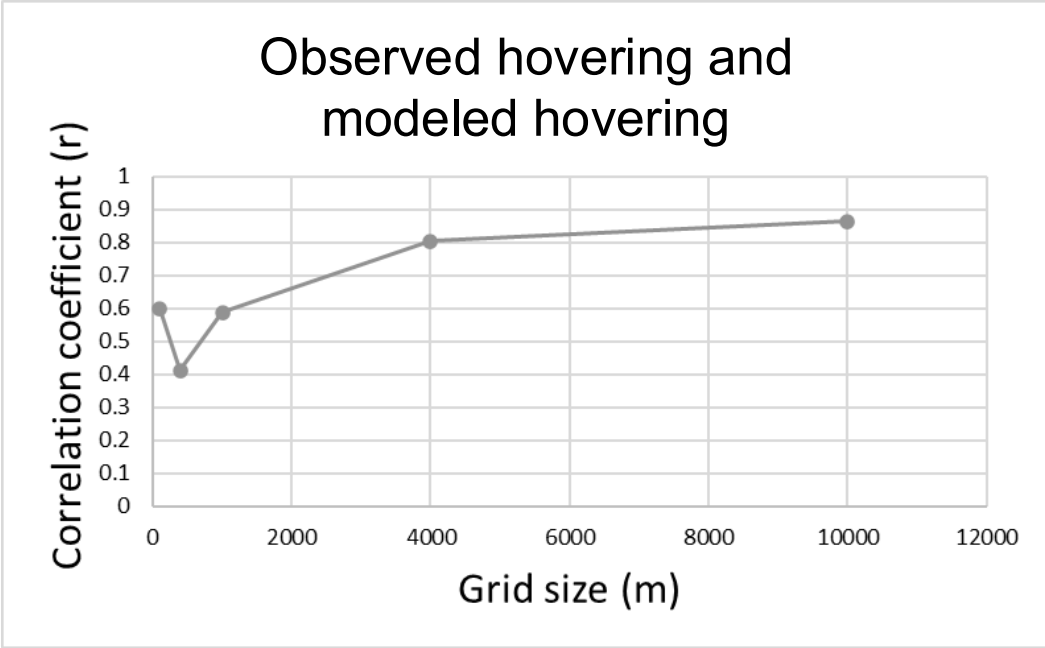


Fig. 5-2 The Correlation coefficient (Spearman's *r*) between the time of observed and modeled a) hovering and that between the time of modeled hovering and the time of b) on-water in each cell when cell size was changed as 100m, 400m, 1km, 4km and 10km. Time was calculated as the number of windows of 30 s classified as the presence of each behavior.

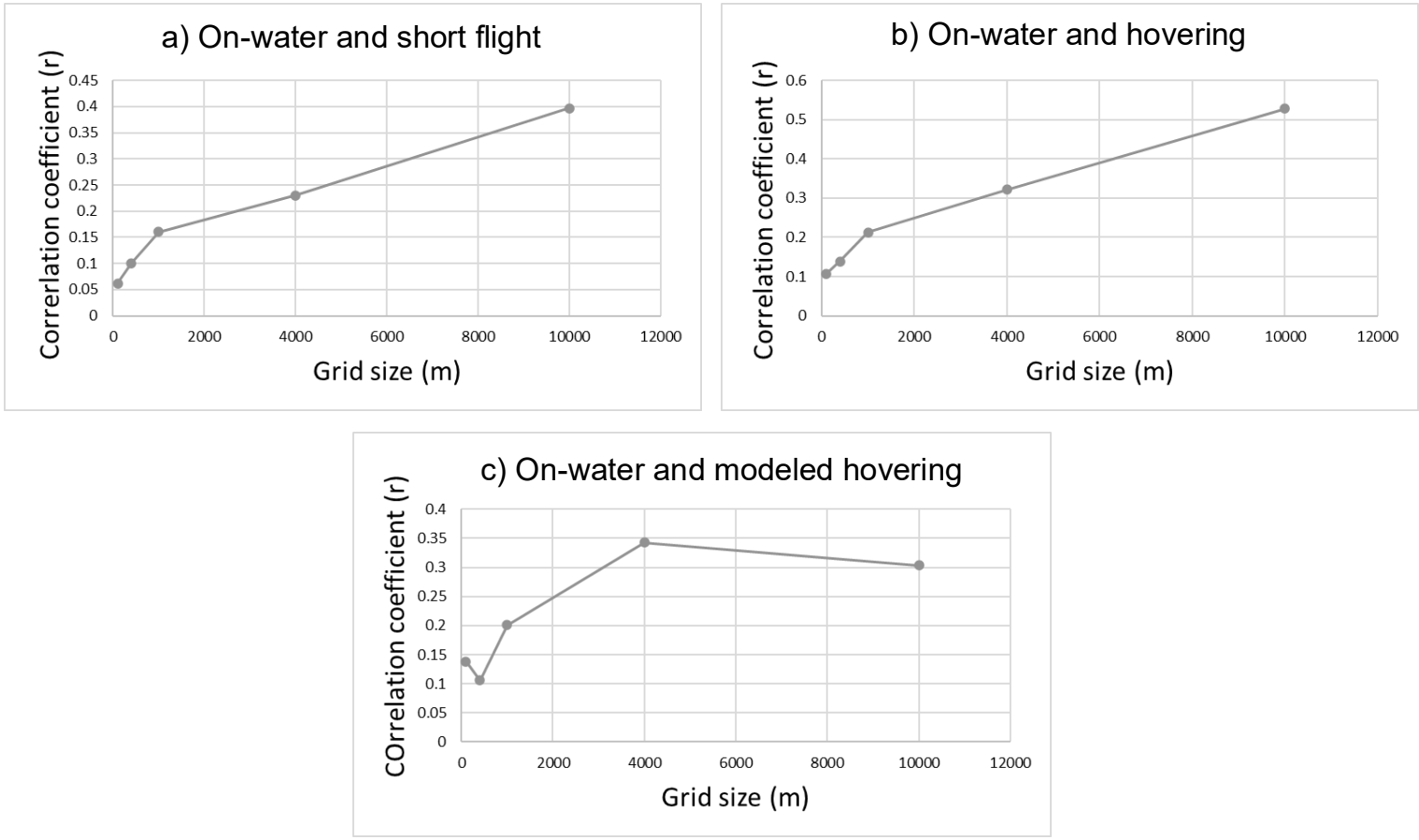


Fig. 5-3 The Correlation coefficient (Spearman's r) between the time of *On-water* and *Short-flight* (a), that between the time of *On-water* and observed *Hovering* (b) and that between the time of *On-water* and *Modelled hovering* (c) in each cell when cell size was changed as 100m, 400m,1km, 4km and 10km.

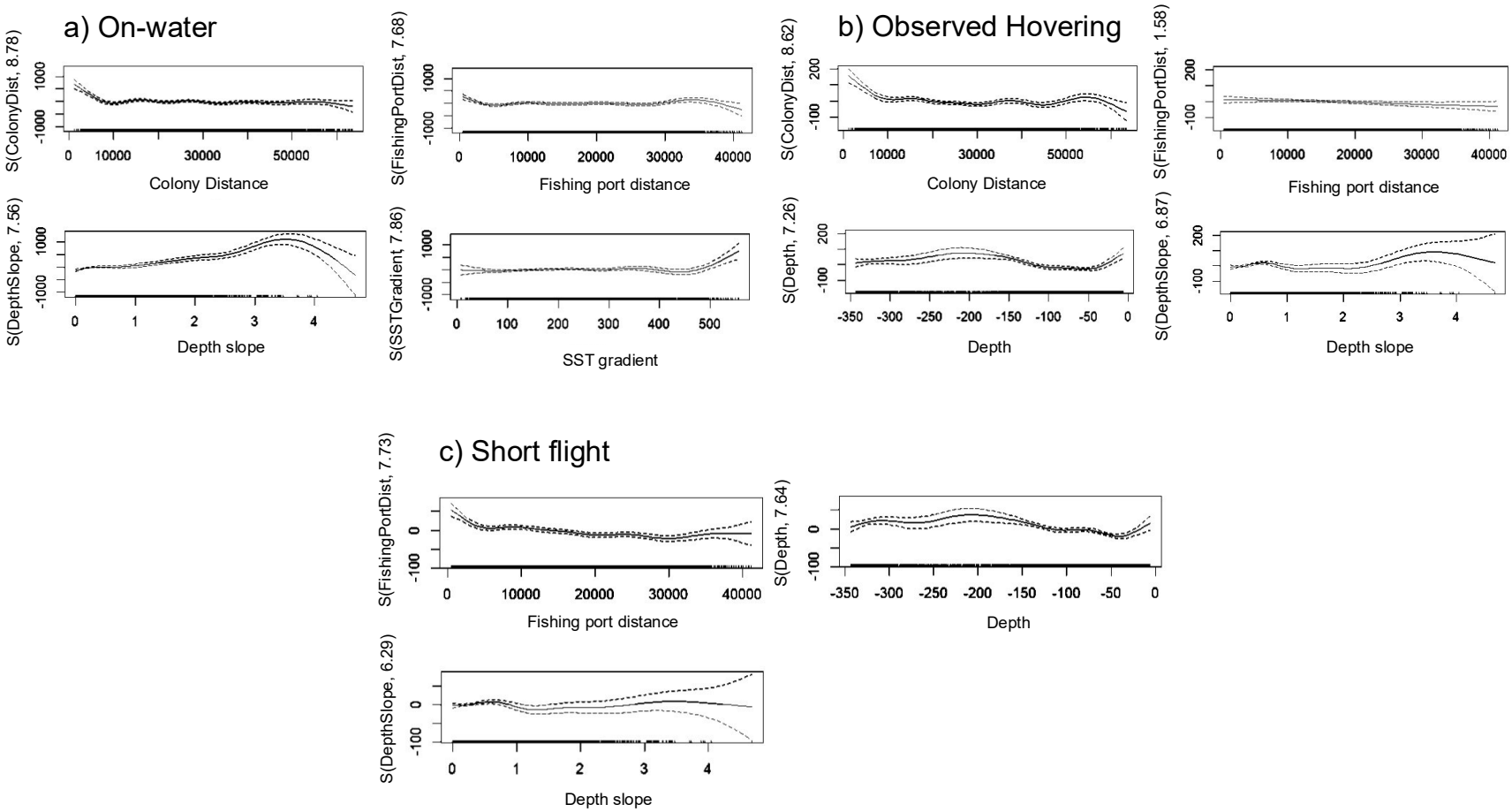


Fig. 5-4 Response curves modeled by the generalized additive models explaining durations of a) on-water b) *hovering*, and c) short-flight inside a 1 km x 1 km grid. The area between dashed lines indicates the 95% confidence interval.

Table 5-1 Selection of top 3 multiple regression models explaining the low-speed, hovering, short flight behaviors of Black-tailed Gulls. Adequate models are in bold letters, and the best models are underlined.

Behaviour	Model	AIC	delta AIC	R^2 of the best model
On-water	**Colony distance + Fishing port distance + Depth slope + SST slope**	**49761.3**	**0**	0.18
	Colony distance + Fishing port distance + Depth slope + SST slope + Depth	**49763**	**1.68**	
	Colony distance + Fishing port distance + Depth slope + SST slope + SST	**49763.1**	**1.75**	
Hovering	**Colony distance + Fishing port distance + Depth + Depth slope**	**39857.4**	**0**	0.12
	Colony distance + Fishing port distance + Depth + Depth slope + SST	**39858.6**	**1.23**	
	Colony distance + Fishing port distance + Depth + Depth slope + SST slope	**39858.8**	**1.46**	
Short flight	**Fishing port distance + Depth + Depth slope**	**35287.1**	**0**	0.09
	Fishing port distance + Depth + Depth slope + SST	**35288**	**0.77**	
	Fishing port distance + Depth + Depth slope + Colony distance	**35288.5**	**1.34**	

5.4 DISCUSSION

I expected that the correlation between modeled and observed hovering could be high across all scales, and that the machine learning approach would be useful in predicting hovering areas. In this chapter, I did not use the presence data of modeled hovering within a certain sample size, but used the raw prediction, which was sufficiently accurate over the 1 km scale. The training data set was also used for prediction in this chapter; thus, the accuracy should be higher than result in Chapter 4. However, I considered that the machine learning approach showed its ability to detect specific spatial patterns of hovering; thus, it can be useful when using GPS data to detect foraging aggregations. The peak in the 100 m scale indicated that the machine learning approach is also be helpful in the scale of foraging aggregation (ca. 10-100 m).

Significant correlations were found between the time observed hovering and on-water and those between the time short-flight and on-water at >10km scale. Therefore, at coarse scale, the areas where birds exhibited on-water, that can be easily measured using only GPS locations, matched well with the areas where birds conducted hovering and short-flight. As the latter two were highly associated with the foraging aggregation, birds foraged intensively in feeding aggregations in areas where birds stayed on the water at the spatial scale of >10 km. At finer scales (<10 km), however, birds did not necessarily show hovering and short-flight in areas where birds spend longer time for on-water.

Krill and epipelagic forage fishes aggregate at the spatial scale of 300-15000 m (Schneider et al. 1986; Simard et al. 1986). The distribution of prey seems to be very patchy during our study period and area (< 1 km, Kurasawa et al .2011). Correlations between the density of seabirds and that of prey are weak at the small (<1 km) scale and strong at the scale of 2-300 km, usually >10 km (Logerwell et al. 1996; Logerwell et al. 1998; Fauchald et al. 2002; Burger et al. 2004; Kurasawa et al .2011). Therefore, it has been hypothesized that seabirds forage in the areas where average prey density is high but they find individual prey patches opportunistically and miss most of prey patches (Fauchald et al .2011). Therefore, at small scales (<10 km), seabirds may form foraging aggregations and resting in different locations but once large cells (>10 km) are set, they would forge and rest within each of them. In fact, individual seabirds are attracted to foraging aggregation over a prey patch through local enhancement at small scale (Fauchald 2009). In black-tailed gulls, hovering was usually associated with the high-local-density aggregation and presence of diving seabirds while short-flight was with large but moderate local-density aggregation. Hovering was exhibited more when getting

closer to colony, whereas short-flight did not. As foraging distribution of diving seabirds are within a range from the colony, surface feeding species, i.e. black-tailed gulls conducted hovering there.

Relatively small-sized bird like black-tailed gull is considered to use less power for landing and taking off when compared to the large-sized bird such as wandering albatrosses (*Diomedea exulans*). The sit-and-wait on water strategy seems effective for foraging small-scale prey patches (Shaffer et al. 2001; Weimerskirch et al. 2007). On-water, thus may not match the prey in small scale for small-sized birds. On the other hand, on-water maybe more reliable in identifying the foraging areas for larger birds.

In the 10 km scale, areas of on-water probably show an overall foraging sites that cover locations of different foraging aggregations. My study indicated that using only GPS speed data to identify productive area in scale of >10 km is useful. However, when analysing what makes prey accessible to seabird, a small-scale analysis matched to the scale of prey patches is necessary, because within a foraging aggregation event, prey is more likely affected by environmental factors on a smaller scale. Since birds will not use areas where they are inaccessible to prey, even in areas of highly productivity, my method will be more helpful when analysing which environmental factors enhance the birds' accessibility to prey. My method successfully provided more helpful information by incorporating environmental factors to predict foraging area outside the area studied.

Chapter 6 Application to sensitivity map

6.1 INTRODUCTION

To provide renewable and clean energy efficiently, the developments of wind farm have been accelerated since 2009 (Windenergie-Agentur Bremerhaven 2009). Being able to stably make use of the wind energy and reduce noise and the impacts to the landscape, deployment of offshore wind farm is also moving forward (Ngai et al. 2004). The offshore wind farm was considered outperforming its high cost, based on its high efficiency (Snyder and Kaiser 2009). However, the risk of impacting the marine ecosystem has attracted concerns and still required studies (Wilson et al. 2010; Kazama et al. 2021). For fish and marine mammals, the risk of changing the existing structure of the food web is of concern (Page et al. 2006). For birds, especially marine seabirds, the direct and indirect impacts on their activity and mortality rates have been evident. The direct impacts include collision between a bird and a rotor blade (Desholm et al. 2006); in the North and Baltic Seas, one wind turbine can lead to a mortality of tens of birds per year (Hüppop et al. 2006). Indirect impacts include barrier effects and habitat loss for birds. Barrier effects lead birds to travel longer distances to avoid wind turbines, especially for birds flying at high-risk altitudes, such as gannets and gulls (Cook et al. 2018). The installation of a wind turbine can potentially occupy the foraging or resting habitat of birds (Fox et al. 2006). Indirect impacts may increase the foraging effort of birds, potentially leading to higher mortality rates of birds or their chicks.

One of the solutions is to develop the sensitive map of seabirds based on the foraging ranges, sensitivity level to disturbance, collision risk and other relevant features of behavioral or population ecology, thus avoiding areas of high risk (Bradbury et al. 2014). A predicted density distribution (based on the environmental factors and spatial locations) of seabirds plays a crucial role in creating a sensitive map. Each grid in the map is evaluated by combining the predicted density distribution and sensitivity level. Sensitivity levels are represented mainly by collision risk (calculated by flight altitudes, maneuverability, percentage of time flying, and nocturnal flight activity) and disturbance and habitat displacement (calculated by disturbance by wind farm structures, ship and helicopter traffic, and habitat specialization). To create a sensitive map, foraging habitat of birds is essential. Birds may increase flight altitude when foraging. Northern gannet fly at medium height around 12 m when commuting but ascend to >30 m when foraging (Cleasby et al. 2015; Garthe et al. 2014). Thus, collision risk is extremely high in foraging habitats. Foraging habitat is also one of the main indicators of the risk of disturbance and

habitat displacement (Kazama et al. 2021). Feeding habitats of surface feeders were difficult to locate using GPS position alone because their surface-feeding behaviors are not determined. Furthermore, the attack on the prey occurs during a short period of the whole foraging phase as I observed in Chapters 2 and 3.

Foraging habitats are predicted based on the environmental factors of foraging locations. At a local scale (<10 km), the locations where birds are moving slowly may not always coincide locations of feeding, because those slow-moving locations contain a long phase of bathing and resting. This study improves the ability to detect the foraging behavior of surface-feeding seabirds. I consider that this study helps increase the accuracy of a sensitive map. The flight altitude during the foraging phase of the surface-feeding seabirds has not been analyzed in previous studies. M-zone flight areas overlap with the areas where black-tailed gulls move slowly (Kazama et al. 2021). Then, whether gulls conduct an M-zone flight when they are foraging has to be tested. As altitude enhances the ability of birds to search foraging sites far away (Collet et al. 2015), birds may conduct M-zone flight between foraging sites to increase the searching efficiency. Thus, I analyzed the flight altitude within a foraging site and during the flight between foraging sites, where I considered birds forming foraging aggregations in Chapter 5.

6.2 MATERIALS AND METHODS

Using the same data set as Chapter 5, I analysed kernel density of time spent for M-zone flight. In this analysis, the behavior of birds was classified as “flight (flapping frequency between 3-6 Hz, or speed > 4.7 m/s, Ma et al. 2022)” or “on-water”. Acceleration loggers were set to record at 25 Hz, and GPS loggers were set to record at a 1 s interval. Considering that the absolute error was approximately 20 m when the number of satellites was six or more, I identified M-zone flight when the altitude of the birds was within the range of 20–140 m, following Mikami et al. (2022). The locations on land were excluded. Besides, altitude data recorded by a GPS logger has a relatively low accuracy (Mikami et al. 2022; Okado et al. 2023). Following Okado et al. (2023), I therefore used the points verified by more than 6 satellites and did not correct errors when altitude was under 0 m. I compared whether there was a significant difference between altitudes of flights (lasting for >5 s) within foraging aggregation sites, between foraging aggregation sites and commuting (*i.e.* flight between foraging aggregation sites and land) using Welch' s t-test. The former category included bouts of birds conducting hovering or short flights, following Ma et al. (2022). Hovering and short flights were excluded because duration was too short for birds to gain height over M-zone.

6.3 RESULTS

Height of flight was 5.4 ± 9.8 m within foraging aggregation sites, 4.0 ± 7.3 m during the flights between foraging aggregation sites, and 5.5 ± 10.7 m in commuting between colony and foraging areas (**Fig. 6-1**): they flew higher during commuting flight than flight between foraging aggregation sites ($p<0.05$). Of the 769166 s flights recorded, 297973 s (39%) were for commuting between colony and foraging areas, 324999 s (42%) were transit between foraging aggregation sites, and 136194 s (18%) was made within foraging aggregation sites. Birds flying within foraging aggregation sites and commuting spent 7% of total time within M-zone and 3% when moving between foraging aggregation sites, respectively (**Table 6-1**). Black-tailed gulls flew in the M-zone in areas along the Hokkaido main land, coast near the colony, and areas of 200 m depth in the west of Teuri Island (**Fig. 6-2**).

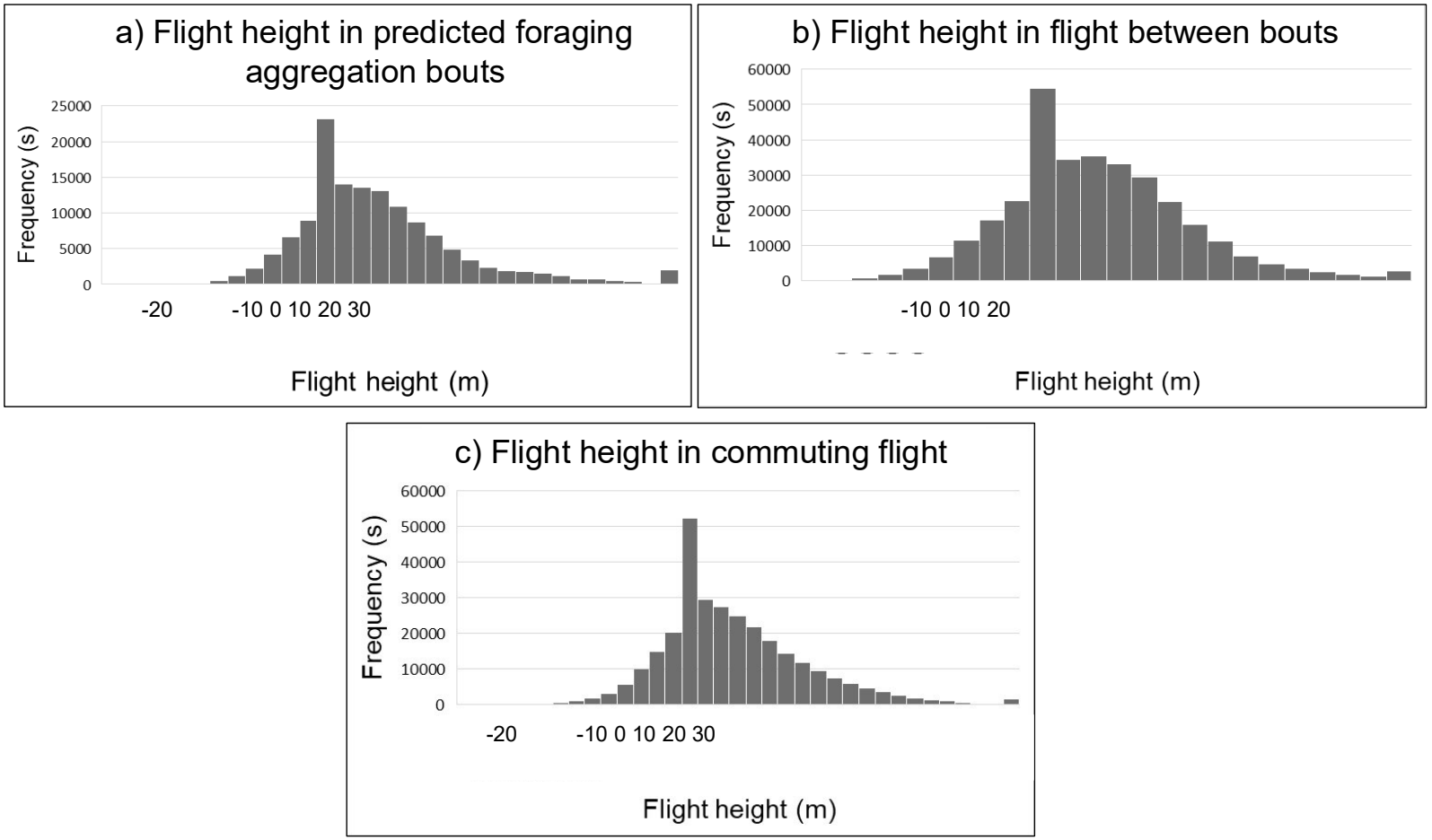


Fig. 6-1 Frequency distribution of flight height in a) bouts of predicted foraging aggregations, b) flight between bouts, c) commuting flight.

Table 6-1 Duration of M-Zone flights in different occasions compared to the total duration recorded.

Site	Duration (s)	M-Zone flight (s)
Sites of foraging aggregations bouts	136194	10065
Sites between bouts	324999	10332
Sites of commuting flight	297973	21632

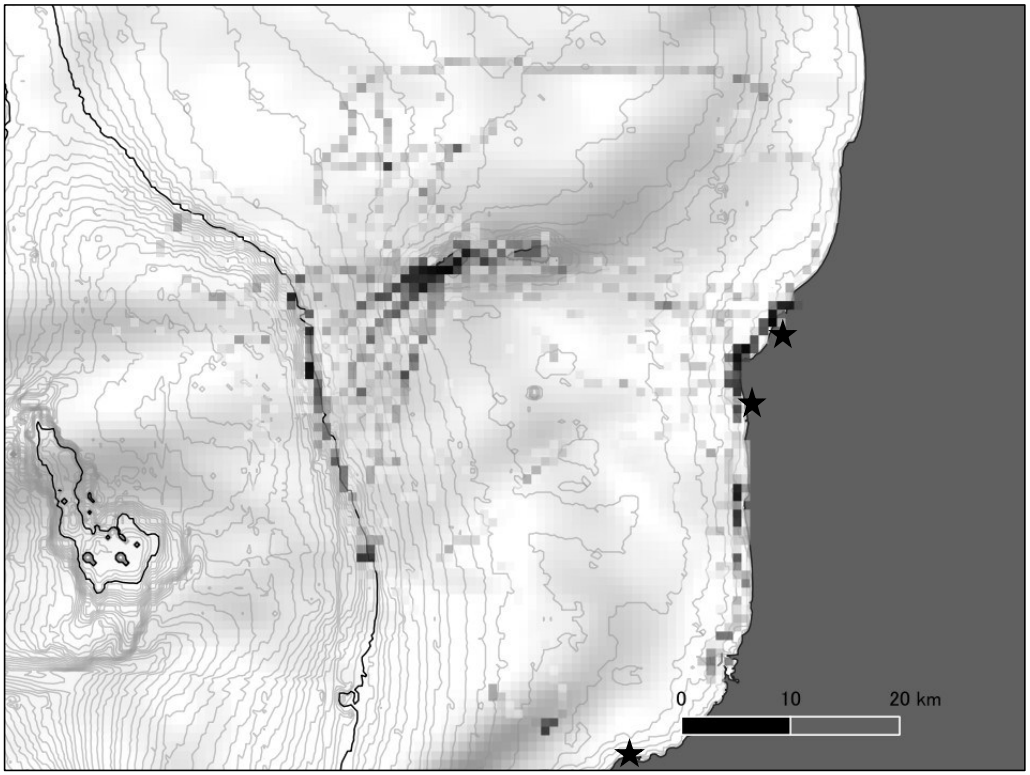


Fig. 6-2 Map showing the standardized frequency of occurrence of M-Zone flight. Dark colors show high duration of M-zone flight within 1 x 1 km grid. Black grid shows highest frequency of occurrence. Stars show fishing ports. Black line highlights 200 m isobath. Shadows show the areas of high SST gradient.

6.4 DISCUSSION

The average proportion of the M-zone flight locations in total time flying was 6%, similar to the result of Mikami et al. (2022), which showed 9% for gulls in Rishiri. They used M-zone when they were travelling to foraging areas as M-zone flights conducted mostly when commuting between the colony and foraging areas, and moving between foraging sites. My results match the previous study that the M-zone flight area was different from the slow-moving area in the black-tailed gull, and M-zone flight was conducted mainly in areas close to the land (Kazama et al. 2021). Birds conducted M-zone flight may be because of the ascending air current close to land, as suggested in Mikami et al. (2022) (**Fig. 6-2**).

When black-tailed gulls were flying within a foraging site or flying between foraging aggregation sites, flight height was similar to commuting. Similar proportion of M-zone between foraging aggregation sites and commuting sites indicates that M-zone flight is also used when generating foraging aggregations, highly used M-Zone areas are similar to areas of foraging aggregation (**Fig. 6-2**; **Fig 5-1**, Chapter 5). In Chapter 2, I observed birds flew often when foraging with other large divers: killer whales, pinnipeds and cormorants. I did not observe those subsurface predators chasing the dense fish school close to surface. When dense prey school is going to be formed, birds may need to stay in the air to get ready to access and the scale of these areas (usually >100 m) is larger than that of foraging aggregations (usually <100 m). Wind speed is generally faster at higher altitude, so the birds can reduce their energy consumption if they fly at higher altitude and close to M-zone in the period when they were flying within foraging sites (Kumagai et al. 2023).

Black-tailed gulls did not ascend to higher altitudes to search for next foraging aggregation sites. The at-sea travelling range of gulls at Teuri is mostly short (<20 km, **Fig. 6-2**). They do not need to gain height over the M-zone when searching (Collet et al. 2015). Probably, a large number of individuals within a foraging aggregation reduces the need for each individual to fly high to search for the next site.

In this study, I improved the ability to locate the foraging areas of a surface feeder, at least around Teuri Island. Birds would be at risk of collision in those areas. Besides, I believe my method improves the accuracy of evaluating the risk of disturbance and habitat displacement as well, because the methods of this study make the habitat usage clearer by highlighting the harbor area and shelf slopes. Wind turbine is considered to affect the

habitat usage of birds on the scales of <1 km to >10 km ((Larsen et al. 2000; Kahlert et al. 2004; Petersen 2005). The new method I propose here can locate foraging areas at a finer scale (<1km), which is useful for planning the wind farm avoidance area of high risk. As seabirds conduct daily commuting flights, avoiding these routes should be crucial (Masden et al. 2009).

Chapter 7 General discussion

7.1 POTENTIAL PREY OF BLACK-TAILED GULLS

The offshore area around Teuri Island is strongly affected by the Tsushima Warm Current, which governs the sea temperature. In this area, sea temperature is considered as the most significant factor affecting prey availability for seabirds (Deguchi et al. 2004). Life history events such as spawning also force prey staying close to the coasts (Fauchald 2009). In the Tsushima Current area, various forage fishes are potentially available for black-tailed gulls. The Japanese sardines (*Sardinops sagax*) aggregates forming a fishing ground within the SST range between 5 and 23.8°C (Muko et al. 2018). On the Japan Sea coasts of Hokkaido, anchovy has been heavily ingested by seabirds when sea surface temperatures (SST) ranged between 12–13 ℃ (Watanuki 2010). Sand lance (*Ammodytes japonicus spp.*) comprises three species around Hokkaido waters, and their specific thermal preference remains unresolved, although A. japonicus is known to be distributes in the water below 25℃ (Akai et al. 2012) and in waters with sandy bottom sediment close to shore (Shibata 2019). Sand lance spawns in April to May in Soya Strait (Miyake 2003) but March to April in Tsugaru Strait (Nara et al. 1987). Habitats of age-0 greenling (*Pleurogrammus azonus*) are in the Sea of Japan off the west coast of Hokkaido and adults spawn in mid-September through early December (Takashima et al. 2016), then they are fished in in January to June (Annual report of Hokkaido offshore demersal fishing catch statistics by fishing ground 2002). Walleye pollock（*Theragra chalcogramma*) spawns from December to April in the Sea of Japan (Maeda et al. 1976; Miyake et al. 2008). Black-tailed gulls mainly fed on age-0 greenling and age-0 walleye pollock during their incubation period (Deguchi et al. 2004; Ito et al. 2009; Tomita et al. 2009). Krills (*Thysanoessa longipes* and *T. inermis*) spawn around Teuri Island in March to April (Hanamura et al. 1989). Birds are possibly feed on the krill when SST is under 8℃ (Deguchi et al. 2004; Ito et al. 2009; Tomita et al. 2009). Our study was conducted from the middle of May to early June, and the SST ranged 8℃-12℃ in this period. Black-tailed gulls probably foraged mainly on sardine, sand lance, greenling or walleye pollock in this period. While little is known about the spawning of sand lance, other prey does not spawn during the study period, making them potentially available to the gulls. sand lance remains known, other preys were probably not constrained spatially by spawning behavior. Besides, birds may also feed on fish eggs, other crustaceans and insects in this period (Tomita et al. 2009; Mizutani et al. 2021).

7.2 AREAS WHERE POTENTIAL PREY IS AVAILABLE

Black-tailed gulls spend more time on-water in areas with frontal zone (Chapter 5, Kazama et al. 2018) where prey may be attracted by the enhanced primary production (Schneider et al. 1990). Crustaceans are carried to the front area by upwelling and mean circulation and are accumulated under water because of their negative phototaxis (Simard et al. 1986). The 0-year-old fishes with limited swimming ability may be also accumulated (Kurasawa et al. 2011). Surface feeders may gain the access to prey that were chased, disturbed and injured by subsurface predators (Schneider 1990). Fronts may also enhance the formation of aggregations of marine fish larvae and eggs due to the convergent currents (Sakamoto et al. 1986).

7.3 FORAGING AREA

In Chapter 3, I considered on-water as a mix of swimming, resting, maintenance and surface-seizing behaviors. Birds conducted long swimming sessions and probably they did surface-seizing during these sessions solitarily (Chapter 3). Some birds may spend an extended duration to feed on crustaceans, fish larvae or eggs accumulated in the frontal zone, it is not thought to be the major foraging strategy of black-tailed gulls (Chapter 3). Kazama et al. (2018) suggested that female black-tailed gulls are less competitive than males. In their study, female birds fed on crustaceans, spent significantly longer time on water and used more time in the frontal zone, and fed on crustaceans; it is implied that they fed on crustaceans along the front.

Further, foraging aggregation of black-tailed gulls was formed in shelf break areas where the productivity may be high (Nevitt 2000) and the patches of forage fish may be available. Also, the shelf break may provide refuge suitable for fish to stay (Schobernd et al. 2009). On the small scale, internal waves over the shelf break area enhance surface aggregation of prey such as herring or crustacean, by generating upwelling, thus also enhancing foraging aggregation of top predators (Stevick et al. 2008). Similar area usage has also been reported in black-footed albatross *Phoebastria nigripes*, white-chinned petrel *Procellaria aequinoctialis* and black petrels *Procellaria parkinsoni* (Hyrenbach et al. 2006; Phillips et al. 2006; Freeman et al. 2010). Thus, the small-scale topography in shelf break area can probably enhance the accessibility of prey to seabirds.

7.4 ON-WATER AREA

Black-tailed gulls spend time on-water and forming foraging aggregations in areas with high bottom depth slope (Chapter 5). Steep slopes can increase nutrient supply of surface mixed layer in coastal upwelling regions (Jacox et al. 2011). There is a drop in using areas

of steepest slope, those are areas of small skerries in the sea or around the island, birds flew across those areas but did not stay (Chapter 5). Birds also used areas close to fishing ports (Chapter 5); they frequently use spilled or discarded fish in fishing ports (Kazama et al. 2018).

Most black-tailed gulls typically do not conduct engage in prolonged swimming session during their incubation period (Ma et al. 2022). As what I have discussed, on-water probably relates to the solitarily foraging and prey patches of low swimming ability that accumulate in front. The energy value of these prey is relatively low; energy intake may not be time-efficient. Moreover, stable front, water mass or eddy on a scale below 10 km does not exist in this study area (Tanaka et al. 2008), which makes the foraging area less predictable for birds. On the other hand, prey with higher energy value and also higher swimming ability are less constrained by the front while being attracted by certain seafloor topography such as shelf break, making it more predictable for birds.

7.5 FORAGING AGGREGATION

The ability of seabirds to track fish schools is considered insufficient as suggested by Fauchald et al. (2011). He mentioned that local enhancement helps overcome this problem. Seabird aggregation on a local scale is also very important for diving seabirds which benefit from it. For instance, Japanese cormorants, in years of feeding on epipelagic prey they had a high probability of joining mixed-species aggregations compared to the years on demersal prey (Watanuki et al. 2004). Foraging by aggregation can be more efficient and may be more preferable to most birds.

Locating the area of foraging aggregation may highlight the hot spots for different species of seabirds distributed in this area. The aggregation of surface feeders may indicate higher productivity and biodiversity, providing important information for mapping Ecologically and Biologically Significant Areas while also helping to reduce the survey cost. My study has highlighted various environmental factors associated with different behaviors, which may help better understand the foraging strategy of the seabirds. The differences between on-water and foraging aggregations were significant on a small scale (<1 km), indicating that fine-scale landscape affects birds foraging, maybe through the small-scale upwelling or prey patch, and affects the majority of birds. Analyzing birds and environmental factors at a fine scale is important for identifying high-productivity areas.

In Chapters 2 and 3, turning flight was found conducted in small foraging aggregation where Japanese cormorants or pinnipeds acted as the main subsurface predators, and foraging aggregations formed around the fishing boats. Birds flew around getting ready to pick the fish that were chased below the surface. The fishing boats may play a role similar to the subsurface predators. As I did not know to what extent birds rely on fishing boat, this behavior was not included in this study. Further comparison of birds foraging around a fishing boat using video recorders would be essential, so that we can figure out the effect of human activity on feeding behaviors, which is also an important theme when establishing EBSA.

When applying my method to other surface-feeding species, behavioral analyses should precede because they might forage in a different way in foraging aggregations. Some seabird species may not use different feeding techniques regardless of whether they feed in aggregations or solitarily. At sea, foraging behaviors of other species of seabirds can be examined by using drone and an accelerometer (Chapter 2 and 3).

In black-tailed gulls hovering and short flight were performed between the time when they were plunging and surface-seizing. This study highlights the usefulness of these indirect foraging behavior as an indicator of foraging aggregation informing the productive areas. Comparing to foraging behaviors such as plunging and surface seizing, short flight and hovering can be identified easily using GPS location data (Chapter 4 and 5). In addition, using hovering and short-flight as indicators I found that the bottom topography including depth was an important factor in generating foraging aggregation, though such depth range was not selected as a factor affecting feeding area in the previous study by Kazama et al. (2018). Instead, SST gradient was select as an important determinant by them. However, the SST field is often ephemeral changing temporally and is inadequate to be used in the selection of protected areas. On the other hand, depth is stable over time and should be useful in the selection of Marine Protect Areas. My study helps making full use of hidden messages in seabirds' GPS data.

7.6 CONCLUSION

This study analysed the relation between foraging aggregation and the behaviors of seabirds. It reminded the importance of different behaviors of seabirds when studying their ecology. It may also enhance the understanding of the ecology of seabirds in the aggregation level. For fisheries science, this study provides information on favorable areas for seabirds to form foraging aggregations. It may be a help in reducing the risk of

bycatch in seabirds under global conservation efforts. My study has also shown the possible way of seabird to track fish school. It may also be applied to enhance the fish school detection to improve fishing efficiency. For environmental science, my study enhances the potential value of seabirds' data by providing information for improving accuracy to bird sensitivity map and identifying marine important area. The enhancement of the mapping process should be a benefit for various taxa.

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SUMMARY

To sustain marine biodiversity, the establishment of Ecologically or Biologically Significant Areas (EBSAs) has been recommended. The areas of high density of surface feeding seabirds foraging in aggregation represent high energy flow through the food-web and biodiversity, and can be a surrogate of EBSA. Although GPS dataloggers have been widely used to track small to large seabirds, identifying foraging areas has remained difficult. To develop a technique to locate foraging aggregations using biologging, the

behaviors of individuals in the foraging aggregation were recorded using a drone. Hovering and short flight indicated the high-density foraging aggregations with diving seabirds and the large but low-density foraging aggregations, respectively. As short flight was identified precisely using GPS data, the accuracy of identification of hovering by body acceleration and GPS locations was tested using footage of simultaneously mounted video loggers and the accuracy was high as ～90%. Then, hovering was modeled by LSTM machine learning using GPS data of train group and a comparison with observed hovering in test group gave the accuracy of the presence of modeled hovering within 30 s window as 91% but with individual variation. Areas where birds conducted on-water matched well with those where birds conducted hovering or short flight at coarse scales (> 10 km) but these did not match at fine scales (< 1000 m). On-water occurred in areas of front while short flight and hovering occurred in areas of shelf break. This study also has indicated that identifying location of foraging aggregation would be important to wind farm sensitivity map and provides useful information for finding EBSA.

要約

海洋生物多様性を保つために、生態学的または生物学的に重要な地域（EBSA）を設定することが推奨されている。海鳥の採餌集団は、2 つの基準、高い生産性と生物多様性を示しているため、EBSA を特定するのに役立つ。海鳥は集団で採餌するため、採食集団の位置を特定することで生産性の高い地域を予測できるだろう。GPS は海鳥の研究では広く使用されているが、GPS データのみから採餌場所を特定することはこれまで困難であった。この問題を解決するため、まずドローンとビデオカメラで採餌集団内の個体の行動を記録し分析したところ、ホバリングは潜水性海鳥を含む高密度の採餌集団を示し、短距離飛行では密度は低いが大規模な採餌集団を示すことがわかった。次に、GPS 位置と体加速度を組み合わせて個体の行動の連続的変化を推定し、身体に装着したビデオデータロガーで観察した実際の行動と比較して、GPS 位置と体加速度による行動分類の精度をテストしたところ、その精度は高く（～90%）、軌跡に沿ってすべての行動を 1 秒単位で判定できた。短距離飛行は GPS データだけで定義できるので、ホバリングのありなしを、GPS データだけで、30 秒ウィンドウで LSTM 機械学習によって、GPS 位置と体加速度で判定した Hovering を教師データとしてモデルし、他の個体のデータをテストデータとし、混合行列で精度判定したところ、91% だった。また、観測ホバリング、短距離飛行と水面滞在についてスケールを変えてその分布をみたところ、10 km 以上の大スケールではおよそ一致したが、＜1000 ｍの小スケールではこれらの位置が異なる場所が多く見られた。また 1 k ｍスケールでこれらと環境要因の関係をモデル化したところ、漁港から

の距離と島からの距離に加え、水面滞在は SST 勾配の影響を受け、ホバリングと短距離飛行は水深の影響を受けていた。この技術の応用としては、洋上風力発電の感受性マップ作成するにあたり、EBSA を特定するにあたり、採餌集団の位置を特定して有用な情報を提供できることを議論した。