



# Individual foraging location, but not dietary, specialization: implications for rhinoceros auklets as samplers of forage fish

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**ABSTRACT:** Forage fish are ecologically important to the marine environment, creating a wasp-waist trophic structure whereby many piscivorous diets are composed of a low diversity of mid-trophic species. Despite the importance of these species, knowledge of their abundance, distribution, and interactions with predators is often limited. On Middleton Island, Alaska, USA, we coupled biologging (GPS-depth logging) with long-term diet observations to examine the use of rhinoceros auklets *Cerorhinca monocerata* chick diets as an ecologically relevant method to sample forage fish in the Gulf of Alaska. Individual rhinoceros auklets did not specialize on select prey items but did specialize on 1 of 2 foraging sites, foraging either in coastal waters or the continental shelf. The majority of forage fish in bill-loads were captured in the top 15 m of the water column. Prey composition in auklet bill-loads varied among and within sampling years (2003–2016). Capelin *Mallotus villosus* dominated auklet diets during the cold-water period with negative Pacific Decadal Oscillation values (2008–2013), whereas Pacific sand lance *Ammodytes hexapterus* were more common in warmer years. Bill-load composition changed within years, with sand lance and capelin delivered to younger chicks, and larger fish, like sablefish *Anoplopoma fimbria*, being introduced as the chicks aged. Auklets returned with sand lance in foraging areas where trawling detected none, implying that auklets can potentially detect fish availability at finer resolutions than conventional methods. In conclusion, auklets responded to variation in forage fish among and across years. These changes in seabird diet could expand our knowledge of changes in availability of important prey species.

**KEY WORDS:** Seabird foraging · *Cerorhinca monocerata* · Gulf of Alaska · Individual specialization · Capelin

## INTRODUCTION

Understanding the interactions of predators with their prey is important for the conservation and management of ecosystems. Such interactions are particularly important for piscivorous species, such as seabirds, and fishing vessels, which can also compete with one another for prey (Hatch & Sanger 1992, Velarde et al. 2013). As is prevalent in many sub-

boreal marine ecosystems (Barrett et al. 1987, Martin 1989), fish species diversity and abundance in the Gulf of Alaska follow a wasp-waist structure with a small number of intermediate trophic level forage fish playing a large role in ecosystem function. Forage fish are important prey items for a variety of commercial fish species in the Gulf of Alaska, including walleye pollock *Gadus chalcogrammus*, herring *Clupea pallasii*, sablefish *Anoplopoma fimbria*, and

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Pacific salmon *Oncorhynchus* spp. (Ormseth 2014). While not directly competing with fisheries for adult fish, Alaskan seabirds feed on the juvenile forms of these fish (Hatch & Sanger 1992, Bertram & Kaiser 1993). Due to their size, these juveniles are classified as forage fish (until they reach maturity and become economically important), a group that also includes Pacific sand lance *Ammodytes hexapterus* and capelin *Mallotus villosus*. Sand lance and capelin are of no direct economic importance, but are of great ecological importance, providing the bulk of many piscivorous diets, including those of seabirds, marine mammals, and the adult forms of harvested fish species (Beacham 1986, Hatch & Sanger 1992, Trites et al. 2007).

Monitoring of forage fish diversity and abundance in the Gulf of Alaska is incomplete (Ormseth 2012). Scientific trawls are performed biennially (formerly triennially) over a 3 mo period, from west to east, using nets originally designed for adult salmon capture (mesh size of 127 mm; Ormseth 2014), allowing high rates of escapement of small, agile forage fish (Ormseth et al. 2016). Using seabirds and their dietary samples as indicators of changes in forage fish availability and abundance, in parallel with conventional trawling methods, could mitigate these biases (Siddig et al. 2016, Sydeman et al. 2017). During the breeding season, seabirds forage at sea and return to the colony to feed their chicks, creating an opportunity to estimate forage fish availability by examining the proportion of prey in seabird diets from a terrestrial point source that simplifies logistics.

When tracked using biologgers to determine where and when prey captures occur, seabirds hold the potential to act as indicators of forage fish occurrence in the environment (Hatch & Sanger 1992, Piatt et al. 2007, Brisson-Curadeau et al. 2017). However, seabirds themselves have potential biases. In particular, individual seabirds may specialize on particular prey items (Woo et al. 2008, Elliott et al. 2009, Ceia & Ramos 2015), and consequently their diet may not be representative of forage fish abundance (Hatch 2013). Furthermore, diet and foraging tactics may change depending on parental demands, leading to prey switching; birds with chicks are known to have a different diet than birds without chicks due to behavioural constraints (Davoren & Burger 1999, Elliott et al. 2010a). Finally, birds may only sample certain areas, because they return to key hotspots (Davoren et al. 2003, Regular et al. 2013), or depths, because of physiological constraints (Kato et al. 2003, Kuroki et al. 2003, Cunningham et al. 2017). Coupling longitudinal dietary analyses of individual birds with bio-

logging can help answer some of those questions by quantifying the degree of individual diet and foraging specialization, and how that might change through the breeding season (Brisson-Curadeau et al. 2017).

There is growing awareness that 'generalist' seabird populations are actually composed of individual dietary specialists (Woo et al. 2008, Ceia & Ramos 2015). Such dietary specialization is thought to reflect individual foraging 'personalities', whereby different individuals specialize on particular foraging tactics, such as particular depths or flight distances (Woo et al. 2008, Regular et al. 2013). For example, individuals may vary in their ability to metabolize lactate, leading to variation in their willingness to dive beyond their aerobic dive limit (Woo et al. 2008). Alternatively, some individuals may forage in particular regions (Regular et al. 2013). For instance, rhinoceros auklets *Cerorhinca monocerata* in California (USA) forage off the continental shelf, sampling only a small amount of the available space, despite having a rather broad diet (Wilkinson et al. 2018). Individual murrelets (*Uria* spp.) specialize on particular benthic prey items, including spawning capelin, kelp forest fish, or sandy bottom fish, and consequently individuals specialize on the same foraging locations year after year (Elliott et al. 2009, Regular et al. 2013). Similarly, individual northern gannets *Sula bassana* tend to specialize on particular foraging areas year after year (Wakefield et al. 2015). Understanding the degree that individual dietary specialization influences foraging specialization, and vice versa, would help understand limitations in the use of seabirds as indicators.

The rhinoceros auklet (hereafter referred to as 'auklet') is a diving seabird that feeds its chick via bill-loads containing multiple prey items per bill-load. Bill-loads with high energy content reduce offspring nutritional stress (Will et al. 2014, 2015). Auklets return to the colony to feed their offspring once each day, during late night/early morning hours, as opposed to alcid species that make several feeding trips daily (Bertram & Kaiser 1993, Davoren & Burger 1999). Auklets return to the colony with whole fish, allowing for reliable sampling of prey items (Davoren & Burger 1999). From previous studies in the Gulf of Alaska, auklet bill-loads generally contain forage fish species like capelin, sand lance, and herring, and the juvenile forms of predatory fish like salmon and sablefish (Thayer et al. 2008, Eby et al. 2017). Auklets appear to sample whatever small, pelagic fish species are obtainable in waters surrounding their colonies, with no bias for a particular species (Vermeer & Westheim 1984). When bluetthroat argentinines *Nan-*

*senia candida* appeared off the coast of British Columbia in 1978, an unprecedented event, this fish species appeared in both the bill-loads of auklets and salmon diets in the area (Vermeer & Westrheim 1984).

In our study, we answered several questions to gauge the viability of using auklet bill-loads as indicators of changes in forage fish availability and abundance in the Gulf of Alaska. Bill-loads were collected from auklets to investigate individual specialization in prey selection, analyse prey species availability and age distribution in surrounding waters, and determine whether species occurrence in bill-loads reflected environmental changes over time in the Gulf of Alaska. Previous work at our study site on black-legged kittiwakes *Rissa tridactyla*, a surface-feeding gull, demonstrated increased capelin occurrence in the diets of kittiwakes during the 2008–2013 cold water period (Hatch 2013). We expected a similar result in the bill-loads of auklets for our study, as kittiwake diets on Middleton Island have shown similar trends to historic auklet bill-load data on Middleton Island, notably, for sand lance proportions in the diet (Thayer et al. 2008, Hatch 2013). In addition, some of the sampled auklets were fitted with miniature biologging devices (GPS units and time-depth recorders, TDRs) to examine the foraging behaviour, including foraging locations and dive depth, of these birds. From these questions, we can evaluate any biases that may occur when using auklets as indicators of forage fish availability, such as individual specialization in prey items or inconsistent foraging depths, and how changes in prey composition of auklet bill-loads across years, and foraging locations for these bill-loads, compare to other surveys of forage fish in the Gulf of Alaska.

## MATERIALS AND METHODS

### Study location, bill-load collection, and prey identification

Bill-loads ( $n = 2228$ ) were sampled from the Middleton Island auklet colony ( $59^{\circ} 25' 42''$  N,  $146^{\circ} 19' 48''$  W), Gulf of Alaska, from late June to mid-August from 2003–2016. The birds were captured by researchers hidden next to runways, either with dipnets, by hand, or by setting up knock-down nets across runways. A bill-load is a bundle of prey items held in a bird's beak that are delivered to the chick (Hatch 1984, Baird 1986, Gaglio et al. 2017). Prey items can be identified to the lowest taxonomic level, and morphometric measurements can help determine

prey age-classes (Hatch & Sanger 1992, Bertram & Kaiser 1993). Collected bill-loads were sealed in zip-lock bags and refrigerated. If an auklet escaped after an attempted capture, but dropped its bill-load, the sample was labeled as 'partial', due to the uncertainty that the whole bill-load was dropped. Prey scattered around the surface of the nesting habitat and collected opportunistically ('ground-loads') were excluded from this study.

Since 2010, each auklet and its corresponding bill-load were identified by its US Fish and Wildlife Service metal band number, whenever possible (Table 1). Bill-loads have been collected from 254 uniquely banded individuals ( $n = 524$  bill-loads). Of the unique auklets sampled, bill-loads were collected once from 127 individuals. Bill-loads were collected multiple times from the remaining 127 individuals, with 74 individuals being collected from twice. Only 53 auklets had their bill-loads collected  $>2$  times, with 1 individual being sampled 11 times. Prey items within each bill-load were identified to species within 24 h of collection. Due to inconsistent taxonomic identification at the species level among sampling years, the various salmon, rockfish (*Sebastes* spp.), and greenling (*Hexagrammos* spp.) species were collectively labeled as salmon spp., rockfish spp., and greenling spp., respectively. Prey species comprising  $<1\%$  of the total bill-load biomass for all years combined were lumped as an 'Other' category, which included: atka mackerel *Pleurogrammus monopterygius*, eulachon *Thaleichthys pacificus*, Pacific sandfish *Trichodon trichodon*, Pacific saury *Cololabis saira*, prowlfish *Zaprora silenus*, three-spined stickleback *Gasterosteus aculeatus*, opalescent inshore squid *Doryteuthis opalescens*, walleye pollock, Pacific cod *Gadus macrocephalus*, and unidentified gunnel (family Pholididae), octopus, prickleback (family Stichaeidae), sculpin (superfamily Cottoidea), and snailfish (family Liparidae) species.

Prey items were weighed to the nearest 0.1 g, and total length (mm) was measured from the tip of the

Table 1. Total number of uniquely banded auklets captured and number of prey items collected from individual banded auklets for sampled years where band number was recorded

Year	Auklets (n)	Prey items (n)
2010	12	49
2012	31	313
2013	17	77
2015	132	1107
2016	136	1836

snout to the tip of the caudal fin. Any invertebrates were measured from the most anterior end to the most posterior end. Incomplete prey items were identified to species and then weighed, but length was not recorded. Age class (either age-0 or age-1+) composition was analysed for 3 prey species based on their total length: capelin 0 (young-of-the-year;  $\leq 50$  mm), 1+ year old ( $> 50$  mm), and sand lance and herring 0 ( $\leq 100$  mm) and 1+ year old ( $> 100$  mm; Hart 1973, Hatch & Sanger 1992). For age class composition analysis, we compared percent composition for each species as opposed to percent biomass to avoid the bias of older fish being larger and therefore accounting for a larger percent of that species' biomass. Total weight, species count, and prey item count were noted for each bill-load. All bill-loads were associated with a date and an average chick age (days) based on the average hatch date of chicks for that given year (except 2014, where hatch date was estimated by the average hatch date of the surrounding years). Chick age was then binned into 2 wk intervals to split the chick-rearing period into 4 quarters for analysis purposes.

### Biologging data collection and dive analysis

A time-depth recorder (TDR; LAT 1500, Lotek Wireless; sampling rate: depth every 2–6 s, temperature every 20 s) or a TDR and a global positioning system (GPS) logger (Alle, Ecotone Telemetry; sampling rate: every 15–30 min depending on satellite availability) were attached to captured auklets. From 2012–2016, 61 auklets were deployed with a TDR (18 in 2012, 4 in 2013, 14 in 2015, and 3 in 2016) or a GPS and a TDR (6 in 2015, and 16 in 2016). TDRs (~3.2 g) were fitted to the left tarsus with a combination of a tarsus cradle, zip-ties, and Tesa tape. Tesa tape was used to tape the GPS units (~4.5 g) to the 4 central retrices of the bird's tail or feathers from the lower back, ensuring that neither the device nor the tape blocked the preen-gland of the bird. Superglue was applied to secure the tape to the device. The combined weight of the devices (~9.5 g) was  $1.87 \pm 0.13\%$  (SD) of the bird's body mass. Several birds were weighed before deployment and after recapture and there was no significant difference in mass (g) between these times (paired *t*-test:  $t_5 = 0.73$ ,  $p = 0.50$ ). However, tags of a similar percent of body mass are known to influence prey delivery rates and abandonment rates in other alcids (Whidden et al. 2007, reviewed by Elliott et al. 2010b). As auklets typically returned each night, we do not think that prey delivery rates were greatly al-

tered, but other components of foraging behaviour may have been impacted.

For the GPS units, a base station and antenna were placed close to the deployed runway to wirelessly upload collected data to the base station as auklets returned to the colony. This allowed for data collection if recapture proved difficult. For the TDR units, auklets needed to be recaptured to retrieve the data. To accomplish this, runways were left undisturbed for ~72 h, and on the third night after deployment, thick-meshed impact nets were set up to recapture individuals. Upon recapture, devices were removed and the birds were weighed. TDR and GPS data were obtained from 30 and 17 auklets, respectively, and 36 auklets were recaptured during this study, with GPS data from an additional 6 auklets being retrieved via uploads to the base station.

Individual dives were determined using a Microsoft Excel (for Mac, Version 14.1.0) macro (dives were defined as  $> 2$  m in depth, to ensure dives were for foraging purposes; Kuroki et al. 2003). The following variables were extracted from these dives: date, time, maximum depth achieved (m), and duration (s). Of the 36 recaptured auklets with TDRs, 19 individuals returned data that could be associated with their bill-load (5 in 2012, 3 in 2015, and 11 in 2016). We assumed that the full bill-load was caught within the last 10 dives the auklets performed before recapture. As auklets can capture multiple fish in a single dive (Duffy et al. 1987), we reason that the last 10 dives represent an adequate number of dives for larger bill-loads to be caught, and may be an overestimation for smaller bill-loads. If a single species in a bill-load comprised over 75% of the prey items for that sample, the bill-load was classified as a single-species bill-load. The other recaptured individuals either did not return with a bill-load when captured, or the battery of the TDR died before capture and thus the final dives could not be associated with the bill-load.

### Statistical analysis

Analyses for individual auklets' specialization were performed using the RInSp package (Zaccarelli et al. 2013) in R v3.2.5 (R Core Team 2016). Specialization was determined using the equation for individual niche variation within a population (Roughgarden 1974):

$$\text{TNW} = \text{WIC} + \text{BIC} \quad (1)$$

where TNW is total niche width, i.e. the variance in prey species biomass among all bill-loads; WIC, the

within-individual component, is the variance among prey species found among and within all of an individual's bill-loads; and BIC, the between-individual component, is the variation in bill-loads among individuals (Bolnick et al. 2003). A high BIC (and consequently a low WIC/TNW) implies a large degree of specialization among individuals (Bolnick et al. 2003). An  $E$  index, the measure of average pairwise dissimilarity in the overlap of bill-load contents between all sampled individuals, was calculated as an additional index for specialization, where a value approaching 1 suggests specialization and a value approaching 0 is the inverse (see Araújo et al. 2008, Zaccarelli et al. 2013 for more detail). Due to the large disparity in the number of times each individual was caught, an adjusted  $E$  ( $E_{\text{adj}}$ ) was calculated to minimize bias of those birds whose bill-loads were represented by a single sample. Likewise,  $E_{\text{adj}}$  was calculated using proportion of prey in an individual's diet and then averaging those proportions for each prey species, as opposed to summing the number of items for all prey species per individual and then determining the proportion of use across the population. A Monte Carlo resampling with 999 replicates was used to derive the  $E_{\text{adj}}$  and WIC/TNW analyses.

Non-metric multi-dimensional scaling (NMDS; Kruskal 1964) was performed on bill-load data (prey biomass) to detect any changes across and within years for all prey species and age classes for select prey (capelin, herring, and sand lance). NMDS uses stress as a quantitative way to determine the goodness of fit, where a stress of 0.05 is considered an excellent representation in reduced dimensions, <0.1 is good, <0.2 is acceptable, and <0.3 provides a poor representation. Decreasing stress is correlated with an increasing number of axes or dimensions (determined via a scree plot). Prey biomass NMDS analysis was conducted using 4 dimensions, while age NMDS analysis was conducted using 3 dimensions (stresses were 0.097 and 0.075, respectively). Shepherd stress plots were used to determine the reliability of these analyses by plotting the relationship between actual dissimilarities between objects and ordination distances, where a larger  $R^2$  value indicates a reliable analysis (linear  $R^2 = 0.921$ ,  $0.976$  and non-metric  $R^2 = 0.991$ ,  $0.995$  for prey and age NMDS, respectively). Correlations between prey and age class occurrence in bill-loads and prey biomass NMDS ordinations were performed, and coefficients  $\geq 0.4$  were considered biologically relevant (Gladics et al. 2015). Generalized linear models (GLMs; Gaussian family, identity link function) were used to determine the influence of year and average days since hatch on the

3 NMDS dimensions for the prey and age-class analyses (NMDS axis as the dependent variable, and year and chick age as independent variables). All NMDS analyses were performed using the R package 'vegan' (Oksanen et al. 2017).

Pearson correlation was performed between dive depth and dive duration (s). ANOVAs (with Bonferroni adjustments for multiple comparisons) were used to identify any differences in average maximum dive depth as a function of hour of day, differences in prey depths from bill-loads of TDR-equipped auklets, and differences in bill-load mass within and among years (bill-load mass as dependent, year and chick age as independent variables). We then plotted locations of GPS tracks, and compared those to locations recorded for diet items by fisheries trawls. Results are reported as mean  $\pm$  SD, unless otherwise stated. All analyses were performed using R v3.2.5 and graphed with the ggplot2 package (Wickham 2009).

## RESULTS

### Individual specialization

Auklet bill-loads from 2003–2016 ( $n = 2228$ , banded and unbanded) contained 22 different prey species. Bill-loads from banded auklets ( $n = 524$ ) had a WIC/TNW of 0.65 ( $p = 0.56$ ,  $n = 254$  individuals) and an  $E_{\text{adj}}$  of 0.56. Individual differences accounted for 35% of the variation in bill-load composition. On average, bill-loads contained  $5.7 \pm 4.5$  prey items (maximum = 30 items) from  $1.8 \pm 1.0$  species (maximum = 7 species), and 51% of all bill-loads sampled contained more than 1 prey species. The average bill-load weight was  $28.2 \pm 12.6$  g (maximum = 122 g). Bill-loads were significantly heavier in 2013 compared to 2007, 2014, and 2015, and were heavier in 2006 compared to 2007, 2011, 2014, and 2015 (GLM analysis; Table 2). Bill-loads were significantly heavier in Weeks 3–4 of chick rearing ( $\beta = 2.38$ ,  $z = 3.31$ ,  $p < 0.01$ ) and Weeks 5–6 ( $\beta = 2.96$ ,  $z = 4.03$ ,  $p < 0.01$ ) compared to Weeks 1–2, and were significantly lighter in Weeks 7–8 compared to Weeks 5–6 of chick rearing ( $\beta = -2.72$ ,  $z = -2.77$ ,  $p = 0.03$ ) across all years.

### Bill-load mass and composition

Prey composition of bill-loads changed throughout the season during the majority of years sampled (Fig. 1). Capelin or sand lance were consistently the most consumed species, in biomass, for the first 2 wk

Table 2. Mean  $\pm$  SD weight of rhinoceros auklet bill-loads for each year that was significantly different in bill-load weight compared to other years. Post hoc comparisons included with estimates ( $\beta$ ) give direction of significance. Significant values ( $p < 0.05$ ) are shown in **bold**

Year	Mean $\pm$ SD (g)	2005		2006		2007		2011		2012		2013	
		$\beta$	p	$\beta$	p	$\beta$	p	$\beta$	p	$\beta$	p	$\beta$	p
2016	29.01 $\pm$ 12.30	3.09	0.73	-2.89	0.76	5.18	3.46	2.98	2.11	-0.74	1.00	-2.39	0.64
2015	25.78 $\pm$ 11.95	0.00	1.00	-5.98	<b>&lt;0.01</b>	2.08	1.43	-0.12	-0.08	-3.83	<b>0.01</b>	-5.48	<b>&lt;0.01</b>
2014	27.05 $\pm$ 11.20	0.66	0.40	-5.31	<b>0.04</b>	2.75	1.71	0.55	0.36	-3.17	0.35	-4.81	<b>&lt;0.01</b>
2013	31.55 $\pm$ 13.56	5.48	3.49	-0.50	1.00	7.57	4.97	5.37	3.73	1.65	0.97	-3.85	<b>&lt;0.01</b>
2012	29.65 $\pm$ 15.17	3.83	2.49	-2.15	0.97	5.92	3.93	3.72	2.61				
2011	26.86 $\pm$ 12.51	0.11	0.06	-5.86	<b>0.04</b>	2.20	1.24						
2007	23.33 $\pm$ 10.70	-2.09	-1.12	-8.06	<b>&lt;0.01</b>								
2006	32.35 $\pm$ 11.50	5.98	3.27										
2005	25.22 $\pm$ 10.69												

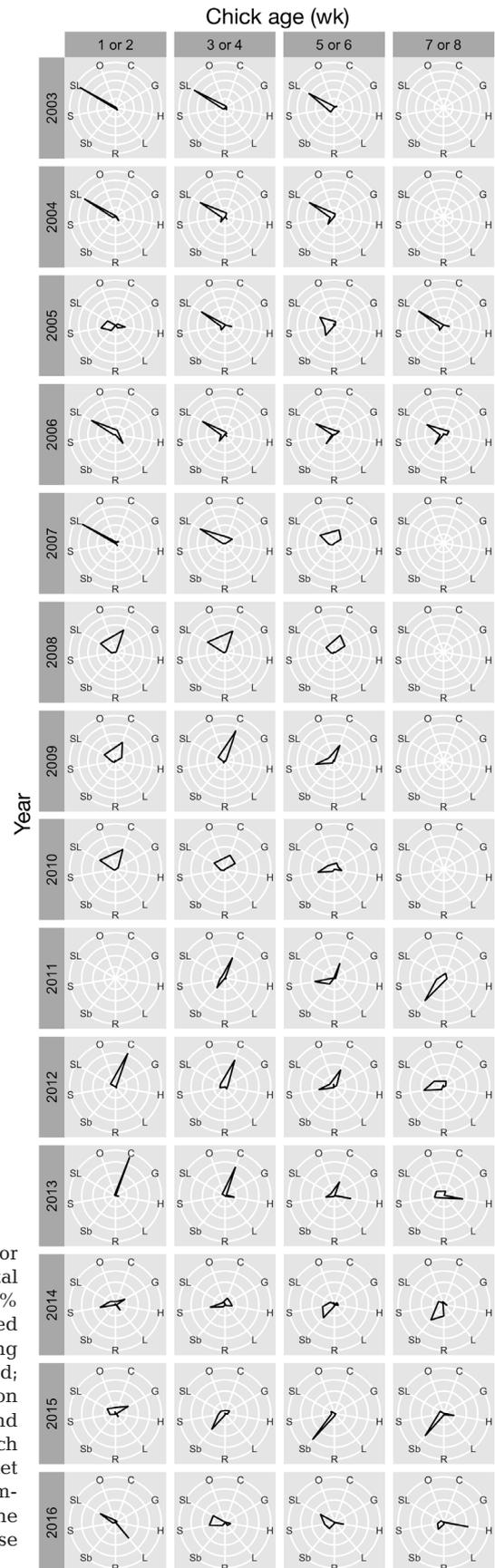


Fig. 1. Percent biomass for each species whose total biomass accounted for  $>1\%$  of the total biomass sampled (C: capelin; G: greenling spp.; H: herring; L: lingcod; R: rockfish spp.; S: sablefish; SL: sand lance, O: other) for each year and rhinoceros auklet chick age (2 wk bins) combination. Circles within the plots represent an increase of 25% biomass

of chick age, except in 2005 and 2014–2016 (Fig. 1). During Weeks 3–4 of chick age, larger fish species, such as salmon and sablefish, began to appear more frequently in bill-loads (Fig. 1). This increase of larger fish species in bill-loads continued into Weeks 5–8 of chick age, notably in recent years (Fig. 1). In earlier sampling years, larger fish species in bill-loads were of equal or lower proportions compared to the relative biomass of sand lance or capelin in bill-loads. Thus, the relative biomass of sand lance, and to a lesser extent capelin, in bill-loads stayed consistent during the latter half of chick rearing (Fig. 1).

Across years, sand lance was the most prevalent species in bill-loads (percent biomass; Fig. 2). Sand lance relative biomass decreased from 2008 to 2013, as capelin relative biomass increased in bill-loads (Fig. 2). Salmonids fluctuated the least across years, having little influence on the NMDS ordination, despite their large presence in bill-loads (Fig. 2, Table 3). Sablefish biomass increased in bill-loads from 2014–2016 with a peak in 2015, where this species comprised 45.7% of the sampled bill-load biomass for that year (Fig. 2). Bill-loads containing herring were more common in recent years (2013–2016), although herring did appear in sizeable amounts in 2005 (Fig. 2). NMDS axes were positively and negatively correlated with select prey species (Table 3). Year had a significant effect on axes NMDS1 ( $t = 6.14$ ,  $p < 0.01$ ), NMDS2 ( $t = -2.17$ ,  $p = 0.04$ ), and NMDS3 ( $t = -3.16$ ,  $p < 0.01$ ), and chick age had a significant effect on NMDS1 ( $t = 7.16$ ,  $p < 0.01$ ).

Capelin did not show large variation in their age class compositions across years and within years, while sand lance did not show large variation within years (Fig. 3). Age-1+ capelin comprised a minimum

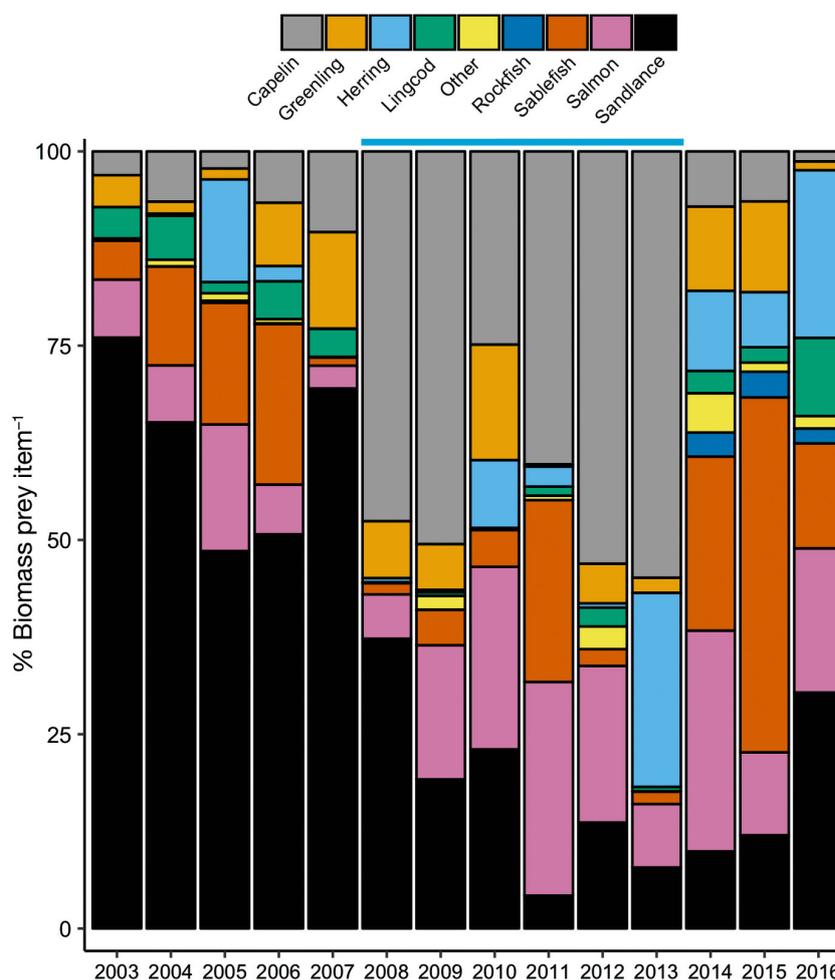


Fig. 2. Percent biomass of all prey species in rhinoceros auklet bill-loads for each year sampled. The blue bar at the top of the graph represents cold years (negative Pacific Decadal Oscillation)

Table 3. Correlations of prey species (percent biomass) for all prey species with non-metric multi-dimensional scaling (NMDS) axes 1, 2, 3, and 4. Values of  $R^2 \geq 0.4$  were considered biologically relevant and are highlighted in **bold**

Prey items Common name	Species	Axes			
		NMDS1	NMDS2	NMDS3	NMDS4
Capelin	<i>Mallotus villosus</i>	-0.090	<b>-0.600</b>	0.175	-0.194
Greenling spp.	<i>Hexagrammos</i> spp.	-0.261	0.152	-0.124	<b>0.520</b>
Herring	<i>Clupea pallasii</i>	<b>0.641</b>	-0.104	0.144	0.013
Lingcod	<i>Ophiodon elongatus</i>	<b>-0.664</b>	0.220	-0.293	-0.256
Other		0.118	0.036	<b>-0.587</b>	-0.262
Rockfish	<i>Sebastes</i> spp.	<b>1.040</b>	<b>0.885</b>	0.096	-0.272
Sablefish	<i>Anoplopoma fimbria</i>	<b>0.419</b>	0.233	0.190	0.076
Salmon	<i>Oncorhynchus</i> spp.	0.127	-0.109	-0.133	0.150
Sand lance	<i>Ammodytes hexapterus</i>	-0.365	0.247	0.168	-0.037

of 73.3% of the capelin captured during all chick ages when capelin was caught, except when chicks were 1 or 2 wk old in 2005 (Fig. 3). In contrast to capelin, sand lance and herring age composition fluctuated widely

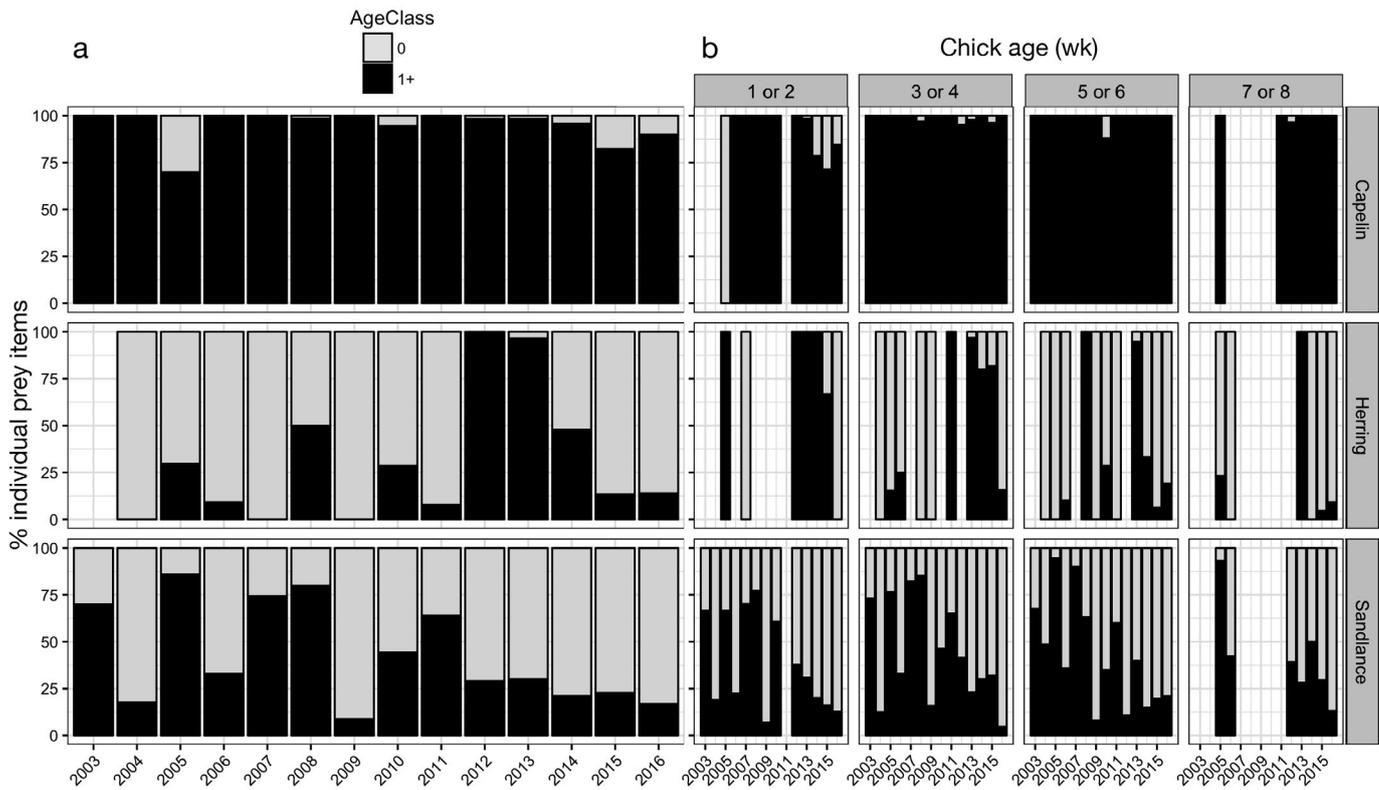


Fig. 3. Percent age composition of prey items collected (a) for year and (b) for each rhinoceros auklet chick age (2 wk bins) per year. Each graph or set of graphs represents a different species: capelin (top), herring (middle), and sand lance (bottom) in auklet bill-loads. Bill-loads were not collected during all chick ages in some years

across years. Age-0 herring comprised 71.4% of herring caught in 2010, but dropped to 3.4% in 2013 (herring were non-existent in 2012 bill-loads; Fig. 3). In 2014, age-0 and age-1+ individuals were equal in herring composition, but age-0 herring began to dominate total herring composition in the 2015 and 2016 breeding seasons (84.0 and 86.1% composition, respectively; Fig. 3). Herring were infrequent in bill-loads prior to Weeks 5–6, and when individuals did occur, the majority were age-1+ herring. In 2016, however, age-0 herring were more prominent during early chick rearing than age-1+ individuals (Fig. 3).

Prior to 2012, sand lance age classes had a cyclical pattern (Fig. 3). After 2012, large variations in sand lance age class were not seen, and these years were dominated by age-0 sand lance, where this age class comprised at least 50% of all individual sand lance for each chick age (Fig. 3). Similarly to the prey composition NMDS, year had a significant effect on axes NMDS1 ( $t = 2.92$ ,  $p < 0.01$ ) and NMDS3 ( $t = -4.72$ ,  $p < 0.01$ ), and chick age had a significant effect on NMDS2 ( $t = -2.55$ ,  $p = 0.01$ ). NMDS1 and NMDS2 were associated with age-0 capelin ( $R = 0.49$ ,  $0.70$ ), age-0 herring ( $R = 0.57$ ,  $-0.44$ ), and age-1+ herring ( $R = 0.62$ ,  $0.55$ ). The remaining age classes had an

$R < 0.4$ , and no age class had an association with  $R > 0.4$  for NMDS3.

### Auklet dive behaviour

Dive duration increased with maximum dive depth ( $n = 39985$  dives,  $t = 192.75$ ,  $p < 0.01$ ; Fig. 4). Auklets dived to an average depth of  $9.20 \pm 6.73$  m (maximum = 52.24 m) with an average duration of  $39.24 \pm 25.10$  s (maximum of 168 s). Depth and number of dives fluctuated with time of day (depth:  $F_{22, 39397} = 41.22$ ,  $p < 0.01$ ; dive count:  $F_{22, 1821} = 3.01$ ,  $p < 0.01$ ). Specifically, shallower dives were documented at dusk and dawn, and more dives were documented near dusk and dawn than at night or midday (Fig. 5). Depth during the last dive bout prior to arrival at the colony varied as a function of prey species captured ( $F_{8, 151} = 5.76$ ,  $p < 0.01$ ). Sand lance were caught at significantly deeper depths than capelin ( $\beta = 3.01$ ,  $t = 4.94$ ,  $p < 0.01$ ) and salmon ( $\beta = 2.75$ ,  $t = 3.77$ ,  $p < 0.01$ ), but not herring ( $p = 1.00$ ; Fig. 6). Mixed species bill-loads of sand lance and capelin were caught significantly shallower than pure sand lance ( $\beta = -3.04$ ,  $t = -4.17$ ,  $p < 0.01$ ), but not compared to pure capelin bill-loads ( $p = 1.00$ ).

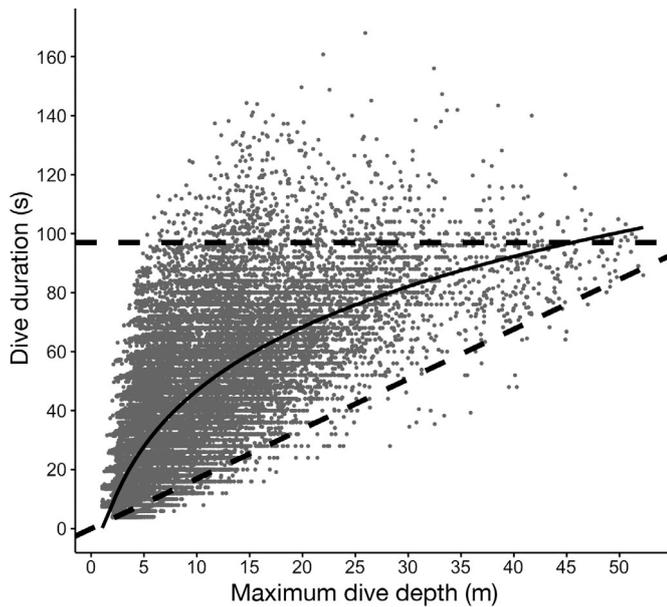


Fig. 4. Maximum dive depth and dive duration for rhinoceros auklets on Middleton Island, Alaska, USA. The solid line is the logarithmic function of dive duration and maximum depth. Based on a diving metabolic rate of  $6.31W$  from Shoji et al. (2016) and oxygen stores of  $30.5\text{ ml}$  from Yamamoto et al. (2011), a  $550\text{ g}$  alcid is expected to have an aerobic dive limit of about  $97\text{ s}$  (upper dashed line). A small number of individuals apparently exceeded their aerobic dive limit, necessitating substantial anaerobic respiration, leading to lengthy surface intervals to metabolize lactate at the surface. Given an average transit rate of  $1.18\text{ m s}^{-1}$ , auklets must have a minimum dive duration of  $1.69\text{ s}$  per metre of depth (lower dashed line). A small number of individuals apparently swam faster than the average transit rate

### Auklet foraging behaviour

Auklets foraged in 2 distinct patches, with the northern patch extending up to  $82\text{ km}$  and the southern patch extending up to  $66\text{ km}$  from the colony (Fig. 7). These birds foraged mostly between Middleton and Montague Island ( $60^{\circ}2'16.1''\text{ N}$ ,  $147^{\circ}28'41.9''\text{ W}$ ; Fig. 7). Five birds returned with bill-loads that could be associated with their GPS track, and 2 of those birds returned from the northern waters with sand lance in their bill-loads, a species that forage fish trawl surveys deemed absent in that area. All auklets foraged within government trawling areas, but there was no temporal overlap between our GPS equipped birds and government surveys.

### DISCUSSION

Auklet foraging behaviour and prey selection among and within years were associated with extrinsic environmental factors rather than with individual specialization. This could indicate that prey diversity found in their bill-loads is reflective of prey availability in surface waters, instead of active selection for specific prey species. In addition, other factors such as chick nutritional demands may influence prey choice and cause prey switching. Auklet dive behaviour varied with light levels and prey diel vertical migration. Auklets were able to detect prey species in foraging areas where previous surveys have deemed

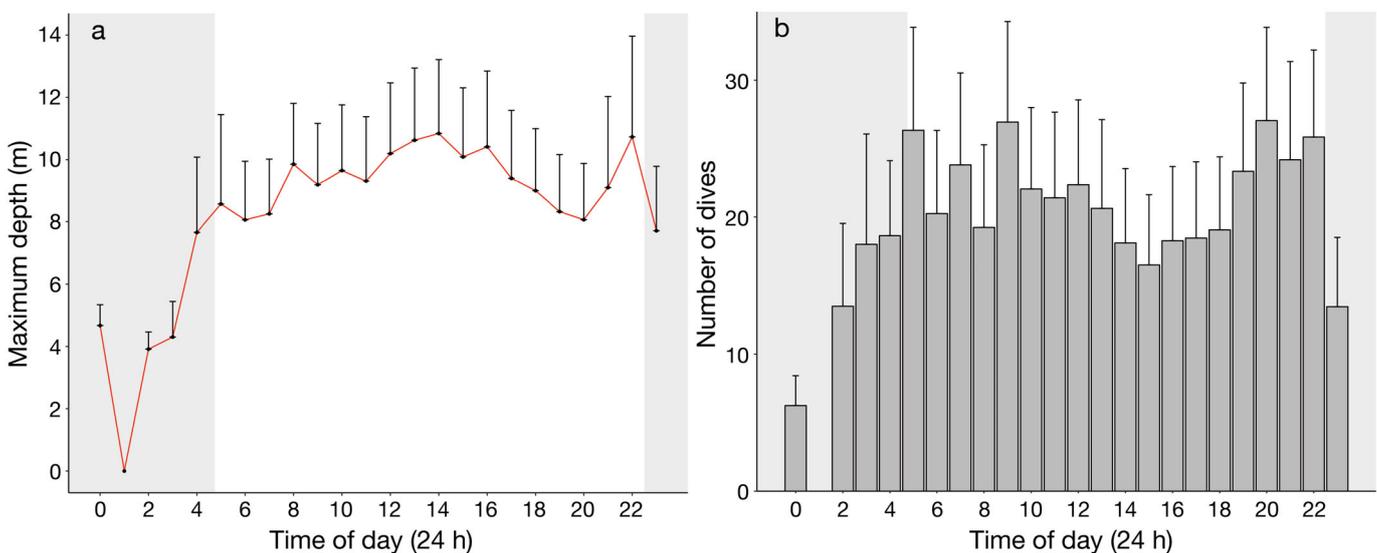


Fig. 5. Mean  $\pm$  SD (a) maximum depth achieved and (b) number of dives performed for each hour of the day. The grey shaded areas designate hours of darkness, with the transition from grey to white representing sunrise and sunset on 23 July, the median day of sampling during the breeding season

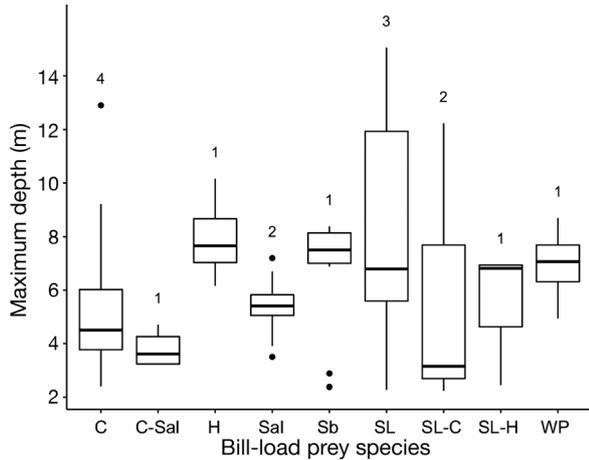


Fig. 6. Box plots showing mean maximum depth achieved for each species or species-combination in sampled bill-loads (C: capelin; H: herring; Sal: salmon spp.; Sb: sablefish; SL: sand lance; WP: walleye pollock). Average dive depth was determined from the final 10 dives, prior to capture, of individual rhinoceros auklets equipped with time-depth recorders. Bill-loads containing the same species were combined. Numbers above box plots indicate the number of bill-loads sampled for that species (or species combination). Each box plot indicates the shallowest dive depth, lower quartile, median, upper quartile, and deepest dive depth. Black dots indicate outliers

them sparse or absent, and to track changes in age classes. Based on these results, we support the use of auklet diet as an ecological monitoring tool that can be used in parallel with conventional surveying methods to detect changes in forage fish availability and, in turn, changes in the marine environment.

### Individual specialization versus environmentally induced flexibility

Differences among individuals in bill-load composition accounted for 35% of the variation in bill-load composition, but those differences were not statistically significant. In contrast, individual specialization accounted for 73% of the variation in bill-load composition in thick-billed murres *Uria lomvia* (Woo et al. 2008, Elliott et al. 2009, Provencher et al. 2013). Perhaps environmental factors swamped any potential individual preferences, and chick diet was closely linked to environmental variability. Similarly, Vermeer (1980) found that auklets switched prey species during times of decreased prey availability.

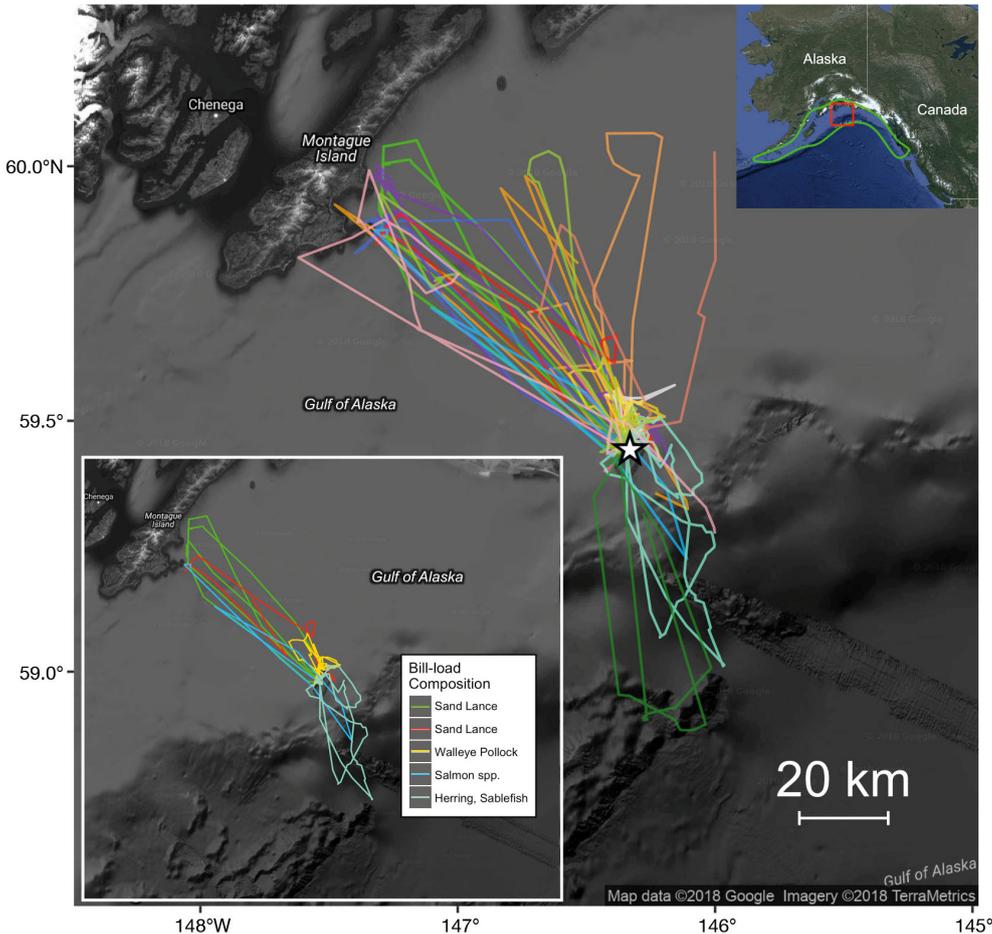


Fig. 7. Foraging tracks of 17 chick-rearing rhinoceros auklets equipped with GPS units. Each colour in the main figure represents the foraging track of an individual auklet over a 3–5 d span. The inset in the top right corner shows the approximate foraging area of the auklets (red box) and the approximate survey area for government trawls (green outline) in the Gulf of Alaska. The inset in bottom left corner shows the foraging tracks for the 5 birds that returned with a bill-load, and the legend describes the bill-load composition of the last foraging trip performed by those birds prior to recapture. The star on the main map denotes the breeding colony at Middleton Island

Apparently, auklets forage on a dominant prey species during times of high availability (i.e. good capelin years), but switch to other prey when availability decreases; individual bill-load composition is determined by what is available when foraging, as opposed to individual specialization. Interestingly, despite the low dietary individual specialization, individuals had high repeatability in foraging destinations (Fig. 7), as was also the case for other alcids (Elliott et al. 2009, Regular et al. 2013).

### Changes in prey and age-class composition within and across years

Auklet bill-loads mostly comprised small, schooling, epipelagic fish, as was the case elsewhere. Sand lance was a dominant prey item in British Columbia (Canada) and Washington (USA) auklet colonies (Wilson & Manuwal 1986, Bertram et al. 1991, Burger et al. 1993), as well as the Teuri Island, Japan, colony (Takahashi et al. 2001, Senzaki et al. 2014). Capelin, lingcod *Ophiodon elongatus*, and sablefish were rare prey items in British Columbia, Washington, and California (Vermeer & Westrheim 1984, Bertram & Kaiser 1993, Davoren & Burger 1999), while rockfishes and greenling species were common (Thayer et al. 2008, Carle et al. 2015). One Pacific saury was captured by auklets on Middleton Island, despite the increased occurrence of this forage fish in the aforementioned colonies south of Middleton Island (Vermeer & Westrheim 1984, Wilson & Manuwal 1986, Carle et al. 2015).

Average bill-load mass ( $28 \pm 13$  g) for auklets on Middleton Island was comparable to values recorded elsewhere (Bertram & Kaiser 1993, Burger et al. 1993, Takahashi et al. 2001). Lower bill-load mass during the warm water 'anomaly' and El Niño conditions post-2013 (Cavole et al. 2016) could be explained by the crash in capelin during those warmer years (Fig. 2). Auklets on Middleton brought back equal proportions of mixed-species bill-loads compared to single-species bill-loads, as distinct from studies in British Columbia (60% of bill-loads contained a single species; Burger et al. 1993) and Japan (93–99% of bill-loads contained a single species; Takahashi et al. 2001, Senzaki et al. 2014). Similar to Japan and British Columbia colonies (Bertram et al. 1991, Takahashi et al. 2001), bill-loads increased during mid-chick-rearing before decreasing prior to chick fledging. The increase early in the season could reflect growing offspring demand as well as availability of larger fish as the season progresses (such as juvenile salmon; Miller et al. 2012).

Life history patterns of several prey species are evident in our results. Sand lance do not migrate during spawning and lay adhesive eggs that are resistant to ocean currents (Field 1988). Thus, sand lance are generally found in the same location on a yearly basis, explaining their continual appearance in bill-loads for all chick ages (Fig. 1). In contrast, the increasing appearance of salmonids in the diet of auklet chicks as they aged is probably because juvenile salmon leave estuaries in July and enter the Gulf of Alaska's continental shelf (Welch et al. 2003, Miller et al. 2012). Simultaneously, they began to appear in auklet bill-loads (Weeks 3–8; Fig. 1). Similarly, larval herring remain in nursery grounds until June, when they metamorphose into young-of-the-year or age-0 herring (Norcross et al. 2001). In July, the age-0 herring join age-1 herring before entering the Gulf of Alaska in schools of all age classes in August (Norcross et al. 2001). This life cycle is evident in the auklet bill-loads, where herring became most apparent in Weeks 5–8 (mid-July to August; Fig. 1). Increased age-0 herring years were generally followed by increased age-1 herring years before returning to age-0 years (Fig. 3). Age-0 herring individuals tended to increase in bill-loads later in chick rearing (chick age 5–8 wk), perhaps due to their migration pattern (Norcross et al. 2001).

The most striking change in bill-load composition across years was the substantial increase of capelin during 2008–2013, followed by its severe decline in 2014 when a warm water 'anomaly' occurred (Cavole et al. 2016). Capelin was absent from seabird diets during years of increased sea surface temperatures (Hatch 2013, Sydeman et al. 2017). Sand lance was more abundant (percent biomass) in auklet bill loads during the warmer period pre-2008, but did not respond rapidly post-2013. This trend was also seen in historical bill-load data from Middleton Island, where sand lance dominated bill-load biomass in the 1990s during periods of increased sea surface temperatures (Thayer et al. 2008). Sand lance age class fluctuated in bill-loads during the initial sampled years of this study similar to other studies (Bertram & Kaiser 1993, Hatch 2013). Recently, age-0 individuals became the predominant age class of sand lance (Fig. 3). This may suggest that recruitment of age-1 sand lance from the previous year's age-0 sand lance was lower during recent, warmer seasons, as increased sand lance abundance and recruitment are associated with high zooplankton abundance, which is directly linked to colder temperatures and increased salinities (Barber & Chavez 1983, Ware & Thomson 1991, McFarlane & Beamish 1992).

### Auklet dive behaviour

Previous research on the dive behaviour of auklets is limited to 1 colony in Japan (Kato et al. 2003, Watanuki & Sato 2008, Yamamoto et al. 2011) and a brief analysis of dive behaviour at St Lazaria in Alaska (Will et al. 2015). Burger et al. (1993) recorded maximum depth of auklets in British Columbia using capillary tubes, a technique since shown to lead to erroneous values (Elliott & Gaston 2009). Maximum dive depth at Middleton Island (52.24 m) was similar to maximum depths found at Teuri Island, Japan (Kato et al. 2003, Kuroki et al. 2003, Watanuki & Sato 2008). Average dive depth and duration for Middleton Island auklets were within the ranges of those observed at Teuri Island, Japan:  $9.2 \pm 6.7$  m (at Middleton) and  $39.2 \pm 25.1$  s versus  $12.1 \pm 5.5$  m and  $42.7 \pm 17.7$  s (Kato et al. 2003), and  $14 \pm 1.8$  m and  $53 \pm 8$  s (Kuroki et al. 2003), and were similar to the duration predicted for a 500 g alcid (Will et al. 2014, Shoji et al. 2016). The deeper average dive depth in Japan could be attributed to the pursuit of Japanese anchovy, a major prey species in the diet of Teuri Island auklet chicks (Takahashi et al. 2001, Senzaki et al. 2014); anchovies have a larger range in depth compared to sand lance and herring (Hourston & Haegele 1980, Ohshimo & Hamatsu 1996). Dive duration increased with maximum depth in agreement with Kuroki et al. (2003), with dive duration bounded by the aerobic dive limit at the upper limit and requirements to transit to depth at the lower limit (Fig. 5).

Increased dive frequency corresponded with dawn and dusk on Middleton Island (Fig. 6). This was also the case at Teuri Island (Kato et al. 2003, Kuroki et al. 2003). In contrast, auklets dived primarily near dusk at Seabird Rocks, British Columbia (Davoren & Burger 1999). The higher latitude of Middleton Island ( $59^{\circ}25'N$ ), compared to Teuri Island ( $44^{\circ}25'N$ ) or Seabird Rocks ( $48^{\circ}45'N$ ), means that dawn was earlier and dusk was later than at those sites. This extended period of light may explain why auklets performed dives at almost every hour of the day at Middleton Island (Fig. 5), which was not evident on Teuri Island (Kuroki et al. 2003). Diving throughout the day is also comparable to other alcid species at higher latitudes. For example, thick-billed murres at Hakluyt Island (Greenland;  $77^{\circ}26'N$ ) and Kongsfjorden (Spitsbergen, Norway;  $72^{\circ}N$ ), and dovekeys *Alle alle* at Kap Brewster ( $70^{\circ}10'N$ ) and Kap Höegh ( $70^{\circ}43'N$ ), Greenland, respectively, dived continuously for 24 h and had no discernable pattern in dives throughout the day (Mehlum et al. 2001, Falk et al.

2002, Harding et al. 2009). The lull in the number of dives auklets performed from 23:00–03:00 h (Fig. 5) corresponds to their nightly visitations to the burrow to feed their offspring.

Auklet dives increased in depth as the day progressed, peaking at 14:00 h before they began to decrease (Fig. 5). This trend has been seen in auklets on Teuri Island (Kato et al. 2003, Kuroki et al. 2003) and in other alcid species (Benvenuti et al. 2001, Paredes et al. 2008, Elliott & Gaston 2015). Visibility at deeper depths is a limiting factor for diving seabirds (Wilson et al. 1993, Regular et al. 2011, Elliott & Gaston 2015). However, prey behaviour also influences diving behaviour (Wilson et al. 1993, Elliott & Gaston 2015). Zooplankton undergo diel vertical migration, giving planktivorous fish an opportunity to forage on the transitioning zooplankton at dusk and at the surface throughout the night until the zooplankton return to deeper depths before dawn (Burger et al. 1993, Kato et al. 2003). Sand lance, herring, juvenile salmon, and Japanese anchovies have all been found to forage in surface waters (<10 m; Hart 1973, Field 1988, Ohshimo & Hamatsu 1996, Miller et al. 2012). Thus, auklets may forage during times of high prey availability at shallow depths (dusk), before returning to the colony.

We found significant differences between prey species and their capture depths. Specifically, capelin were caught at shallower depths than salmon and sand lance (Fig. 6). Sand lance prefer locations with depths of 40–50 m (Robards et al. 1999, Ostrand et al. 2005, Robinson et al. 2013), and capelin and adult Pacific salmon have been documented at shallower depths than those preferred by sand lance (Garthe et al. 2000, Ishida et al. 2001). However, because these fish species undergo crepuscular foraging, maximum depths are not as relevant when auklets collect bill-loads prior to returning to the colony at dusk. Indeed, all bill-loads were caught within 15 m of the water's surface, a quarter of the maximum depth auklets have been known to achieve (Burger et al. 1993, Watanuki & Sato 2008).

Auklets travelled farther from the colony than previous observations (Cody 1973, Deguchi et al. 2010), but were within the maximum foraging range estimated for this species (Kato et al. 2003). Maximum foraging distance for Middleton birds was roughly twice the distance for auklets at the Farallon Islands, California (~27 km; Wilkinson et al. 2018). Moreover, whereas birds at the Farallon Islands foraged primarily over the shelf, most birds at Middleton Island moved away from the shelf edge, and towards coastal waters. Auklets foraged in both the shallow, northern

continental shelf (<100 m) and the deeper, southern continental slope (200–4000 m; Hatch 2013). Using 2 separate foraging areas, potentially consisting of different prey availability (i.e. sablefish spawn in deeper waters near the continental slope; Sigler et al. 2001, Hatch 2013), could allow for an increased diversity of prey species to be exploited.

### Auklets as samplers of forage fish populations

The use of seabirds to identify trends in forage fish data is a recurring idea in the literature (see Vermeer & Westrheim 1984, Hatch & Sanger 1992, Cury et al. 2011). Conventional sampling methods can be costly and are accompanied by methodological challenges, including fish avoidance behaviour (Suuronen et al. 1997, Misund et al. 1999), poor sampling equipment (Ormseth 2014, Ormseth et al. 2016), and forage fish patchiness that leads to disparity in sampling (Vermeer & Westrheim 1984). Historically, insight on forage fish estimates in the Gulf of Alaska have been determined by incidental catch in bottom trawls, although in recent years (2011–2013), pelagic trawls have been performed in pre-determined areas (Ormseth 2012, Ormseth et al. 2016). However, both of these trawl methods have innate sampling biases in their equipment and methods.

In this study, GPS-equipped auklets returned with sand lance captured in surface waters between Middleton Island and Montague Island (Fig. 7). As sand lance is a dominant prey item in auklet bill-loads, and many GPS-equipped auklets foraged in northwestern waters, we can conclude that sand lance is present in this area. However, trawling data from 2007–2013 detected no sand lance in the water around Middleton Island or the majority of the central Gulf of Alaska (see Fig. 3 in Ormseth 2014). It is possible that sand lance may be available across the Gulf of Alaska, but trawling only detects this species in areas of high abundance, such as the Western Gulf of Alaska (Ormseth 2014). As seabirds actively forage for fish, they may be better suited to display changes in the environment, if they take prey species in relative proportions to actual forage fish abundances.

In some systems, seabird diet can predict future fisheries catch (Velarde et al. 2013, Wells et al. 2017). However, for several seabird species, colony metrics, including diet, are often poor indicators of independently measured prey stocks, except at low stock levels (Piatt et al. 2007, Cury et al. 2011, Brisson-Curadeau et al. 2017). One potential cause is prey switching, as observed in our study, such that sea-

birds switch to alternate prey once abundance drops below a critical threshold. Additional research is needed to address potential confounding factors, such as differences in dietary and foraging behaviour between sexes or age classes (see Elliott et al. 2010a, Carle et al. 2015, Cunningham et al. 2017). Neither trawling nor seabird diets are comprehensive enough to adequately gauge forage fish abundance independently, but could be used in combination to monitor changes in the marine food chain. Using seabird data to monitor forage fish availability and abundance, perhaps by monitoring several Gulf of Alaska colonies (Sydeman et al. 2017), is a cost effective way to collect data on widely distributed ecologically important fish, including the difficult to monitor juvenile stages.

In sum, rhinoceros auklets were effective samplers of forage fish availability in the top 15 m of the Gulf of Alaska. Individual auklets did not show marked specialization, implying that they had the flexibility to alter their diet in response to prey availability. Indeed, auklets displayed temporal changes in forage fish availability within and among years. Capelin dominated auklet diet during the cold-water period with negative Pacific Decadal Oscillation values (2008–2013), whereas Pacific sand lance were more common in warmer years. Bill-load composition changed within years, with sand lance and capelin delivered to younger chicks, and larger fish, like sablefish, being introduced as the chicks aged. Auklets also returned with sand lance from a foraging area where trawling detected none, implying that auklets can potentially detect fish availability at finer resolutions than conventional methods. We strongly encourage the use of auklets across the Gulf of Alaska as one of the samplers of forage fish availability in this region.

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