ARTICLE IN PRESS

Deep-Sea Research Part I xxx (xxxx) xxx–xxx

Contents lists available at ScienceDirect

Deep-Sea Research Part I

journal homepage: www.elsevier.com/locate/dsri

Variation in zooplankton prey distribution determines marine foraging distributions of breeding Cassin's Auklet

Douglas F. Bertram[a,b,*], David L. Mackas[c], David W. Welch[d,1], W. Sean Boyd[b], John L. Ryder[a,2], Moira Galbraith[c], April Hedd[a,3], Ken Morgan[e], Patrick D. O'Hara[e]

[a] Simon Fraser University, Centre for Wildlife Ecology, Department of Biological Sciences, 8888 University Drive, Burnaby, B.C., Canada V5A 1S6
[b] Environment and Climate Change Canada, Canadian Wildlife Service, 5421 Robertson Rd., Delta, B.C., Canada V4K 3N2
[c] Department of Fisheries and Oceans, Institute of Ocean Sciences, 9860 West Saanich Road, P.O. Box 6000, Sidney, B.C., Canada V8L 4B2
[d] Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, B.C., Canada V9R 5K6
[e] Environment and Climate Change Canada, Canadian Wildlife Service, c/o Institute of Ocean Sciences, 9860 West Saanich Road, P.O. Box 6000, Sidney, B.C., Canada V8L 4B2

ARTICLE INFO

Keywords:
Zooplankton distribution
Cassin's Auklet
Marine habitat use
Neocalanus
Deep-sea copepods
Ptychoramphus aleuticus
Marine National Wildlife Area

ABSTRACT

To investigate the causal basis for patterns of seabird foraging distributions during breeding we integrated data from ship-board seabird and zooplankton surveys, aerial radio telemetry, and colony-based research programs. We examined the marine distributions of Cassin's Auklet (*Ptychoramphus aleuticus*) breeding on Triangle Island, in the Northeast Pacific off the coast of B.C., Canada using surveys conducted in 1999, 2000, and 2001. Concurrently, we sampled zooplankton at 16 stations along a cross shelf transect in the vicinity of Triangle Island. In 1999 and 2000, when populations of the preferred copepod prey *Neocalanus cristatus* were available at deep-water stations (1000–2000 m), the majority of the auklets were concentrated SW of the colony 40–75 km offshore and parallel to, but 35 −50 km beyond the shelf break in deep water (1200–2000 m). Birds did not fly farther out to sea to where prey was five times more abundant when *N. cristatus* could be found at lower abundance levels, closer to the colony. In 2001, *N. cristatus* were virtually absent at the deep-water stations, likely as a result of massive salp (family Salpidae) aggregations which may have consumed and displaced the seabirds' preferred prey. We demonstrate that while birds were still able to locate and provision chicks with *N. cristatus* in 2001, they had to forage farther away from the colony in order to do so. Our telemetry results are generally consistent with analyses of at-sea distributions of Cassin's Auklets derived from ship-board surveys (1990–2010) both of which have contributed to the design of the proposed Scott Islands marine National Wildlife Area, the first of its kind in Canada.

1. Introduction

The examination of marine habitat use by breeding seabirds is a fundamental step required to gauge ecosystem function, vulnerability to anthropogenic threats around colonies, and to inform conservation efforts (Hunt et al., 1999; Robinette et al., 2007; Wilson et al., 2009; Nur et al., 2011; Benoit-Bird et al., 2013; Davoren, 2013; Gaston et al., 2013; Lascelles et al., 2015; Manugian et al., 2015; Sydeman et al., 2015; Fifield et al., 2017; Santora et al., 2017).

In the Northeast Pacific, 26 nautical miles off of Vancouver Island, British Columbia, is Triangle Island, the largest and most diverse seabird colony on Canada's West Coast (Rodway, 1991). In addition, the world's largest population of Cassin's Auklet (*Ptychoramphus aleuticus*) breeds on Triangle Island (Rodway and Lemon, 2011).

Cassin's Auklets are small seabirds (~180 g) of the family Alcidae that use their wings both for flying and for propulsion underwater in search of prey such as copepods, krill, and small fish. Cassin's Auklet's maximum dive depth averages 22 m, with a mode of 40 m (Burger and Powell, 1990). Like most seabirds, Cassin's Auklets have long lives (Bertram et al., 2005; Morrison et al., 2011), delayed maturity, and low reproductive output (females usually lay a single egg per year on colonies in BC). The nestling is fed regurgitations each night by both

* Corresponding author at: Environment and Climate Change Canada, Wildlife Research Division, c/o Institute of Ocean Sciences, 9860 West Saanich Road, P.O. Box 6000, Sidney, B.C., Canada V8L 4B2.
E-mail address: douglas.bertram@dfo-mpo.gc.ca (D.F. Bertram).
[1] Present address: Kintama Research Services, Ltd., 4737 Vista View, Nanaimo, B.C., Canada V9V 1N8.
[2] Present address: Environmental Programs, Yukon Department of Environment, P.O. Box 2703, Whitehorse, Y.T., Canada Y1A 2C6.
[3] Present address: Environment and Climate Change Canada, Wildlife Research Division, Mount Pearl, NL, Canada A1N 4T3.

http://dx.doi.org/10.1016/j.dsr.2017.09.004
Received 28 February 2017; Received in revised form 8 September 2017; Accepted 9 September 2017

parents (Hedd et al., 2002), who carry food in a gular pouch.

Breeding success on Triangle Island has been linked to the timing of availability of large bodied copepod prey in surface waters (Bertram et al., 2001, 2017; Hipfner, 2008). The preferred *Neocalanus* copepods exhibit strong seasonal vertical migration linked to their developmental and reproductive cycle. These copepods are 'interzonal migrants' and are therefore only available to diving seabirds for a brief period before the stage V copepodites leave surface waters to reproduce and complete their life cycle at bathypelagic depths (400–700 m, Mackas et al., 1998). Breeding failures can occur when timing of copepod prey availability and predator breeding are mismatched due to warm ocean temperature anomalies.

Since seabirds are long lived and have many years to breed, life history theory (Roff, 1992; Stearns, 1992) predicts that to maximize lifetime reproductive success parents should limit investment in their current offspring and be reluctant provisioners (cf Drent and Daan, 1980), particularly in years of poor prey availability, to safe guard themselves for future reproductive efforts (see Burke and Montevecchi (2009), Jacobs et al. (2013)). It has been estimated that Cassin's Auklet breeding farther south need to consume 67% of their body mass per day in euphausiids during chick rearing (Hodum et al., 1998) and it is known that breeding birds of the family Alcidae are close to their maximum working capacity and "energetic ceiling" (Elliott et al., 2013; Regular et al., 2014). In addition, breeding colonial seabirds like Cassin's Auklet are central-place foragers and central-place foraging theory (Orians and Pearson, 1979) predicts that prey items close to the colony will be preferred over prey items distant from the colony (see Elliott et al. (2009)).

A tracking study using aerial telemetry around Triangle Island demonstrated that the marine foraging distributions (home range estimates) of the auklets during the chick-rearing periods of 1999 and 2000 were similar in size and overlapped but were larger and non-overlapping in 2001 when birds were dispersed more widely and foraged farther from the colony (Boyd et al., 2008). The telemetry work of Boyd et al. (2008) was part of an integrated ecosystem study which combined ship-based sampling for zooplankton with aerial telemetry to track breeding seabirds, and colony-based research on nestling diet and growth. Here we report the concurrent (1999, 2000, 2001) sampling for zooplankton distribution and abundance along a cross shelf transect, which was designed to pass near Triangle Island (see Figs. 1a, 2a, 3a).

The objective of our study was to examine the foraging locations and distances from the breeding colony, within and among years, in relation to the distribution and abundance of *Neocalanus* copepods and euphausiids (*Thysanoessa* spp. and *Euphausia pacifica)*, key zooplankton prey groups for the seabirds in British Columbia (Bertram et al., 2001, 2009; Hedd et al., 2002; Hipfner, 2008, 2009). We compared our aerial telemetry results with analyses of at-sea distributions of Cassin's Auklets, derived from ship-board transect surveys.

2. Methods

Field work was conducted at Triangle Island (50°52'N 129°05'W), the largest and most diverse seabird colony in Western Canada, with a long history of seabird research, recognized as an internationally Important Bird Area (Scott Islands Group, BC006) and with the land protected as a provincial Ecological Reserve (Anne Vallée). The remote and rugged seabird colony is in a unique oceanographic position at the northern end of the California Current Ecosystem, 26 nautical miles offshore of the northern tip of Vancouver Island in the North Pacific, the outermost of the Scott Islands. We conducted an integrated ecosystem study of Cassin's Auklet foraging ecology by forming a partnership among the Fisheries and Oceans Canada (DFO), Environment Canada, and Simon Fraser University, Centre for Wildlife Ecology. We present data on (1) marine distributions of birds from air-borne radio telemetry (1999–2001) and ship board transect surveys (1990–2010); (2) nestling diet on Triangle Island (1999–2001); and (3) regional zooplankton surveys (1999–2001). When there was more than one zooplankton survey in a year we present the zooplankton results for the cruise which was closest in time to the telemetry flights to best match the timing of the dates of plankton sampling and dates when marine bird foraging locations were determined.

2.1. Marine distributions of Cassin's Auklet

We measured marine bird distribution patterns in two ways which addressed different time frames and different resolutions of spatial scale. The first method tracked individual breeding birds using air-borne very-high frequency (VHF) telemetry at specific times for periods ranging from days to weeks, over three breeding seasons. This allowed us to compare the foraging locations within and between years as well as in relation to a concurrent zooplankton sampling program at sea. The second method used seabird density data derived from at-sea strip transect surveys onboard ships of opportunity over a 20 year period. We compared our aerial telemetry results with analyses of at-sea distributions of Cassin's Auklets, derived from ship-board transect surveys.

2.1.1. Aerial Radio telemetry

We attached 2.2 g VHF transmitters to breeding Cassin's Auklet in 1999 (n = 39), 2000 (n = 35), and 2001(n = 38) on Triangle Island. The radio signals from individual birds were detected from a de Havilland Beaver float plane fitted with antennae, flying at high altitude (~3000 m) covering surveys grids (up to 5.1 million ha) over the open ocean. The VHF radio telemetry methods are presented elsewhere in detail (Boyd et al., 2000, 2008; Ryder et al., 2001; McFarlane Tranquilla et al., 2005). We assumed that the Cassin's Auklet detection locations, based on VHF radio telemetry represented marine areas where adults foraged during the day for self-maintenance, and also where they captured prey for delivery to their single nestling upon returning to the colony at night. In this report we use a single detection to represent the location of each bird that was closest in time to the zooplankton sampling date. We visualized locations with the 95% Kernel Home Ranges (KHR) previously reported by Boyd et al. (2008) based on telemetry data collected for all of the tagged birds during the same year. We use the term "kernel home range" or KHR throughout to be consistent with the work of Boyd et al. (2008).

2.1.2. At-sea strip transect surveys

The at-sea data were collected by skilled observers placed on ships of opportunity (i.e., whenever possible) to conduct seabird counts using fixed-width strip transects (see Kenyon et al. (2009) for detailed methodology and summaries for data collected). A density surface was created for Cassin's Auklet (birds/km^2) based upon two decades (1990–2010) of at-sea survey data, collected during the chick rearing period (May-July) in the vicinity of the Triangle Island (at-sea bird observations are shown in Fig. 4b to represent the number of surveys and spatial extent). This density surface represents an average May-July distribution over these 20 years. To create the density surface a negative binomial Generalized Additive Model (GAM) was used based on Cassin's Auklet at-sea abundances as the response variable, and location (latitude and longitude as Equal Area Albers coordinates in metres) and square-root transformed depth as predictor variables. Effort was used as an offset variable, and effort was log transformed to be consistent with log link function of the negative binomial GAM. The GAM was developed using the Mixed GAM Computation Vehicle (MGCV) package in R (R Development Core Team, 2008), with thin-plate regression splines as smooth terms for both location (bivariate with 40 knots) and square-root depth (2 knots). The GAM was developed using Restricted Maximum Likelihood to estimate the smoothing parameters with inflated model degrees of freedom (gamma = 1.4) to reduce model overfitting as suggested by Wood (2016). The GAM was then used to predict Cassin's Auklet densities onto a 1 × 1 km grid (BC Albers Equal Area projection) to produce a density surface.

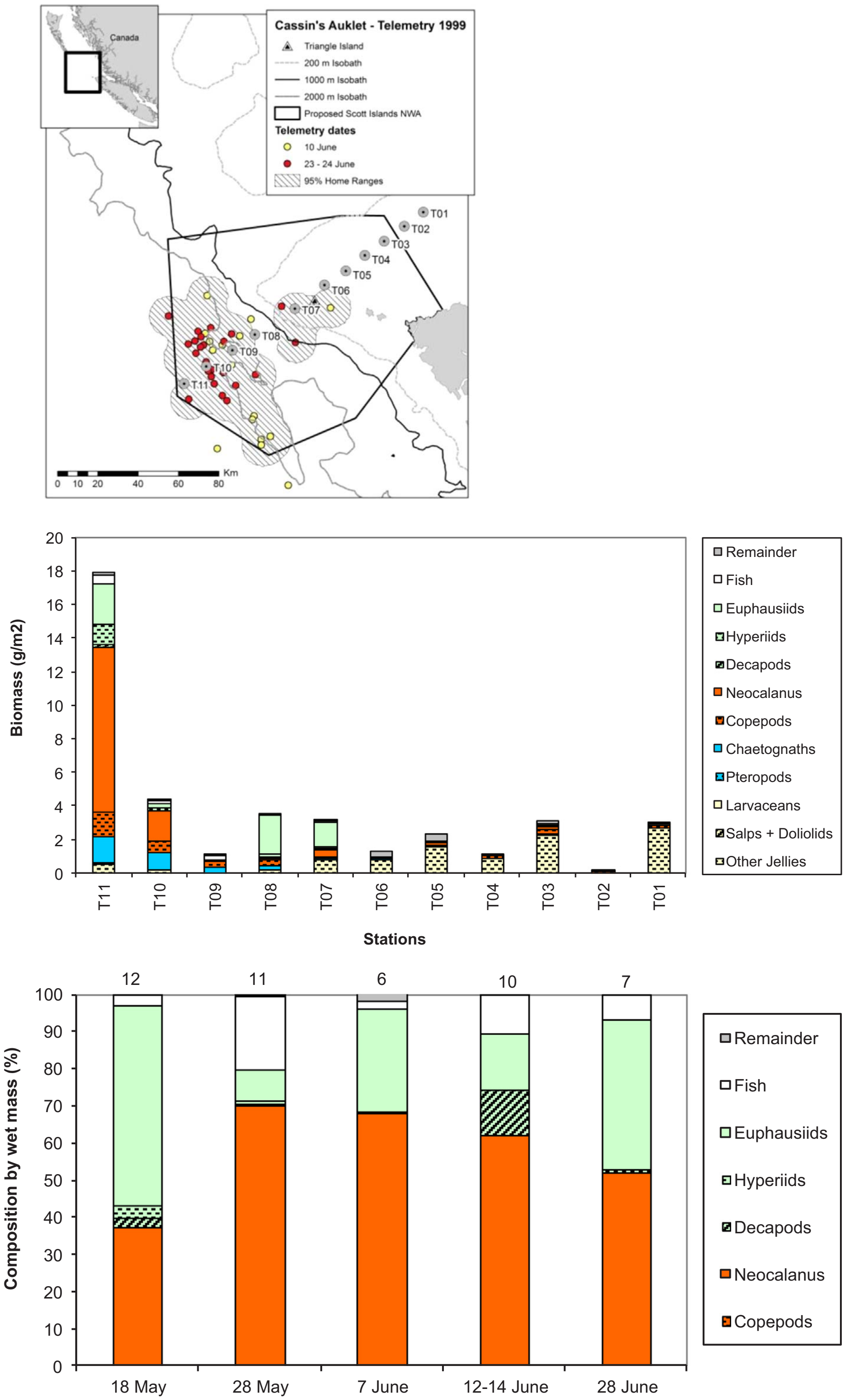

Fig. 1. (a) The marine distribution of individual Cassin's Auklets breeding on Triangle Island on 10 and 23–24 June 1999. Depth contours show the continental shelf break (200 m) and slope (1000 m and 2000 m) region. Shown also are the 95% Kernel Home Ranges of foraging birds (from Boyd et al. (2008)) and the proposed boundaries for the marine National Wildlife Area (Environment Canada, 2013). (b) Spring season zooplankton gradients along the Triangle transect, 23–24 June 1999. (c) Nestling diet (regurgitated from provisioning parents) of Cassin's Auklet during the 1999 breeding season. The number of diet samples is shown above the bars.

2.2. Nestling diet sampling

The diet of nestling Cassin's Auklet was sampled on Triangle Island at 10 d intervals (n = 2–39), from mid-May until the end of June in each year (1999, 2000, 2001). Adult birds, returning to the colony at night were captured and we collected meals intended for nestlings by assisting the parents to regurgitate the contents of their gular pouch into a funnel (see Hedd et al. (2002) for more detailed methods). Zooplankton identification and enumeration was conducted by the same taxonomist who performed the ship-based zooplankton work (MG) to ensure consistency (see below). Zooplankton in the nestling diet was grouped into the following categories: Copepods, Decapods, Euphausiids, Fish, Hyperiids, *Neocalanus*, & Remainder.

2.3. Zooplankton sampling

We established a cross–shelf transect of sampling stations with two variants (T and CS) and conducted cruises in 1999, 2000, and 2001. The

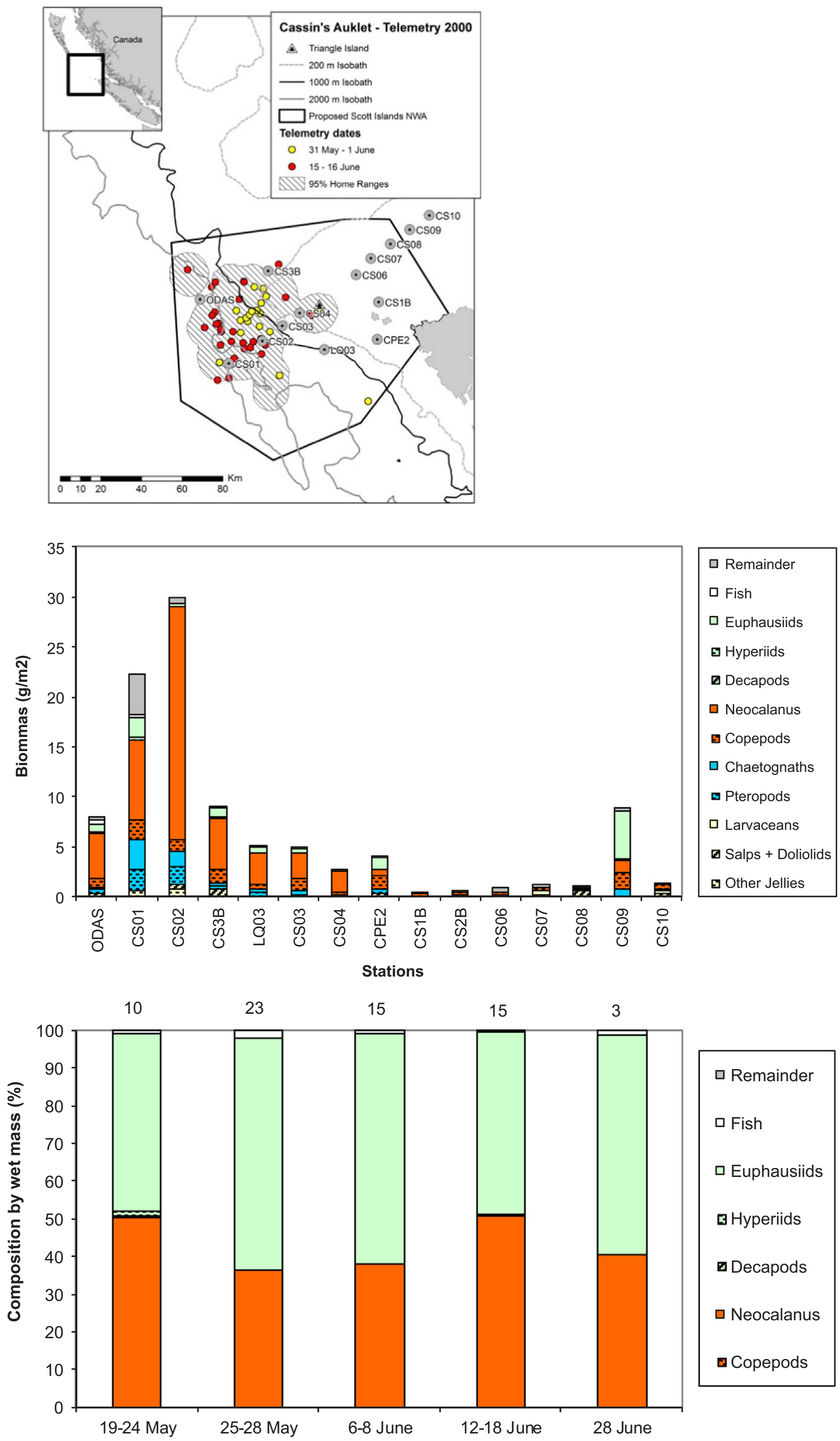

Fig. 2. (a) The marine distributions of individual Cassin's Auklets breeding on Triangle Island on 31 May, 1 June and 15–16 June 2000. Depth contours show the continental shelf break (200 m) and slope (1000 m and 2000 m) region. Shown also are the 95% Kernel Home Ranges of foraging birds (from Boyd et al. (2008)) and the proposed boundaries for the marine National Wildlife Area (Environment Canada, 2013). (b) Spring season zooplankton gradients along the Cape Scott transect, 9–10 May 2000. (c) Nestling diet (regurgitated from provisioning parents) of Cassin's auklet during the breeding season in 2000. The number of diet samples is shown above the bars.

T (Triangle, Fig. 1a) line was conducted on the CCGS *W.E. Ricker* in June and the CS (Cape Scott) line was conducted on the CCGS *John P. Tully* in May of each year. The Tully cruises also sampled from additional stations near the CS line (Fig. 2a). Vertical bongo tow plankton samples were taken at each station (near bottom to surface on the continental shelf, 250 m to surface over the continental slope and beyond). Zooplankton identification and enumeration was done by a single observer (MG). Methods of plankton collection and data presentation are described in detail elsewhere (Mackas et al., 2007). We present the zooplankton results (in g/m^2 at each station) for the cruise which was closest in time to the telemetry flights in each year to best match the timing of the dates of plankton sampling and dates when marine bird foraging locations were determined. To facilitate comparison with bird diets, the zooplankton were assigned to the following groups: Copepods, Chaetognaths, Decapods, Euphausiids, Fish, Hyperiids, Larvaceans, *Neocalanus*, Pteropods, Salps + Doliolids, Other jellies, Remainder.

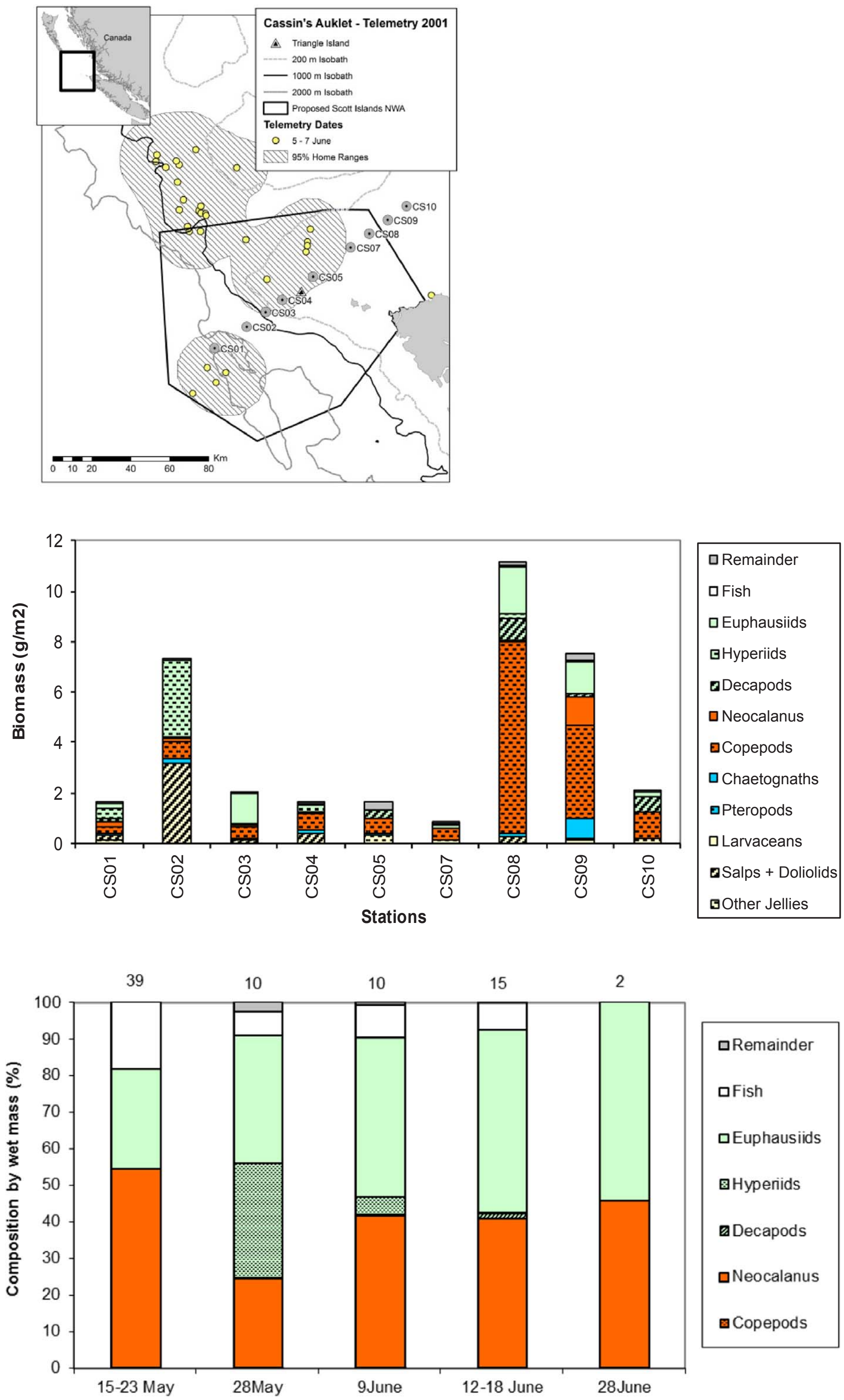

Fig. 3. (a) The marine distributions of individual Cassin's Auklets breeding on Triangle Island on 5, 6, and 7 June 2001. Depth contours show the continental shelf break (200 m) and slope (1000 m and 2000 m) region. Shown also are the 95% Kernel Home Ranges of foraging birds (from Boyd et al. (2008)) and the proposed boundaries for the marine National Wildlife Area (Environment Canada, 2013). (b) Spring season zooplankton gradients along the Cape Scott transect, 31 May 2001. (c) Nestling diet of Cassin's Auklet during the breeding season in 2001. The number of diet samples is shown above the bars.

3. Results

The 1999 telemetry data indicated that Cassin's Auklets were located primarily in deep waters SW of Triangle Island with the largest KHR polygon centered and extending along the 2000 m isobath and a smaller polygon located over the 200 m and 1000 m isobaths (Fig. 1a). On 10 June the birds were detected along the transect line near stations T8 and T9 and up to 80 km south of the line (ca. 100 km away from the colony). Two weeks later (23–24 June), the birds were more tightly clustered, centered close to station T10. Concurrent zooplankton sampling on 23–24 June demonstrated significant concentrations (2 g/m^2) of the deep-water-dependent copepod *Neocalanus cristatus* (Fig. 1b) at station T10. *N. cristatus* was the dominant prey delivered to nestlings on Triangle Island throughout the 1999 breeding season, and accounted for 35–66% of the diet during the zooplankton sampling and telemetry survey periods (Fig. 1c). It is noteworthy that station T11 had five times as much *N. cristatus* as station T10 on 23–24 June, but the majority of Cassin's Auklets were detected closer to the colony, at or near T10.

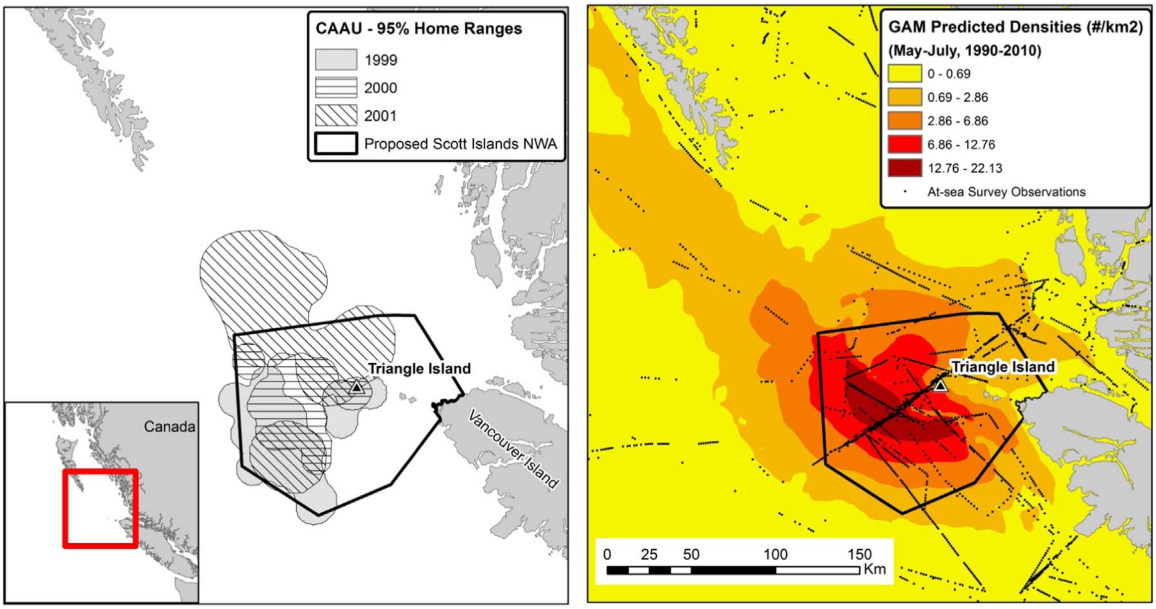

Fig. 4. (a) Overlay of 95% Kernel Home Ranges from 1999, 2000, and 2001 in relation to the proposed boundaries for the marine National Wildlife Area (Environment Canada, 2013). (b) Ship-board surveys (May-July 1990–2010) showing the location of areas surveyed, and the predicted densities of Cassin's Auklets based upon General Additive Modelling (GAM). Also shown are the proposed boundaries for the proposed marine National Wildlife Area (Environment Canada, 2013; Canada Gazette, 2016).

The year 2000 telemetry data showed that the seabirds were again primarily foraging offshore in deep-waters, W of Triangle Island, with the KHR polygon covering a wider range of isobaths (200 m, 1000 m, and 2000 m). On 31 May-1 June birds were 40–50 km W of the colony, between stations CSO2, CS3B, and ODAS (Fig. 2a). The zooplankton sampling on 9–10 May (Fig. 2b) showed dense concentrations of *N. cristatus* at all deep-water stations, with a peak value of 24 g/m^2. Even the station nearest to Triangle Island, situated on the continental shelf, had a relatively high concentration of *N. cristatus* (2 g/m^2). Euphausiids were also present at deep-water stations, including CSO1with densities of ~2 g/m^2. Station CSO9, close to a deep-water trench (900 m), showed high concentrations of *N. cristatus* and euphausiids, but no Cassin's Auklets were observed that far onto the shelf during the surveys aerial survey. Later in the breeding season (15–16 June), tagged, breeding adults were located in roughly the same general area, albeit farther from the colony. From 19 May through 28 June, *N. cristatus* represented 36–51% of the nestling diet, with the remainder being primarily euphausiids (Fig. 2c).

In contrast to 1999 and 2000, there were far fewer Cassin's Auklets detected close to the zooplankton sampling transect line in 2001. Most tagged birds were detected up to 100 km NW of the colony, near the offshore mouth of a marine canyon (delineated by the 200 m and 1000 m isobaths, Fig. 3a). The zooplankton sampling that occurred within one week of the aerial survey flights revealed low concentrations of *N. cristatus* and euphausiids at deep-water stations (Fig. 3b). In contrast to other years, salps, doliolids, and hyperiid amphipods dominated deep-water stations (Fig. 3b). Despite *N. cristatus* and euphausiids remaining a dominant component of the nestling diet (Fig. 3c) in 2001, the *N. cristatus* component was the lowest on record (24%) on the diet sampling date (28 May) closest to the zooplankton sampling date (31 May; Fig. 3c). At that time (28 May) hyperiid amphipods were observed at record levels (~30%) in the nestling diet. More birds were recorded foraging over the shelf in 2001 than in previous years.

3.1. General at-sea spatial distribution during breeding season

The home ranges based on telemetry overlapped considerably in 1999 and 2000 with the largest concentrations of Cassin's Auklet offshore, in deep water (Fig. 4a). In contrast, the 2001 home range showed much less overlap with the previous years and indicated that the birds moved considerably more northward in that year alone. The general spatial pattern over 20 years (i.e., based on the GAM output) predicts densities of Cassin's Auklet distribution during the months of May, June, and July to be highest directly offshore of Triangle Island, in waters > 1000 m (Fig. 4b). Densities were also predicted to be relatively high to the north along the shelf break.

4. Discussion

Our results demonstrate that in 1999 and 2000 the Cassin's Auklets nesting on Triangle Island foraged in deep waters (1800, 1400 m respective averages, Boyd et al., 2008) well beyond the continental shelf where their preferred prey, *N. cristatus* and euphausiids, were abundant. The life history of these prey require deep-water oceanic habitats, so it is not surprising that Cassin's Auklet were foraging in deep offshore waters. Indeed, the close proximity of Triangle Island to deep waters and predictable zooplankton biomass may explain why the world's largest Cassin's Auklet population nests there (Mackas and Galbraith, 1992). Although the birds can easily fly long distances, our data support the concept that they do not fly any farther than they need to in order to forage. In 1999, the timing of the telemetry and the zooplankton sampling occurred on the same day, and thus provided a particularly relevant snapshot of what was available to the auklets in surface waters around the colony. The birds foraged near station T10 where *N. cristatus* was available at ~ 2 g/m^2 and did not fly farther to station T11 where prey density was five times higher (than T10). Our results could be explained and modelled using aspects of foraging and life history theories but such treatment is beyond the scope of this empirical study.

We found that auklets shifted north to an alternative foraging area to track their preferred prey distribution in 2001. In stark contrast to 1999 and 2000, in 2001 there were very few *N. cristatus* or euphausiids at the deep-water (1000–2000) stations and foraging birds were generally not found in these regions, SW of the colony. Salps were present in extraordinary densities at offshore stations (DLM, MG pers. obs., Mackas and Coyle, 2005). Salps are deep-water residents that can form extensive colonies in surface waters (Mackas and Galbraith, 1992). They consume and displace zooplankton which could account for the virtual absence of preferred prey at deep-water stations in 2001. The auklets must have consumed salps, particularly on 28 May 2001, because hyperiid amphipods were found in the nestling diet and these amphipods are commensal with jellies like salps (Gasca and Haddock, 2004). Despite the paucity of *N. cristatus* and euphausiids at deep-water stations (1000–2000 m), the nestling diet composition revealed that the foraging parents found their preferred prey at different locations (see also Santora et al. (2011)) north of the colony over a large submarine canyon (200–1000 m) on the shelf break. In 1999 and 2000, 95% Kernel Home Range (KHR) estimates coincided and were similar in size; but in 2001, there was almost no overlap with the previous years and the KHR was much larger (Boyd et al., 2008), with birds flying farther away from the colony and appearing to forage over a much wider area. Within limits (e.g., Ronconi and Burger, 2008), parent seabirds can buffer changes in prey availability by working harder (Burger and Piatt, 1990; Bertram et al., 1996), and flying further from the nesting site in search of prey. It is noteworthy that nestling growth rates in 2001 (4.5 g/d, n = 58) were close to the long term running average at the time (4.7 g/d), but lower than the exceptionally good years of 1999 (5.4 g/d, n = 57) and 2000 (5.3 g/d, n = 63; DFO, 2002).

Our telemetry work contrasts with similar research in California where Cassin's Auklets foraged within 30 km of the colony (Adams et al., 2004a) at stable locations associated with a highly productive marine region located downstream from a major upwelling zone near Point Conception (Adams et al., 2004b). In California, the birds consumed primarily euphausiids on the shelf break and larval and juvenile fishes that were concentrated at a persistent cyclonic eddy located in the western Santa Barbara Channel.

In addition, at-sea surveys around the Southeast Farallon Island breeding colony highlighted persistent areas of high use by foraging Cassin's Auklets around Cordell Bank and the Farallones Escarpment, areas in which krill consistently occur (Manugian et al., 2015). Although persistent foraging hotspots were identified the authors argued that predator prey relationships likely vary with local and wide scale oceanographic conditions which can lead to changes in seabird densities in response to variability in krill and forage fish abundance (see also Sydeman et al. (2015)). Note that *Neocalanoid* copepods are a dominant member of the spring mesozooplankton community in the subarctic North Pacific and Bering Sea but their distribution does not extend as far south as California and consequently they are unavailable to planktivorous seabirds in the region.

Neocalanus copepods are also important prey for other small alcids such as the Least, Crested, and Whiskered Auklets (*Aethia pusilla*, *A. cristatella*, *A. pygmaea*), which breed in the Aleutian Islands (Bond et al., 2011b) and northern Bering Sea (Hunt et al., 1993; Gall et al., 2006). An early study coupling seabirds and oceanography in the Chirikov Basin (Hunt et al., 1990) demonstrated that Least Auklets foraged in greatest numbers where *Neocalanus* was present and the water was strongly stratified, and where prey was concentrated near the surface around the breeding colony on St. Lawrence Island (40–65 km, Obst et al., 1995). Additional research confirmed that nestling survival of the Least Auklets and Crested Auklets was enhanced when they were fed more *Neocalanus* on St. Lawrence Island (Gall et al., 2006; Sheffield Guy et al., 2009). An important contrast with diet studies in other northern regions (our study and colonies in the Aleutian Islands, Bond et al., 2011b) is that Chirikov Basin averages less than 50 m depth. *Neocalanus* are advected into the St. Lawrence colony area by the Anadyr Current which originates from the deep Bering Sea (Springer et al., 1989; Hunt et al., 1990) and the copepods cannot complete their life cycles at the shallow depths on the shelf. On St. Lawrence Island, interannaul differences in nestling survival, and diet of Least and Crested auklets, is likely associated with the strength of the cold, nutrient-rich Anadyr Current, which passes in close proximity to the seabird colony and influences zooplankton productivity, distribution (Gall et al., 2006) and hence foraging locations of auklets.

In our study system, the foraging Cassin's Auklet tended not to use waters over the continental shelf and headed to the offshore deep water habitats of their preferred prey. Zooplankton prey are usually transported seaward during summer by upwelling processes (Mackas and Coyle, 2005) and by westward currents around Scott Island during the breeding season (Borstad et al., 2011). Rapid nestling growth is positively associated with dietary levels of *N. cristatus* (Bertram et al., 2001, 2017; Hedd et al., 2002; Hipfner, 2008, 2009) and Cassin's Auklet will seek their preferred prey in waters on the shelf break and beyond when the copepods are present. However, the exact foraging locations in relation to the colony can vary among years by up to 100 km as our results demonstrate, and therefore, are less predictable on a smaller spatial scale. Our data, coupled with other studies of breeding planktivorous auklet foraging locations collectively indicate that results are colony specific and will be strongly influenced by the presence and distribution of preferred prey, the habitat needs of prey throughout their life cycle in relation to depth, regional currents patterns, and spatial patterns of other zooplankton predators and competitors.

Our research has contributed to the rationale for the boundaries of a marine National Wildlife Area (mNWA, Environment Canada, 2013; Canada Gazette, 2016, Figs. 1–4), which will provide protection for a wide range of marine life. This is first time that Canada has used seabird foraging locations to help define a protected area. The boundaries proposed for the mNWA encompass the highest predicted densities of the GAM output based on twenty years of at-sea survey data (1990–2010), as well as the 1999 and 2000 VHF telemetry-generated home ranges, and the southern part of the 2001 home range. The consistency between the GAM output based on at-sea survey data with the KHRs based on tracking data indicates that birds observed at sea were likely from Triangle Island.

The proposed mNWA was based upon multiple considerations, and many species of seabirds including breeding Cassin's Auklet (Environment Canada, 2013). The mNWA would comprise 11,546 km^2 of entirely marine environment, composed of internal waters, the territorial sea and the exclusive economic zone of Canada. The Scott Islands proposal reflects Canada's commitment to the United Nations Convention on Biological Diversity, to conserve at least 10% of its coastal and marine area by 2020 in order to conserve marine biodiversity (Canada Gazette, 2016).

The proposed mNWA does not include all of the known Cassin's Auklet foraging areas but represents a major advance because it includes significant amounts of deep-water habitat, which were missing from a much smaller proposed area (0.591 km^2), prior to our telemetry study (Kenyon et al., 2007; M. Dunn, pers. comm.). Protection of such deep-water foraging habitats near Triangle Island is important because oil discharges from ships are highly likely to occur in the region. The proposed mNWA would be supported by increased surveillance in the region for ship-based discharges, which should act as a deterrent to pollution (O'Hara et al., 2013) and thus benefit all seabirds and marine life in the ecosystem. Prohibitions against fishing for the forage species Pacific sand lance (*Ammodytes personatus*), Pacific saury (*Cololabis saira)*, and North Pacific krill (*Euphausia pacifica*) will also benefit upper trophic level predators including seabirds, marine mammals and fishes in the proposed mNWA. Ongoing graduate studies of Cassin's Auklet foraging tracks using GPS tags will further inform decisions regarding the proposed boundaries for the Scott Islands mNWA (J. M. Hipfner, pers. comm.).

Measures of seabird foraging and reproductive performance can provide unique insights into marine ecosystems and can act as indicators of changes in prey populations (e.g., Piatt et al., 2007; Parsons et al., 2008). The establishment of a mNWA around the Scott Islands could help to ensure the support required to gauge seabird population trends and their causes in the Northeast Pacific through ongoing long term research and monitoring at Triangle Island, the sentinel seabird colony at the northern tip of the California Current Ecosystem.

Our research demonstrates the value of annual time series monitoring data and the value of integrating multiple sources of data to address issues which concern the conservation and management of marine species. The integrated ecosystem program on Triangle Island continues, and is the longest running time series of its kind in BC. Ongoing integrated research and monitoring will be able to detect changes in marine food webs in relation to ocean climate change (e.g., Bond et al., 2011a; Bertram et al., 2017), which could lead to temporal and spatial shifts in prey populations and, in turn, changes in the foraging distributions and success of breeding seabirds.

Acknowledgements

"Nestucca" Oil Spill Trust Fund (Anonymous, 1992; see also USFWS 2004) grants to Gary Kaiser, DFB, DLM and DWW supported this ecosystem-level study. Additional financial support was received from the Canadian Climate Change Action Fund and the Canadian Nature Federation and their partners BirdLife International and Bird Studies Canada grants to DFB; Natural Sciences and Engineering Research Council of Canada grants to Fred Cooke, Simon Fraser University (SFU) Centre for Wildlife Ecology, the Canadian Wildlife Service, and the Ocean Sciences Division of the Department of Fisheries and Oceans. Permission to work on Triangle Island (the Anne Vallée Ecological Reserve) was provided by B.C. Parks. We could not have conducted the study without the major efforts of the field crews on Triangle Island, or the crew and officers aboard the vessels CCGS *John P. Tully* and CCGS *W.E. Ricker*. Connie Smith arranged for permits and provided logistic support through SFU. Thanks to Cooper Air for the Beaver flights and Canadian Coast Guard and West Coast Helicopters for helicopter support. Michael Dunn discussed historical marine conservation efforts and Greg Jones offered updates on the status of the proposed marine National Wildlife Area. George Hunt and an anonymous reviewer helped us to improve the manuscript.

References

Adams, J., Takekawa, J.Y., Carter, H.R., 2004a. Foraging distance and home range of Cassin's Auklet nesting at two colonies in the California Channel Islands. Condor 106, 618–637.

Adams, J., Takekawa, J.Y., Carter, H.R., 2004b. Stable foraging areas and variable chick diet in Cassin's auklets (*Ptychoramphus aleuticus*) off southern California. Can. J. Zool. 82, 1578–1595.

Anonymous, 1992. The Canada-British Columbia Netucca Agreement. Province of British Columbia Order of the Lieutenant Governor in Council. Order in Council No. 955. ⟨http://www.bclaws.ca/civix/document/id/oic/arc_oic/0955_1992⟩ (accessed 7 September 2017).

Benoit-Bird, K.J., Battaile, B.C., Heppell, S.A., Hoover, B., Irons, D., Jones, N., Kuletz, K.J., Nordstrom, C.A., Parades, R., Suryan, R.M., Waluk, C.M., Trites, A.W., 2013. Prey patch patterns predict habitat use by top marine predators with diverse foraging strategies. PLoS One 8 (1), e53348. http://dx.doi.org/10.1371/journal.pone.0053348.

Bertram, D.F., Welham, C.V.J., Ydenberg, R.C., 1996. Flexible effort in breeding seabirds: adjustment of provisioning according to nestling age and mass. Can. J. Zool. 74, 1876–1881.

Bertram, D.F., Mackas, D.L., McKinnell, S.M., 2001. The seasonal cycle revisited: interannual variation and ecosystem consequences. Prog. Oceanogr. 49, 283–307.

Bertram, D.F., Harfenist, A., Smith, B.D., 2005. Ocean climate and El Niño impacts on survival of Cassin's Auklets from upwelling and downwelling domains of British Columbia. Can. J. Fish. Aquat. Sci. 62, 2841–2853.

Bertram, D.F., Harfenist, A., Hedd, A., 2009. Seabird nestling diets reflect latitudinal temperature-dependent variation in availability of key zooplankton prey populations. Mar. Ecol. Prog. Ser. 393, 199–210.

Bertram, D.F., Harfenist, A., Cowen, L.L.E., Koch, D., Drever, M.C., Hipfner, J.M., Lemon, M.J.F., 2017. Latitudinal temperature-dependent variation in timing of prey availability can impact Pacific seabird populations in Canada. Can. J. Zool. 95 (3), 161–167. http://dx.doi.org/10.1139/cjz-2016-0197.

Bond, A.L., Jones, I.L., Sydeman, W.J., Major, H.L., Minobe, S., Williams, J.C., Byrd, G.V., 2011a. Reproductive success of planktivorous seabirds in the North Pacific is related to ocean climate on decadal scales. Mar. Ecol. Prog. Ser. 424, 205–218.

Bond, A.L., Jones, I.L., Williams, J.C., Byrd, G.V., 2011b. Diet of auklet chicks in the Aleutian Islands, Alaska: similarity among islands, inter-species overlap, and relationships to ocean climate. J. Ornithol. 153. pp. 115–129.

Borstad, G., Crawford, W., Hipfner, J.M., Thomson, R., Hyatt, K., 2011. Environmental control of the breeding success of rhinoceros auklets at Triangle Island, British Columbia. Mar. Ecol. Prog. Ser. 424, 285–302.

Boyd, W.S., Ryder, J.L., Shisko, S.G., Bertram, D.F., 2000. At-sea foraging distributions of radio-marked Cassin's Auklets breeding at Triangle Island, British Columbia. Technical Report Series No. 353. Canadian Wildlife Service, Pacific and Yukon Region, British Columbia.

Boyd, W.S., McFarlane Tranquilla, L., Ryder, J.L., Shisko, S.G., Bertram, D.F., 2008. Variation in marine distributions of Cassin's Auklets (*Ptychoramphus aleuticus*) breeding at Triangle Island, British Columbia. Auk 125 (1), 158–166.

Burger, A.E., Piatt, J.F., 1990. Flexible time budgets in breeding common murres as buffers against variable prey abundance. Stud. Avian Biol. 14, 71–83.

Burger, A.E., Powell, D.W., 1990. Diving depths and diet of Cassin's auklet at Reef Island, British Columbia. Can. J. Zool. 68, 1572–1577.

Burke, C.M., Montevecchi, W.A., 2009. The foraging decisions of a central place foraging seabird in response to fluctuations in local prey conditions. J. Zool. 278, 354–361.

Canada Gazette. 2016. Scott Islands Protected Marine Area Regulations. Vol. 150, No. 53. http://www.gazette.gc.ca/rp-pr/p1/2016/2016-12-31/html/reg1-eng.php?pedisable=false (accessed 3 January 2017).

Davoren, G.K., 2013. Distribution of marine predator hotspots explained by persistent areas of prey. Mar. Biol. 160, 3043–3058. http://dx.doi.org/10.1007/s00227-013-2294-5.

DFO, 2002. 2001 Pacific Region State of the Ocean. DFO Science Ocean Status Report 2002 (2002). Bertram, D.F., and Gaston, A.J. 2002. Seabird reproductive performance on Triangle Island and in Laskeek Bay (Queen Charlotte Islands). pp 39–41.

Drent, R.H., Daan, S. 1980. The prudent parent: energetic adjustments in avian breeding. Ardea (Tijdschrift van de NOU), jaargang 68, 225–252.

Elliott, K.H., Woo, K.J., Gaston, A.J., Benvenuti, S., Dall'Antonia, L., Davoren, G.K., 2009. Central-place foraging in an Arctic seabird provides evidence for Storer-Ashmole's halo. Auk 126 (3), 613–625.

Elliott, K.H., Le Vaillant, M., Kato, A., Gaston, A.J., Ropert-Coudert, Y., Hare, J.F., Speakman, J.R., Croll, D., 2013. Age-related variation in energy expenditure in a long lived bird within the envelope of an energy ceiling. J. Anim. Ecol. http://dx.doi.org/10.1111/1365-2656.12126.

Environment Canada. 2013. Regulatory Strategy for the Designation of the Proposed Scott Islands Marine National Wildlife Area. Amendment to Schedule I of the Wildlife Area Regulations: Proposed Scott Islands National Wildlife Area. Available from http://www.ec.gc.ca/ap-pa/default.asp?lang=En&n=A66BB7F1-1 [accessed 6 Sept 2016].

Fifield, D.A., Hedd, A., Avery-Gomm, S., Robertson, G.J., Gjerdrum, C., McFarlane Tranquilla, L.A., 2017. Employing predictive spatial models to inform conservation planning for seabirds in the Labrador Sea. Front. Mar. Sci. 4, 149.

Gall, A.E., Roby, D.D., Irons, D.B., Rose, I.C., 2006. Differential response in chick survival to diet in least and crested auklets. Mar. Ecol. Prog. Ser. 308, 279–291.

Gasca, R., Haddock, S.H.D., 2004. Associations between gelatinous zooplankton and hyperiid amphipods (Crustacea: peracarida) in the Gulf of California. Hydrobiologia 530/531, 529–535.

Gaston, A.J., Elliott, K.H., Ropert-Coudert, Y., Kato, A., Macdonald, C.A., Mallory, M.L., Gilchrist, H.G., 2013. Modeling foraging range for breeding colonies of thick-billed murres *Uria lomvia* in the Eastern Canadian Arctic and potential overlap with industrial development. Biol. Conserv. 168, 134–143.

Hedd, A., Ryder, J.L., Cowen, L.L., Bertram, D.F., 2002. Inter-annual variation in the diet, provisioning and growth of Cassin's Auklet at Triangle Island, British Columbia: responses to variation in ocean climate. Mar. Ecol. Prog. Ser. 229, 221–232.

Hipfner, J.M., 2008. Matches and mismatches: ocean climate, prey phenology and reproductive performance in a zooplanktivorous seabird. Mar. Ecol. Prog. Ser. 368, 295–304.

Hipfner, J.M., 2009. Euphausiids in the diet of a North Pacific seabird: annual and seasonal variation and the role of ocean climate. Mar. Ecol. Prog. Ser. 390, 277–289. http://dx.doi.org/10.3354/meps08209.

Hodum, P.J., Sydeman, W.J., Visser, G.H., 1998. Energy expenditure and food requirement of Cassin's Auklets provisioning nestlings. Condor 100, 546–550.

Hunt Jr., G.L., Harrison, N.M., Cooney, R.T., 1990. The influence of hydrographic structure and prey abundance on foraging of least Auklets. Stud. Avian Biol. 14, 7–22.

Hunt, G.L., Harrison, N.M., Piatt, J.F., 1993. Foraging ecology as related to the distribution of planktivorous auklets in the Bering Sea. In: Vermeer, K., Briggs, K.T., Morgan, K.H., Siegel-Causey, D. (Eds.), The Status, Ecology, and Conservation of Marine Birds of the North Pacific. Can. Wildl. Serv. Spec. Publ., pp. 18–26.

Hunt, G.L., Mehlum, F., Russell, R.W., Irons, D., Decker, M.B., Becker, P.H. 1999. Physical processes, prey abundance, and the foraging ecology of seabirds. In: Adams, N.J, Sloto, R.H. (Eds.). In: Proc. 22nd Int. Ornithol. Congr. Birdlife South Africa,Durban, 2040–2046.

Jacobs, S.R., Elliott, K.H., Gaston, A.J., 2013. Parents are a drag: long-lived birds share the cost of increased foraging effort with their offspring, but males pass on more of the costs than females. PLoS One e54594. http://dx.doi.org/10.1371/journal.pone.0054594 PMID: 23382921.

Kenyon, J.K., Amey, K., Moore, K., Dunn, M., 2007. The Canadian Wildlife Service's British Columbia Marine Bird Area of Interest Database. Technical Report Series No. 479. Canadian Wildlife Service, Pacific and Yukon Region, British Columbia.

Kenyon, J.K., Morgan, K.H., Bentley, M.D., McFarlane Tranquilla, L.A., Moore, K.E., 2009. Atlas of Pelagic Seabirds Off the West Coast of Canada and Adjacent Areas. Canadian Wildlife Service, Pacific and Yukon Region, British Columbia.

Lascelles, B.G., Taylor, P.R., Miller, M.G.R., Dias, M.P., Oppel, S., Torres, L., Hedd, A., Le Corre, M., Phillips, R.A., Shaffer, S.A., Weimerskirch, H., Small, C., 2015. Applying global criteria to tracking data to define important areas for marine conservation. Divers. Distrib. 1–10. http://dx.doi.org/10.1111/ddi.12411.

Mackas, D.L., Coyle, K.C., 2005. Shelf-offshore exchange processes, and their effects on mesozooplankton biomass and community composition patterns in the northeast Pacific. Deep-Sea Res. II 52, 707–725.

Mackas, D.L., Galbraith, M., 1992. Zooplankton on the west coast of Vancouver Island: distribution and availability to marine birds. Occasional Paper No. 75 In: Vermeer, K., Butler, R.W., Morgan, K.H. (Eds.), The Ecology, Status, and Conservation of

Marine and Shoreline Birds on the West Coast of Vancouver Island. Canadian Wildlife Service, Ottawa, pp. 15–21.

Mackas, D.L., Goldblatt, R., Lewis, A.G., 1998. Interdecadal variation in developmental timing of *Neocalanus plumchrus* populations at Ocean Station P in the subarctic North Pacific. Can. J. Fish. Aquat. Sci. 55, 1878–1893.

Mackas, D.L., Batten, S., Trudel, M., 2007. Effects on zooplankton of a warmer ocean: recent evidence from the Northeast Pacific. Prog. Oceanogr. 75, 223–253.

Manugian, S., Elliott, M.L., Bradley, R., Howar, J., Karnovsky, N., Saenz, B., Studwell, A., Warzybok, P., Nur, N., Jahncke, J., 2015. Spatial distribution and temporal patterns of Cassin's Auklet foraging and their Euphausiid prey in a variable ocean environment. PLoS One 10 (12), e0144232. http://dx.doi.org/10.1371/journal.pone.0144232.

McFarlane Tranquilla, L., Ryder, J.L., Boyd, W.S., Shisko, S.G., Bertram, D.F., Hipfner, J.M., 2005. Diurnal Marine Distributions of Radio-tagged Cassin's Auklets and Rhinoceros Auklets Breeding at Triangle Island, British Columbia. Technical Report Series No. 423. Canadian Wildlife Service, Pacific and Yukon Region, British Columbia Catalogue No. CW-69-5/423E, ISBN 0-662-38691-4, ISSN 0831-6481.

Morrison, K.W., Hipfner, J.M., Blackburn, G.S., Green, D.J., 2011. Effects of extreme climate events on adult survival of three Pacific Auks. Auk 128 (4), 707–715.

Nur, N., Jahncke, J., Herzog, M.P., Howar, J., Hyrenbach, K.D., Zamon, J.E., Ainley, D.G., Wiens, J.A., Morgan, K., Ballance, L.T., Stralberg, D., 2011. Where the wild things are: predicting hotspots of seabird aggregations in the California Current System. Ecol. Appl. 21, 2241–2257.

O'Hara, P.D., Serra-Sogas, N., Canessa, R., Keller, P., Pelot, R., 2013. Estimating discharge rates of oily wastes and deterrence based on aerial surveillance data collected in western Canadian marine waters. Mar. Pollut. Bull. 69, 157–164.

Obst, B.S., Russell, R.W., Hunt, G.L., Eppley, Z.A., Harrison, N.M., 1995. Foraging radii and energetics of least auklets *(Aethia pusilla)* breeding on 3 Bering Sea islands. Physiol. Zool. 68, 647–672.

Orians, G.H., Pearson, N.E., 1979. On the theory of central place foraging. In: Horn, D.J., Stairs, G.R., Mitchell, R. (Eds.), Analysis of Ecological Systems. Ohio State University Press, Columbus, OH, pp. 155–177.

Parsons, M., Mitchell, I., Butler, A., Ratcliffe, N., Frederiksen, M., Foster, S., Reid, J.B., 2008. Seabirds as indicators of the marine environment. ICES J. Mar. Sci. 65, 1520–1526.

Piatt, J.F., Harding, A.M.A., Shultz, M.T., Speckman, S.G., van Pelt, T.,I., Drew, G.S., Kettle, A.B., 2007. Seabirds as indicators of marine food supplies: Cairns revisited. Mar. Ecol. Prog. Ser. 352, 221–234. http://dx.doi.org/10.3354/meps07078.

R Development Core Team, 2008. R: A Language and Environment for Statistical Computing. http://www.R-project.org. R Foundation for Statistical Computing, Vienna, Austria ISBN 3-900051-07-0.

Regular, P.M., Hedd, A., Montevecchi, W.A., Robertson, G.J., Storey, A.E., Walsh, C.J., 2014. Why timing is everything: energetic costs and reproductive consequences of resource mismatch for a chick-rearing seabird. Ecosphere 5 (12), 155.

Robinette, D.P., Howar, J., Sydeman, W.J., Nur, N., 2007. Spatial patterns of recruitment in a demersal fish as revealed by seabird diet. Mar. Ecol. Prog. Ser. 352, 259–268.

Rodway, M.S., 1991. Status and conservation of breeding seabirds in British Columbia. ICBP Technical Publication No. 11: 43-102.

Rodway, M.S., Lemon, M.J.F., 2011. Use of permanent plots to monitor trends in burrow-nesting seabird populations in British Columbia. Mar. Ornithol. 39, 243–253.

Roff, D.A., 1992. The Evolution of Life Histories: Theory and Analysis. Chapman and Hall, New York, NY.

Ronconi, R.A., Burger, A.E., 2008. Limited foraging flexibility: increased foraging effort by a marine predator does not buffer against scarce prey. Mar. Ecol. Prog. Ser. 366, 245–258. http://dx.doi.org/10.3354/meps07529.

Ryder, J.L., Boyd, W.S., Shisko, S.G., Bertram, D.F., 2001. At-Sea Foraging Distributions of Radio-marked Cassin's Auklets Breeding at Triangle Island, B.C., 2000. Technical Report Series No. 368. Canadian Wildlife Service, Pacific and Yukon Region, British Columbia.

Santora, J.A., Ralston, S., Sydeman, W.J., 2011. Spatial organization of krill and seabirds in the central California Current. ICES J. Mar. Sci. 68, 1391–2075.

Santora, J.A., Sydeman, W.J., Schroeder, I.D., Field, J.C., Miller, R.A., Wells, B.K., 2017. Persistence of trophic hotspots and relation to human impacts within an upwelling marine ecosystem. Ecol. Appl. 27, 560–574.

Sheffield Guy, L.M., Roby, D.D., Gall, A.E., Irons, D.B., Rose, I.C., 2009. The influence of diet and ocean conditions on productivity of auklets on St. Lawrence Island, Alaska. Mar. Ornithol. 37, 227–236.

Springer, A.M., McRoy, C.P., Turco, K.R., 1989. The paradox of pelagic food webs in the northern Bering Sea. II. Zooplankton communities. Cont. Shelf Res. 9, 359–386.

Stearns, S.C., 1992. The Evolution of Life Histories. Oxford University Press, NY.

Sydeman, W.J., Thompson, S.A., Santora, J.A., Koslow, J.A., Goericke, R., Ohman, M.D., 2015. Climate-ecosystem change off southern California: time-dependent seabird predator-prey numerical responses. Deep Sea Res Part II 158–170. http://dx.doi.org/10.1016/j.dsr2.2014.03.008.

US Fish and Wildlife Service (USFWS), 2004. *Nestucca* oil spill revised restoration plan. Western Washington Fish and Wildlife Office, Lacey, Washington. 42 p. 〈https://www.cerc.usgs.gov/orda_docs/CaseDetails?ID=961〉 (accessed 7 September 2017).

Wilson, L.J., McSorley, C.A., Gray, C.M., Dean, B.J., Dunn, T.E., Web, A., Reid, J.B., 2009. Radio-telemetry as a tool to define protected areas for seabirds in the marine environment. Biol. Conserv. 142, 1808–1817.

Wood, S. 2016. Package 'mgcv'. R package version,1–7.