PARENTAL INVESTMENT IN THE RHINOCEROS AUKLET (*Cerorhinca monocerata*) AT THE COLONY AND AT SEA OFF SOUTHWESTERN VANCOUVER ISLAND

by
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We accept this thesis as conforming
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ABSTRACT

This study was the first to simultaneously record ocean-based, colony-based and at-sea time budget information for a pursuit-diving seabird. The primary objective was to determine if at-sea time budgets, provisioning and chick growth rates of Rhinoceros Auklets reflected fluctuations in prey availability. The major findings of this study were fourfold. First, auklets showed great plasticity in their foraging strategies and showed flexibility in their daily time budgets when faced with varying prey availability and energetic constraints. Second, auklets showed flexibility in their provisioning behaviour, resulting in increased chick growth rates. These results suggest that auklets are capable of buffering the effects of lowered prey availability, or other adverse conditions, on reproductive success and adult survival. Third, nestling and adult diets reflected both diurnal behaviors and seasonal habitat preferences of auklet prey species. All of these results suggest that auklets may be reasonable indicators of prey availability and prevailing ocean conditions. Fourth, auklets made a consistent switch between both foraging strategies and prey preferences when self-feeding in comparison to when collecting chick meals. Although several studies have documented different diets of seabird adults and chicks, this is the first study to document different foraging strategies used in adult and chick provisioning.

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INTRODUCTION

This study describes at-sea time budgets, chick provisioning and growth rates of chicks of Rhinoceros Auklets (*Cerorhinca monocerata*) during the breeding season. The main goal is to describe the responses of these three parameters to shifts in prey density and distribution. The following chapter reviews the known and hypothesized effects of food limitation on seabirds.

Food limitation was suggested to be one of the major factors regulating the size of seabird populations (Furness and Birkhead 1984). Various aspects of seabird breeding and foraging behaviour, also often reflect changes in the abundance and distribution of their prey populations (Hunt et al. 1990). For instance, changing prey populations have had dramatic impacts on breeding seabirds during El Nino events, including breeding failure, adult mortality and subsequent declines in seabird populations (Barber and Chavez 1983; Hodder and Graybill 1985; Boersma 1977).

Food limitation may have more pronounced effects on seabirds during the breeding season than during the winter. During the winter, prey are generally more scarce but seabirds have lower energetic demands, compared to when rearing chicks, and also are free to track prey populations over vast distances. In contrast, during the breeding season, seabirds are restricted to areas surrounding breeding colonies. When provisioning chicks, seabirds act as central-place foragers and, thus, are even further constrained. A major constraint on central-place foragers is both the time and energy expended during a round trip from the central place (breeding colony) to the foraging site(s) and back to the central place (Orians and Pearson 1979). The central-place foraging/provisioning model predicts that foragers should attempt to minimize travel distances and travel durations to foraging sites (Pyke 1984). If food supply is low in the vicinity of colonies, however, foraging distances must increase. As foraging distances increase, the central-place foraging/provisioning model predicts that foragers should spend more time foraging at foraging sites and collect more food per trip (Pyke 1984). Adults provisioning chicks, however, are generally limited to how much food can be carried per trip; therefore, when foraging distances increase beyond a threshold, breeding success will probably decline.

Food limitation around breeding colonies can occur in three ways:

- prey abundance may decrease, due to active migration, passive transport via oceanic currents or due to reduced ocean productivity;
- prey density may decrease due to increased dispersal, causing prey encounter rates to fall below levels required for efficient foraging;
- prey accessibility may decrease by prey moving deeper in the water column. Although pursuit-diving seabirds are capable of diving to great depths, most Rhinoceros Auklets forage in the upper 10-20 m (Burger et al. 1993).

Throughout this thesis, I refer to the combination of these three components of food limitation as 'prey availability'. Each of these types of food limitation may severely increase energy expenditure of seabirds during the breeding season.

Prey species and size class composition in the area surrounding breeding colonies can also affect seabird breeding success. For instance, if only larger fish species or size classes are available for meals of chicks during chick rearing, chicks may choke trying to swallow them or may starve by not eating them (e.g. Vermeer 1980). In contrast, if only small fish are available during chick rearing, adults may have to expend more energy collecting fish for chicks. This may result in parents being unable to deliver a sufficient mass of fish to their chicks, resulting in reduced growth rates of chicks and maybe even poor body condition of adults (Bertram et al. 1991; Hamer et al. 1991; Ricklefs 1983). One would expect similar results if only prey of low caloric value were available during the breeding season (Ricklefs 1983).

Cairns (1987) proposed that prey availability would sequentially affect activity-time budgets of adults, colony attendance, chick growth, breeding success (e.g. the number of offspring successfully fledged) and ultimately adult survival. He also suggested the range of prey availabilities over which these parameters were likely to be sensitive. First, at moderate levels of prey availability, activity-time budgets and colony attendance were suggested to be the most sensitive. Some seabirds are known to have flexible time budgets when rearing chicks, showing increased durations of foraging trips, or decreased off-duty time spent at the colony, during periods of moderate prey decline (Burger and Piatt 1990; Burness et al. 1994; Uttley et al. 1994; Monaghan et al. 1994; Birkhead and Nettleship 1987; Hamer et al. 1991). More indirect evidence for flexible time budgets was shown through cross-fostering and twinning experiments, where parents were able to successfully rear more chicks or larger chicks (e.g. Shea and Ricklefs 1985). This ability to increase activities related to foraging and provisioning allows seabirds to maintain chick growth and breeding success at consistent levels during periods of moderate prey availability.

The ability of seabirds to buffer declining prey availability depends on the level of effort required to provision chicks adequately when food supply is favorable. Certain species (e.g. albatrosses) may be unable to buffer moderate prey declines because adults already spend the majority of their time provisioning and maintaining their own body condition (Gaston 1985; Cairns et al. 1987). For instance, Laysan and Black-footed albatross parents were unable to rear two chicks in twinning experiments (Rice and Keyon 1962). This may be explained by the low amount of off-duty time that albatrosses spend at the colony during chick rearing (e.g. 0.4% in the Grey-headed Albatrosses; Prince and Francis 1984) and by the high amount of time spent actively flying and foraging (75 - 100%) when away from the colony (Weimerskirch et al. 1993).

When prey availability declines below moderate levels, seabirds capable of time buffering may not be able to further increase their provisioning efforts. During these periods, breeding individuals might balance the demand for allocating resources to rearing young against maintaining adult body condition (Newton 1989). Seabirds are generally long-lived species; therefore, they presumably place more emphasis on successfully raising a high number of offspring throughout their lifetime rather than in any one year. Consequently, seabirds may abandon breeding attempts during periods when prey availability is low. This would increase their own chances for survival and potentially increase the number of offspring produced per lifetime, or their lifetime reproductive success (Newton 1989).

OBJECTIVES

The primary objective of this study was to determine if at-sea time budgets, chick provisioning and chick growth rates of Rhinoceros Auklets reflected fluctuations in prey availability. Understanding the responses of auklets to variable prey availability during the breeding season is important to the development of many foraging, provisioning and life history theories. First, by describing the responses of time budgets and chick provisioning to fluctuating prey availability, the time-buffering hypothesis and various provisioning models, in the context of lifetime reproductive success theory, can be tested. Second, by describing self-feeding and provisioning responses to variable food supplies, parent-offspring conflicts and central-place foraging theory can be tested. This understanding of auklet responses to fluctuating prey availability also may increase the potential of using seabirds as indicators or monitors of prevailing ocean conditions.

The specific goals of this study were fourfold.

- to describe changes in the availability, species composition and size class composition of auklet prey in the study area on three temporal scales (daily, seasonally, annually) (chapter 1);
- to describe fluctuations in time budgets of auklets at-sea in response to daily and seasonal fluctuations in prey availability, with a particular focus on foraging behaviour (chapter 2);
- to describe changes in the prey-tracking behaviour of auklets in response to seasonal fluctuations in prey availability (chapter 3);
- to describe the responses of chick provisioning and growth rates of chicks to interannual variations in prey availability (chapter 4).

For easier flow of the text, most of the statistical results is presented in appendices.

RHINOCEROS AUKLET (*Cerorhinca monocerata*) BACKGROUND

The Rhinoceros Auklet, a member of the marine bird family Alcidae ('alcid'), dives underwater to feed mainly on small schooling fish. This auklet occurs throughout the coastal temperate waters of the north Pacific Ocean, where it breeds on a small number of coastal islands in California, Washington, British Columbia, southeast Alaska and Japan. Numerous aspects of Rhinoceros Auklet breeding biology (Leschner 1976; Wilson 1977; Gaston and Dechesne 1996), chick provisioning behaviour (Vermeer et al. 1979; Bertram et al. 1991; Bertram and Kaiser 1993; Bertram et al. 1996), diving behaviour (Burger et al. 1993; Grover and Olla 1983) and life history strategies (Harfenist 1991; Harfenist 1995; Ydenberg et al. 1995) have been documented, making this seabird an ideal species for this study.

These auklets nest in burrows, which vary from 1-5 m in length. They lay a single-egg clutch and are thought to be monogamous and long-lived (Gaston and Dechesne 1996). During chick rearing, adults return to the colony once each night to feed their chicks, with peak numbers returning just after dusk. Prey delivered by adults to chicks are primarily are small, epipelagic, schooling fish (50-120 mm; Gaston and Dechesne 1996). A number of fish are collected for each chick meal, which are held crossways in the bills of parents. Meals of chicks are collected primarily during daylight hours, although there is some evidence of nocturnal capture (Burger et al. 1993; Gaston and Dechesne 1996).

The timing of breeding varies throughout this species' breeding range and between years of different sea temperature but mainly occurs during the summer (May to August) (Gaston and Dechesne 1996). In southern British Columbia and Washington, burrow-digging peaks in late March and egg-laying in middle to late-May; thus adults concentrate around the colony approximately 2 months prior to egg laying. Incubation lasts approximately 45 days and peak hatching generally occurs in late June to early July. Semiprecocial chicks remain in burrows for approximately 50 days; however, peak fledging dates vary with growth rates and threat of predation (Bertram 1988; Harfenist 1991). Once chicks have fledged, auklets undergo a post-breeding dispersal, generally moving southward (Gaston and Dechesne 1996).

Nestlings of these auklets show high within year variation in growth rates and fledging mass, with nestlings fledging at 40 to 70 days of age and from 45% to 80% of adult body mass (Vermeer and Cullen 1979; Wilson and Manuwal 1986; Harfenist 1991). This variation is thought to result from fitness trade-offs involving the timing of nest departure (e.g. increased safety in burrows versus increased growth rates on the ocean; Ydenberg 1989; Clark and

Ydenberg 1990). Harfenist and Ydenberg (1995) showed that when growth rates of chicks of auklets were high, due to high provisioning efforts by parents, chicks fledged at an earlier age, but higher mass, than those receiving less food. Therefore, intraspecific variability in growth and fledging mass may have evolved due to varying factors (e.g. food supply, risk of predation), resulting in a variety of nestling departure strategies, where each chick judges the advantages and disadvantages of leaving the nest at particular points in its rearing phase (Ydenberg et al. 1995). Since these nest departure decisions may influence fledgling survival (e.g. reduced mass at fledging results in lower chances of survival; Ydenberg et al. 1995), food supplies may regulate the sizes of breeding populations.

STUDY AREA

This study was conducted on and near the Seabird Rocks breeding colony on the west coast of Vancouver Island, just south of Barkley Sound (48°45'N, 125°09'W). This small island (500 by 300 m) is situated on the exposed Pacific coast and supports approximately 130-170 breeding pairs of Rhinoceros Auklets (Rodway 1991; Burger et al. 1993). This colony is small compared to many other Rhinoceros Auklet colonies (e.g. Triangle Island: 41, 680 breeding pairs; Rodway 1991) and is located less than 2 km from the coastline. The concentration of auklets around this colony during the breeding season (A. E. Burger unpublished data) and the concentration of auklets close to shore made this an ideal study area.

Seabird Rocks contains four main habitats: (1) bare rock, (2) salmon berry shrubs, (3) wild rye and tussock grass and (4) shell beaches or drift log areas. These habitats provide nesting sites for a variety of other seabird species, including: Leach's Storm-Petrels (600 pairs), Fork-tailed Storm-Petrels (250 pairs), Cassin's Auklets (200 pairs), Pigeon Guillemots, Tufted Puffins (8 pairs), Glaucous-winged Gulls (400 pairs), Pelagic Cormorants (2-20 pairs), and Black Oystercatchers (20 pairs) (Rodway 1991).

REGIONAL OCEANOGRAPHY

The west coast of Vancouver Island is part of the Coastal Upwelling Domain, which extends from Baja California to the northern tip of Vancouver Island (Mackas

1992; Ware and Thomson 1991). The most striking variations in ocean currents occur on an annual cycle (Freeland 1992), which generally repeats itself each year with similar magnitudes at similar times of the year (Mackas 1992). This annual cycle can be broken down into four periods: Winter (October-January), Spring Transition (February-April), Summer (May-September) and Fall Transition (September or October) (Thomson 1981). Fall Transition usually occurs abruptly after the first major fall storm and, thus, generally only lasts for one to two weeks (Thomson 1981).

During the Winter, the Vancouver Island Coastal Current (VICC) flows along the shelf on the west coast of Vancouver Island in a northwesterly direction and is primarily driven by the outflow from the Fraser River, in the Summer, and the Columbia River, in the Winter (Thomson 1981). In the Winter, southeast winds, or downwelling-favorable winds, enhance the speed of the VICC. This strong current during Winter acts as a barrier to the cross-shelf transport of nutrients and biomass (e.g. plankton, fish eggs and larvae) and as a conduit for the northward migration of biomass (Thomson et al. 1989). During Spring Transition, winds switch to northwesterly, or upwelling-favorable winds (Thomson et al. 1989). Spring Transition can occur abruptly but can also occur over a couple of months with a number of wind direction reversals (Thomson 1981). The abruptness and timing of Spring Transition has been linked to the distribution and abundance of fish larvae, fish adults and invertebrate larvae in the inner shelf area of southwestern Vancouver Island (McFarlane et al. 1995; Ware and McFarlane 1995; Jamieson et al. 1989). Despite the northwesterly winds, the VICC continues in a northwesterly direction during the Summer (Mackas 1992; Simard and Mackas 1989); however, the current strength is reduced. This relaxes both the cross-shelf barrier and the northward transport of organisms (Thomson et al. 1989).

During the Summer, upwelling is the prominent feature of the outer shelf and the shelf-break region, whereas estuarine circulation and, to a lesser degree, tidal mixing are the prominent features of the inner-shelf, or coastal region (McFarlane et al. 1997). Primary productivity is transferred to zooplankton biomass in the outer shelf region on the temporal scale of weeks (Denman et al. 1989), with peaks levels of zooplankton biomass in late spring and early summer (Mackas 1992). Zooplankton biomass in deep water moves from the outer shelf towards the Strait of Juan de Fuca through the Juan de Fuca canyon and other canyons (McFarlane et al. 1997). Once in the Strait of Juan de Fuca, tidal mixing transfers this biomass into surface waters. This water is then carried northward along the west coast of Vancouver Island with the runoff from the Fraser River, via the VICC (McFarlane et al. 1997). Consequently, during the Summer, or upwelling season, the VICC is characterized by warm, low salinity water with both high nutrient and plankton biomass content. The VICC generally follows the coastline as it moves northward, however, onshore (southwest) winds can displace the VICC inshore, whereas, offshore (northeast) winds can displace the VICC further offshore (R. Thomson pers. comm.).

Overall, wind-induced changes in ocean currents in the shelf-break region are important in determining ocean productivity, whereas estuarine circulation primarily determines the transfer of biomass from the outer shelf to near-shore areas during the Summer. Wind-induced displacement of the VICC can also affect the biomass transfer to near-shore areas in the Summer. Therefore, variations in such physical ocean processes during the Summer, when food demands of auklets are the highest, may have an important influence on the breeding success of seabirds.

CHAPTER ONE

CHANGING AVAILABILITY OF RHINOCEROS AUKLET PREY DURING THE BREEDING SEASON

INTRODUCTION

Nestling diets of alcids vary between years in the same breeding colony (Vermeer 1980; Vermeer and Westrheim 1984; Uttley et al. 1994; Monaghan et al. 1994; Hatch 1982). Nestling diets in different colonies, however, vary similarly between years and, thus, are similar in any given year (Bertram and Kaiser 1993; Hatch and Sanger 1992). Independent measures of changing ocean productivity (e.g. upwelling indices, sea surface temperature) and juvenile year classes (e.g. fisheries catches) have been associated with widespread changes in nestling diets (e.g. Bertram et al. 1991; Bertram and Kaiser 1993). Therefore, large scale changes in ocean conditions (Bertram and Kaiser 1993; Hatch and Sanger 1992; Hislop and Harris 1985; Martin 1989; Montevecchi and Myers 1996) and/or fisheries activities (Martin 1989; Montevecchi and Berruti 1991; Montevecchi and Myers 1996; Nettleship 1991) may be responsible for changing diets of seabird nestlings.

Juvenile fish populations in surface waters are difficult to sample using conventional methods and, therefore, little is known of their distribution and behaviour (Hay et al. 1992; Hart 1973). Many researchers have suggested that the diets of auklet and puffin nestlings provide a means of sampling juvenile fish and could be useful in monitoring age classes of certain fish species (Vermeer 1980: Vermeer and Westrheim 1984; Bertram and Kaiser 1993; Burger et al. 1993; Hatch 1982; Hatch and Sanger 1992). Rhinoceros Auklets collect a variety of fish species and year classes (50-120 mm) for their chicks and, thus, are thought to be good samplers of the prey available in proximity to colonies during the breeding season (Hatch and Sanger 1992; Bertram and Kaiser 1993). Auklets may undersample the juveniles of certain species (e.g. herring) when collecting meals for chicks because they are limited by the number of fish that they can carry in their bills. Consequently, other simultaneous measures of prey availability may provide more information on the fish species and age classes in the area. These measures also may provide some insight into the prey preferences of seabirds, which are important when evaluating the potential of using seabird diets as indicators of fish availability.

The first objective of this study was to describe changes in the prey availability in the study area on three temporal scales (interannually, seasonally and daily) and to determine the factors causing these fluctuations. The second objective was to describe interannual and seasonal changes in species composition in the context of the life history of prey species. The ultimate goal was to provide a basis for interpreting auklet behaviour in relation to prey availability in the following chapters.

METHODS

PREY AVAILABILITY

Fluctuations in prey availability were determined in three ways. First, prey availability was determined through unquantified observations of fish schools at the ocean's surface, which were noted during visual observations of the auklets activities at sea (chapter 2). Second, route-focused transects, in which the same route was repeated during each transect, were conducted to describe seasonal and interannual fluctuations in prey density and abundance and auklet densities. Transects were conducted as weather permitted and 87% were conducted in the morning, with only 13% conducted in the evening. Route-focused transects intensively sampled the area surrounding the Seabird Rocks breeding colony (Fig. 1-1), where auklets generally feed during the breeding season (A. E. Burger unpublished data).

During route-focused transects, bird numbers and prey densities were recorded simultaneously in 20-second time blocks (≈100 m) along the transect. Vessel speed was held consistently around 18 km/hr. Birds were observed within 150 m on both sides of the boat and numbers were recorded on a tape recorder every 20 seconds. Prey schools were recorded in the top 40 m of the water column using a 200 kHz echosounder with a paper trace. The echosounder transducer was mounted on the transom of the boat, pointed directly downwards. The depth along the transect route never exceeded 40 m and,

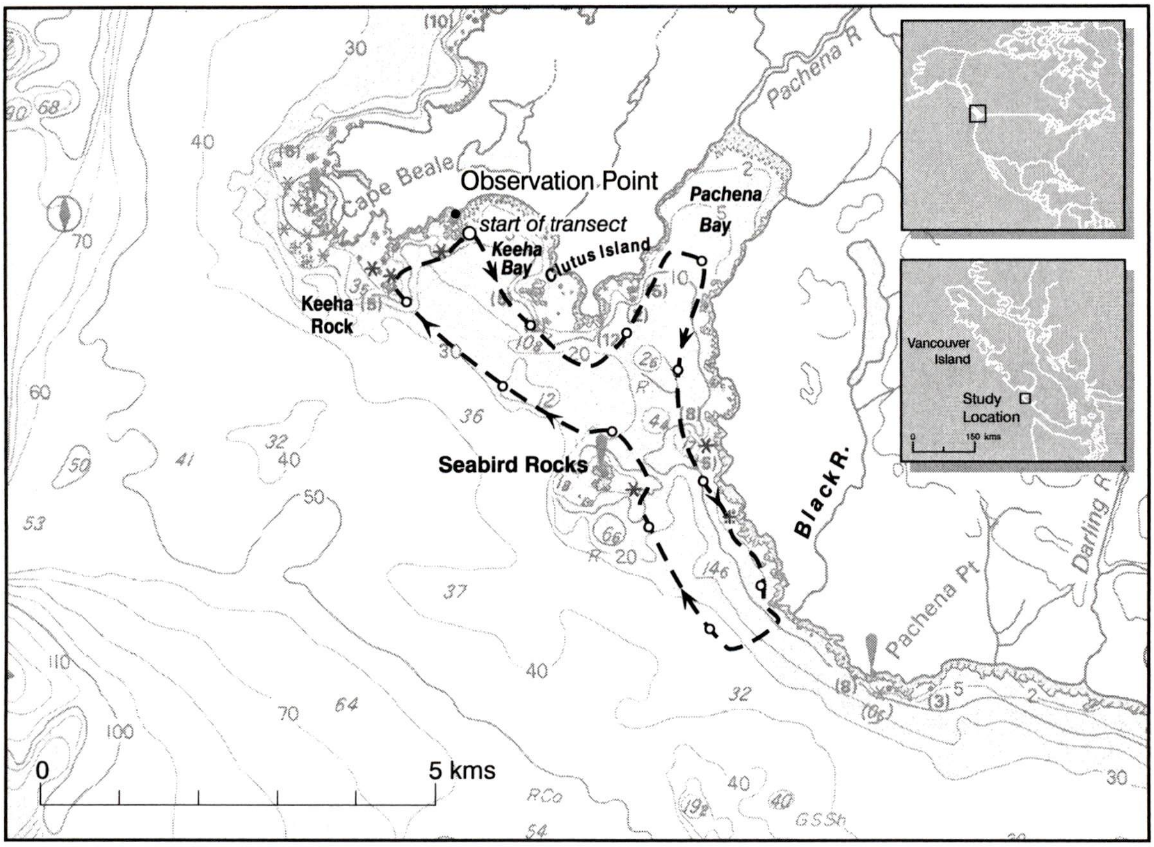


Fig. 1-1. Map of the study area, indicating the transect route and direction plus the point from which the observational scans were conducted.

therefore, the entire water column underneath the boat was sampled. During these transects, sea state, tidal stage, wind speed, wind direction and time of day also were recorded.

Following Piatt (1990), a transparent grid was overlaid on the resulting echosounder paper trace to determine prey densities, with each square representing 20 s horizontal time periods and 2 m vertical depths. Prey densities were then quantified by estimating the percentage cover of prey in each square, for later translation into prey density scores (scale 0-9). Prey density scores were squared prior to analysis to attain a better estimate of biomass (Forbes and Nakken 1972). Discriminating between types of 'prey' on the echosounder paper trace was difficult; however, I conducted field tests by driving over a school of fish near the ocean's surface, where I was able to dipnet some fish and record the school on the echosounder. This allowed the discrimination between schools of small fish and solitary, larger fish on the echosounder paper trace. The probability of euphausiids showing up on the paper trace was low because they generally only migrate into the mid- or upper water column at night.

Third, prey availability was also determined by conducting flock-focused transects, following the methods in Safina and Burger (1985). These transects were conducted to describe the foraging behaviour of auklets in mixed-species feeding flocks and to measure the size, density and species composition of fish schools being exploited by seabird flocks. Each transect was run through a different feeding flock, in which the numbers of each bird species in the flock was counted, fish schooling at the ocean's surface were dipnetted and prey density was measured hydroacoustically, with the 200 kHz echosounder. The length of these transects varied with the size of the flock and extended as far beyond the flock as the distance across the flock. This allowed the water column under feeding birds to be compared with an immediately adjacent area of equal length without birds. After each flock-focused transect, I recorded sea state, tidal height, wind speed, wind direction and time of day. I also recorded the foraging intensity of auklets in the feeding flock, the fish school size observed and the persistence of auklets at the feeding flock after passage by the boat. These three measures were quantified as indices which are defined in Appendix 1-1.

The mean prey density score per route-focused transect was calculated by averaging the squared prey density scores over all 20 s time blocks. Therefore, the mean prey density score for each route-focused transect incorporated both the abundance of prey schools and the density of each school. Two mean prey density scores per flock-focused transect were calculated. The first was calculated by averaging the squared prey density scores in all 20 s blocks located under foraging birds ('flock') and the second was calculated by averaging all 20 s blocks located adjacent to foraging birds ('post-flock'). A number of flock-focused transects were generally conducted in succession and it was hard to determine whether a different fish school was being sampled. Consequently, prey density scores of flock-focused transects conducted in succession were pooled and mean prey density was then calculated for the flock and post-flock areas during each sampling period.

For data analysis, daily and seasonal environmental categories were defined (Appendix 1-2). Daily categories included: time of day, tidal stage and sea state. Only two time-of-day categories were chosen because most transects were conducted in the morning and I wanted to distinguish between dawn light conditions (morning transects) and full daylight conditions (afternoon / evening transects). Seasonal categories included: breeding phases of auklets, prey density periods (incorporating both prey density and abundance), prey accessibility periods and periods of variable wind direction and speed. Wind speed and direction were measured in km/hr at the Cape Beale Light Station and sea state was measured visually using the Beaufort Scale. All of these categories were defined in Appendix 1-2.

Prey densities of route and flock-focused transects were compared between years and between seasonal and daily categories using multi-factor ANOVAs for unbalanced designs. The statistical program SYSTAT was used. SYSTAT computes unbalanced design ANOVAs by creating dummy variables out of the classifying input variable, in which the sum of the effects estimated for the classifying variable is zero (SYSTAT 1992). Interactions between factors, or categories, also were examined if sufficient data were available, or cells were not missing. Due to the unbalanced design of the ANOVAs in this study, the sum of squares associated with one factor depends on the sum of squares for another (Zar 1984). Therefore, careful interpretation of main factor effects is required when an interaction term is significant (Krebs 1989). For instance, if the interaction is disordinal, the two main factors can not be interpreted separately from the interaction and can only be interpreted at each particular level of the main factor (Keppel 1973). If the interaction is ordinal, however, one or both of the main factors may be interpreted separately and may still be interpreted as being significant, regardless of the interaction (Keppel 1973).

Wind speed and sea state were similar among all transects since sampling was impossible in rough weather, thus comparisons could not be conducted on these variables. To compare the total available prey at feeding flocks to the prey being exploited by birds, differences between the prey densities of flock and post-flock areas were analyzed between each environmental category, using Independent sample t-tests. Flock-focused transects also were examined for differences in prey density between prey species, using Independent sample t-tests.

PREY SPECIES / SIZE COMPOSITION

Prey were sampled in two ways to determine annual and seasonal variability in species and size class composition in the study area. First, fish concentrated at the ocean's surface during flock-focused transects were collected using a fine mesh dipnet. Second, fish delivered to chicks at the Seabird Rocks breeding colony were collected by screening burrow entrances and later collecting the fish dropped on the screens and by capturing parents returning to the colony at night with fish for their chicks (chapter 4). Each fish was identified to species, weighed to the nearest 0.5g using a 50 g Pesola spring scale and measured for standard (snout to beginning of caudal fin), fork (snout to tail fork) and total length (snout to tip of tail) to the nearest 0.1 cm (Hart 1973). Three measurements of fish length were collected in order to compare my data with those of other studies. Within each species, different age classes were identified. A comparisons of the number of each species delivered to auklet chicks between years was conducted using a chi-squared test and interannual comparisons of fish length for each species were conducted using Independent sample t-tests.

RESULTS

In 1995, 10 route-focused transects and 10 flock-focused transects were conducted. Prey sampling efforts were concentrated during two time periods: July 21-August 2 (late Rhinoceros Auklet chick rearing) and August 21-23 (post-fledging). A total of 180 fish were collected in these flock-focused transects and 151 were collected in meals of chicks at the colony. In 1996, 23 route-focused transects and 22 flock-focused transects were conducted. Prey sampling efforts were concentrated during three time periods: May 24-June 20 (incubation), July 4-August 5 (chick rearing) and August 20-September 3 (post-fledging). A total of 343 fish were collected in flock-focused transects and 136 fish were collected in meals of chicks at the colony.

PREY AVAILABILITY

INTERANNUAL VARIATIONS

Prey densities of route-focused transects did not differ significantly between years during the same time period (July 21 - September 3; Fig. 1-2). In addition, mean prey densities of flock-focused transects did not differ significantly between years, for both areas underneath bird flocks and areas adjacent to bird flocks (Fig. 1-2).

SEASONAL VARIATIONS

Overall, prey densities of route-focused transects did not differ significantly between seasons (Appendix 1-3). Prey densities of route-focused transects were, however, significantly higher in certain periods in both years. I defined these periods as high prey density periods, with the other transects representing low prey density periods (Fig. 1-3). Between June 13-20 in 1996, fish schools were observed frequently at the ocean's surface during the day. I defined this as a period of high prey accessibility because fish were both concentrated and located in surface waters.

In 1996, comparisons in the mean prey density scores from route-focused transects between seasonal categories showed a significant interaction between prey density and prey accessibility periods. The interaction was ordinal for prey density but disordinal for prey accessibility, suggesting that prey density was significantly higher during particular

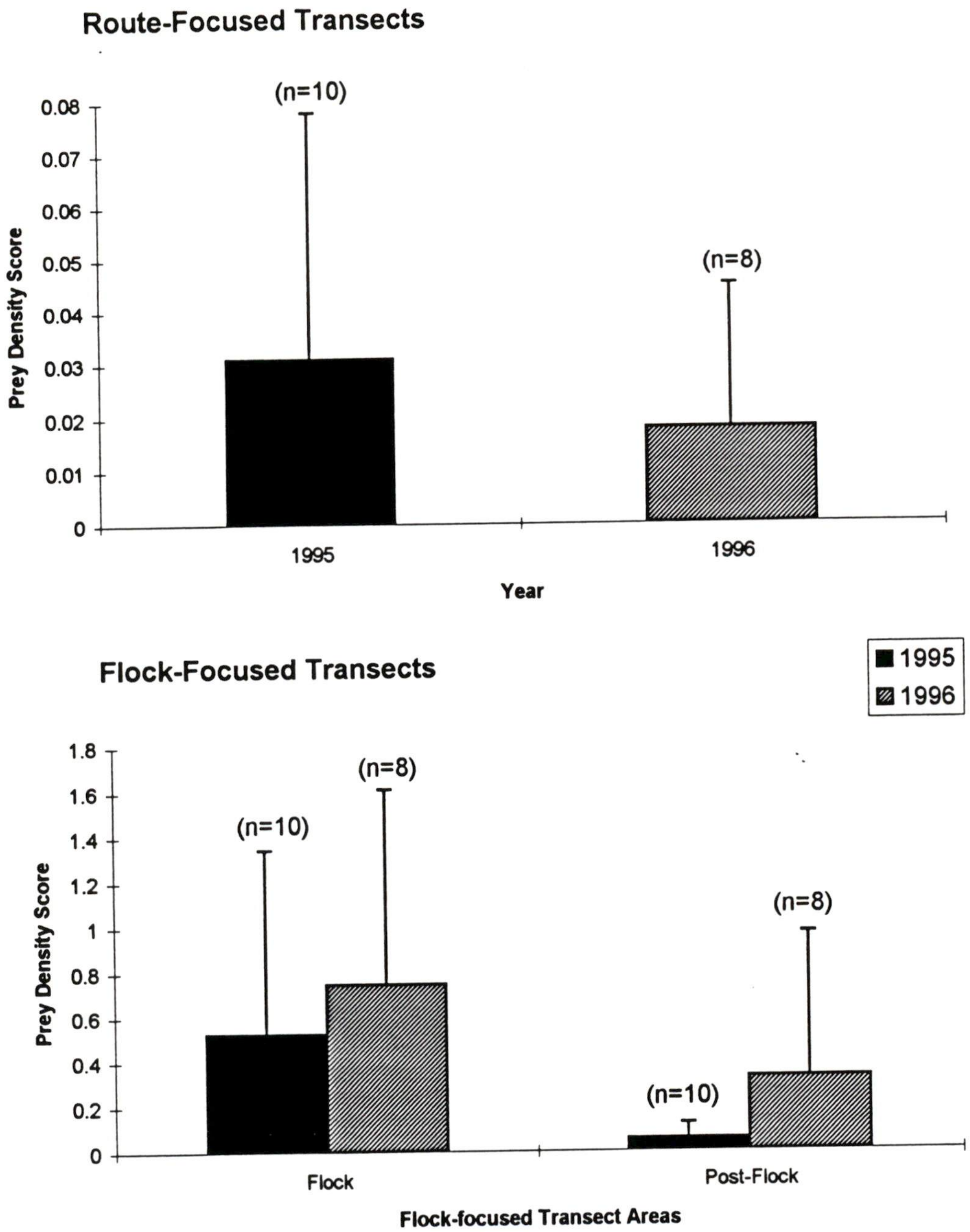
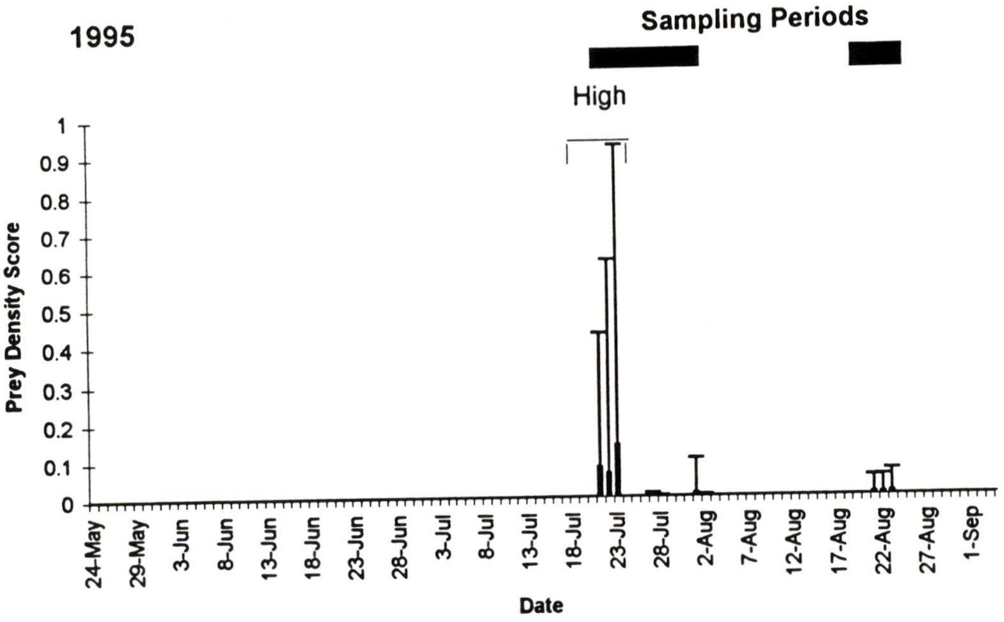


Fig. 1-2. The mean prey density scores (+ SD) of route-focused transects (Independent sample t-test, t=-0.684, df=16, P=0.504, power=0.97) and flock-focused transects (flock areas: t=-0.555, df=16, P=0.584, power=0.95; post-flock areas: t=-1.181, df=16, P=0.203, power=0.95) around the Seabird Rocks breeding colony in 1995 and 1996.



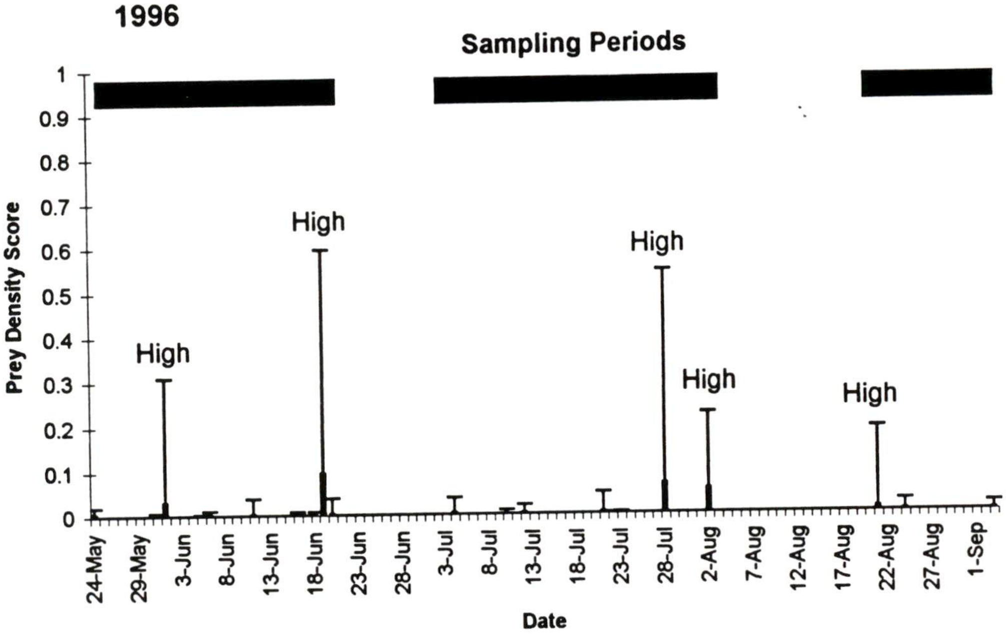


Fig. 1-3. The mean prey density scores (+ SD) of route-focused transects in 1995 and 1996 around the Seabird Rocks breeding colony with high prey density periods indicated.

transects, but the effect of prey accessibility can not be interpreted separately from prey density. No significant difference in prey densities of route-focused transects were found between wind direction categories; however, high prey density periods were preceded by periods of strong northwest to easterly winds followed by a period of strong southeast to westerly winds (Fig. 1-4 and 1-5). Northerly to easterly winds are offshore winds, whereas northwest wind is an along-shore wind that causes offshore flow in surface layers due to the Coriolis force. Consequently, these winds drive the Vancouver Island Coastal Current away from the coast. Southerly to westerly winds are onshore winds, whereas southeast wind is an along-shore wind that causes onshore flow in surface layers due to the Coriolos force. Consequently, these winds drive the VICC towards the coast.

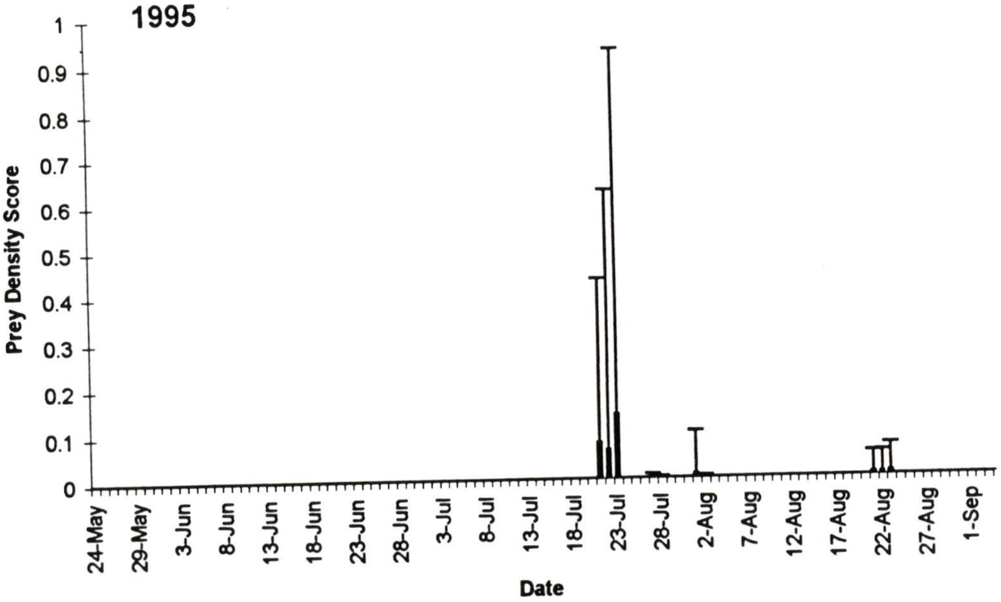
In both years, prey densities of flock-focused transects did not differ significantly between seasons, however, there was a significant interaction between wind direction and prey density in flock areas in 1996 (Appendix 1-3). The interaction was disordinal for both prey density and wind direction, suggesting that these two factors can not be interpreted independently of each other. Prey densities in flock areas did not differ significantly from post-flock areas among seasonal and daily categories (Appendix 1-4).

DAILY VARIATIONS

Prey densities in route and flock-focused transects did not differ significantly between daily categories (Appendix 1-5).

DIFFERENCES BETWEEN PREY SPECIES

Comparisons between flocks associated with schools of sand lance and herring in 1996 showed no significant differences in the prey densities of flock and post-flock areas (Appendix 1-6). Flocks with sand lance and herring also did not occur at different times of the day or at different tidal stages. There were insufficient data for such comparisons in 1995.



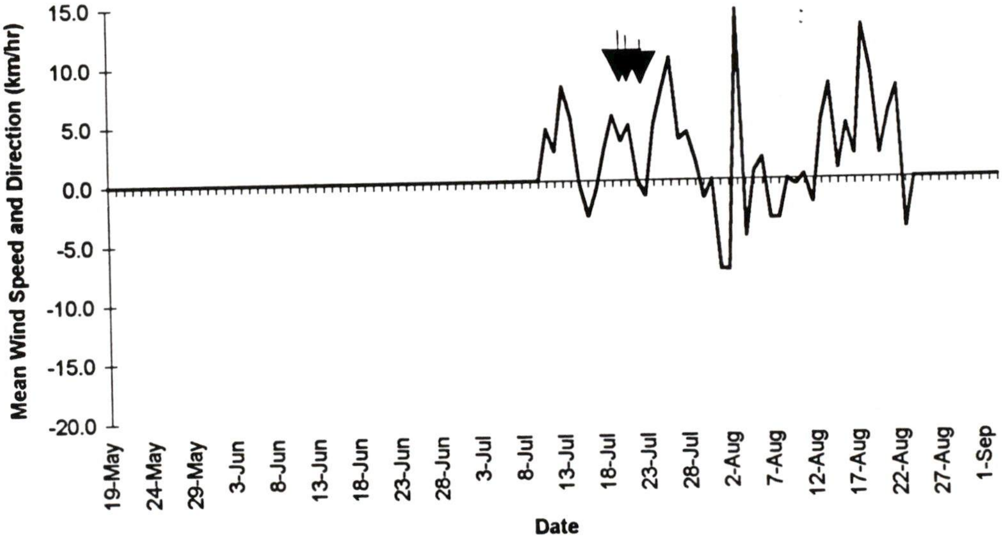
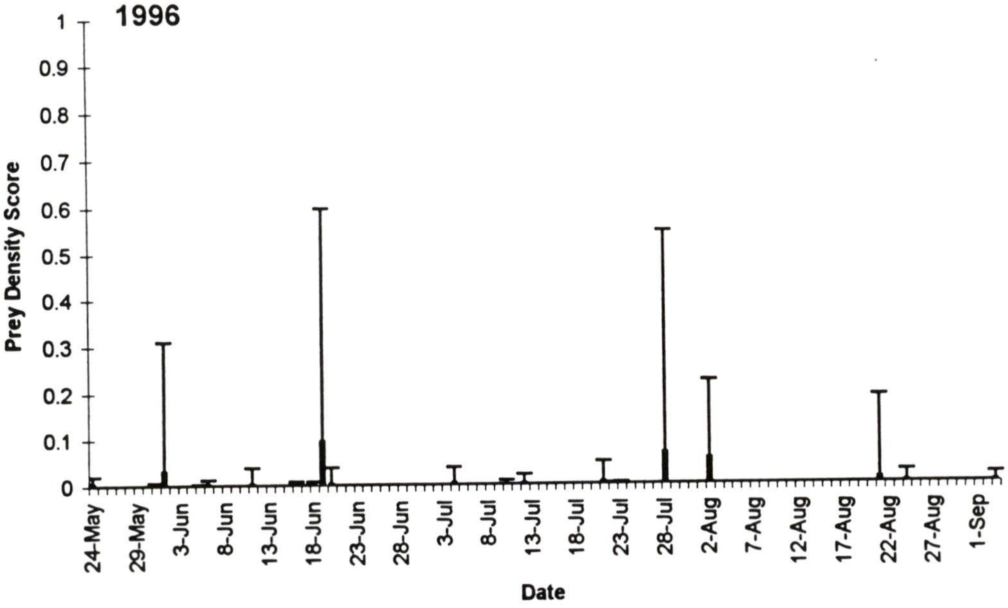


Fig. 1-4. The mean prey density scores (+ SD) of route-focused transects in 1995 around the Seabird Rocks breeding colony and the mean wind speed and direction in the study area. A positive wind value represents southeasterly to westerly winds (drives the Vancouver Island Coastal Current towards the coast) and a negative value represents northwesterly to easterly winds (drives the VICC away from the coast). The high prey density transects are indicated with arrows.



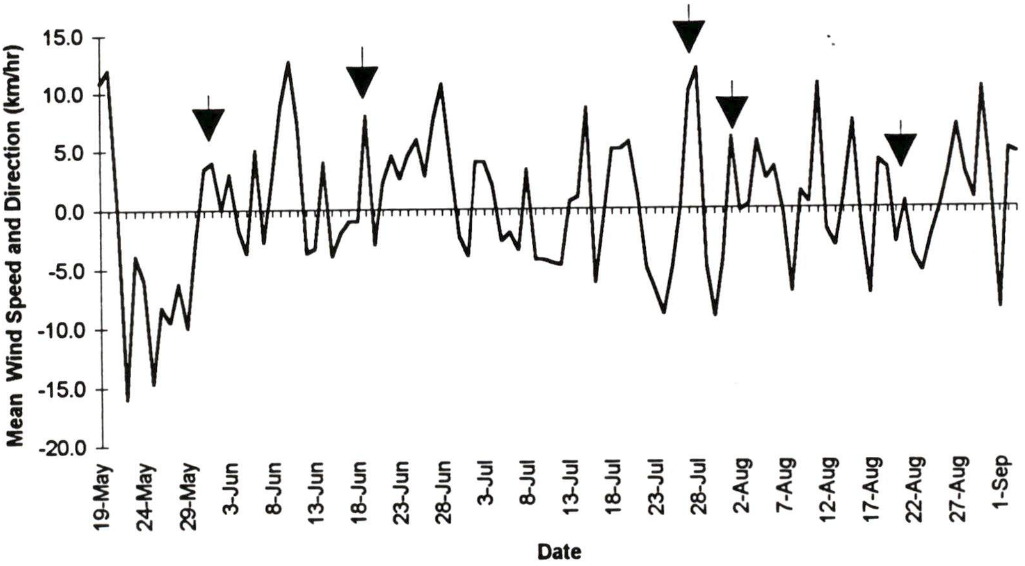


Fig. 1-5. The mean prey density scores (+ SD) of route-focused transects in 1996 around the Seabird Rocks breeding colony and the mean wind speed and direction in the study area. A positive wind value represents southeasterly to westerly winds (drives the Vancouver Island Coastal Current towards the coast) and a negative value represents northwesterly to easterly winds (drives the VICC away from the coast). The high prey density transects are indicated with arrows.

SPECIES COMPOSITION

INTERANNUAL VARIATIONS

In both years, sand lance was delivered to chicks in the highest numbers followed by Pacific salmon species, Pacific herring, surf smelt and other species (i.e. Pacific hake, Pacific tomcod and Pacific sandfish). The percentages by number of each fish species collected in meals of chicks at the colony, however, differed significantly between years, shown by a chi-squared test conducted on the total number of each species in each year (X^2=16.156, df=4, P=0.003; Table 1-1). A lower number and mass of sand lance but a higher number and mass of salmon and herring were delivered to chicks in 1996, compared to 1995. The percentage by number of each fish species collected in meals of chicks also differed significantly between visits within the same year, shown by a chi-squared test conducted on the total counts of each species delivered in each visit per year (1995: X^2=31.474, df=12, P=0.002; 1996: X^2=24.607, df=8, P=0.002; Table 1-1).

Only two fish species were collected from the ocean's surface at feeding flocks in both years: Pacific herring and Pacific sand lance (Table 1-1). Interannual differences in the percent occurrence of species collected at feeding flocks probably do not reflect changes in their availability but rather interannual differences in sampling times during the day. For instance, in 1995, fish at feeding flocks were mainly sampled after 0900 but in 1996 they were also sampled before 0900, which was when sand lance were mainly collected.

SEASONAL VARIATIONS

Differences in species composition in the study area were not documented; however, herring were collected only between June 17 and August 2 in 1996. Samples sizes before and after these dates were low and, thus, this may not reflect migration activity of herring.

Table 1-1. Percentage of total number and of total mass of fish species delivered to chicks of Rhinoceros Auklets in each visit to the Seabird Rocks breeding colony in 1995 and 1996. Percentage of occurrence of fish species collected at feeding flocks containing Rhinoceros Auklets in 1995 and 1996 near the Seabird Rocks breeding colony

Location, Date	sand lance	herring	salmon	surf smelt	other fish	Number of Prey Items
Percent Occurrence						
Colony 1995						
July 4-5	48	0	30	22	0	23
July 14-15	51	5	16	16	2	45
July 24-25	75	15	6	4	0	71
August 3-4	91	0	0	8	0	12
Total	65	12	12	10	1	151
Colony 1996						
July 7-8	42	14	25	8	10	59
July 17-18	68	14	13	2	3	62
July 30-31	7	27	46	13	7	15
Total	50	15	22	6	7	136
Feeding Flock						
1995	17	83	0	0	0	180
1996	59	41	0	0	0	343
Percent of Total Mass						
Colony 1995	31	9	22	36	2	151
Colony 1996	31	14	31	21	2	136

SIZE COMPOSITION

INTERANNUAL VARIATIONS

Two age classes of sand lance and herring were delivered to chicks: sand lance 0+ (juveniles, 40-110 mm) and 1+ (111-180 mm) (Vermeer and Westrheim 1984) and herring 0+ (juveniles, 40-100 mm), 1+ (101-140 mm) (Hart 1973). Juvenile salmon and adult surf smelt were only delivered to chicks, and were not found associated with feeding flocks.

At feeding flocks, the juvenile herring collected were significantly larger in 1996, compared to 1995; however, the juvenile sand lance were significantly smaller in 1996, compared to 1995 (Table 1-2; Appendix 1-7). In meals of chicks, juvenile salmon and sand lance were significantly larger in 1996, relative to 1995, however, juvenile herring were significantly larger in 1995, compared to 1996 (Table 1-2; Appendix 1-7). There were no significant differences in the size of surf smelt, 1+ herring and 1+ sand lance between years.

DIFFERENCES BETWEEN MEALS OF CHICKS AND FEEDING FLOCKS

In both years, sand lance and herring collected at feeding flocks consisted only of age class 0+ fish (Table 1-2). In contrast, sand lance and herring delivered in meals of chicks consisted of both age class 0+ and 1+, resulting in significantly larger fish delivered to chicks, compared to those collected at feeding flocks (Fig. 1-6).

DISCUSSION

SEASONAL VARIABILITY IN PREY DENSITY AND ABUNDANCE

A decline in prey density and abundance during critical food-gathering periods (e.g. chick rearing) may negatively influence the provisioning rates of seabirds, potentially resulting in reduced breeding success. Prey densities in both route-focused and flock-focused transects did not differ between years but did fluctuate significantly within each year. In 1996, the interaction between prey density and prey accessibility was disordinal for the prey accessibility factor. This suggests that fluctuations in prey density during prey

Table 1-2. Mean standard lengths (± SD) of each age class of fish delivered to chicks of Rhinoceros Auklets at the Seabird Rocks colony and found at mixed-species feeding flocks containing auklets near Seabird Rocks in 1995 and 1996. Numbers of fish collected are given in parentheses

Location, Year	0 + sand lance	1 + sand lance	0 + herring	1 + herring	salmon	surf smelt
Colony 1995	79.1 ± 9.7 (71)	119.5 ± 5.1 (27)	71.2 ± 11.6 (13)	129.5 ± 18.4 (5)	87.8 ± 16.0 (18)	134.2 ± 17.9 (16)
Colony 1996	97.6 ± 14.8 (44)	117.2 ± 5.9 (24)	57.1 ± 8.0 (14)	130.8 ± 4.4 (7)	97.8 ± 10.1 (30)	113.8 ± 39.6 (8)
Feeding Flock 1995	74.1 ± 3.6 (42)	-	51.4 ± 11.4 (138)	-	-	-
Feeding Flock 1996	68.0 ± 6.3 (161)	-	53.9 ± 6.9 (202)	-	-	-

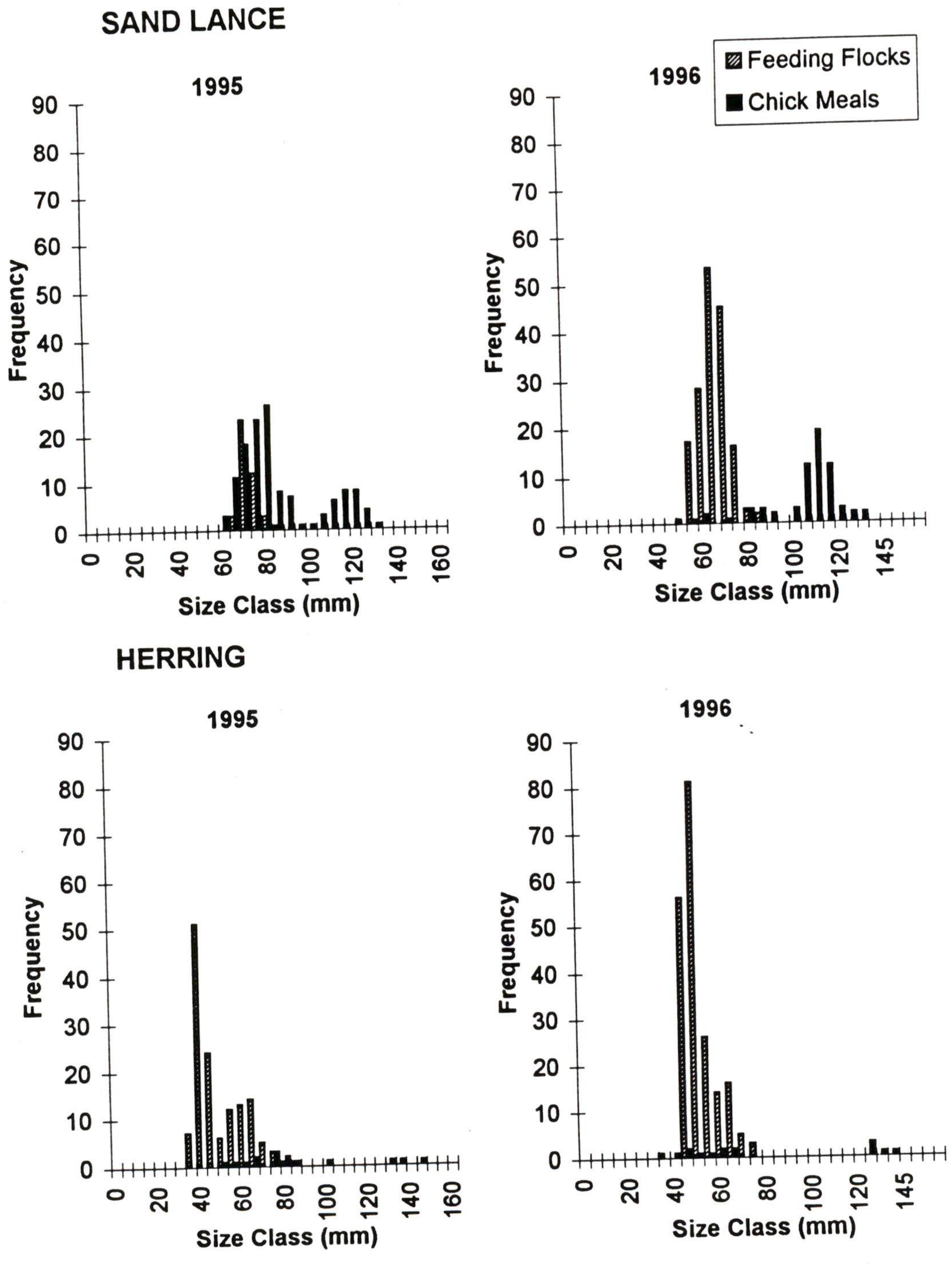


Fig. 1-6. The frequency distribution of 5 mm size classes of sand lance and herring collected at the colony in chick meals of Rhinoceros Auklets and in feeding flocks containing Rhinoceros Auklets in both 1995 and 1996. Sand lance delivered to chicks were significantly larger than those at feeding flocks (Independent sample t-test: 1995: t=7.599, df=138, P<0.0001; 1996: t=19.214, df=227, P<0.0001). Herring delivered to chicks were significantly larger than those at feeding flocks (1995: t=4.569, df=154, P<0.0001; 1996: t=2.810, df=221, P=0.015).

accessibility periods are dependent on prey density periods. In 1996, there was also a significant interaction between prey density and wind direction. This suggests that fluctuations in the prey densities of flock areas at feeding flocks are influenced in combination by prey density periods and wind direction, showing that these two factors can not be interpreted separately. In support, high prey density periods in both years were preceded by periods of strong northwest to east (primarily northwest) winds followed by a period of strong southeast to west winds (primarily southeast and southwest winds) (Fig. 1-4 and 1-5).

Prevailing northwest winds during the Summer result in coastal upwelling and the offshore of water in surface layers (Thomson et al. 1989). When winds change to strong southeast winds during the Summer, upwelling currents relax and downwelling occurs, generally resulting in the onshore flow of surface layers (upper 50m). This causes a shift in surface layer biomass, causing organisms (e.g. plankton and fish) to concentrate on the continental shelf (Thomson et al. 1989). Studies in other areas have shown this inshore advection of organisms (e.g. barnacle, bivalve and gastropod larvae) during the upwelling season when upwelling intensity relaxed or when downwelling conditions were established on the temporal scale of hours to days (Alexander and Roughgarden 1996; Farrell et al. 1991; Roughgarden et al. 1991; Butman 1997). Therefore, strong southeast, or downwelling-favourable winds may have shifted biomass in surface waters inshore at regular intervals within my sampling seasons. Upwelling, however, is a prominent feature of the outer shelf area and only affects the biomass of the inner shelf indirectly through the inshore transport of biomass at depth through deep ocean canyons and the subsequent northward transport via the Vancouver Island Coastal Current (VICC; McFarlane et al. 1997). Consequently, a change in estuarine circulation may explain the fluctuations in prey density and abundance better at the temporal scales that I observed (hours to days).

The path of the VICC may be shifted towards or away from the coast by onshore and (southwest) and offshore (northeast) winds, respectively (Thomson 1981). Since the VICC acts as a northward conduit for zooplankton and other organisms (e.g. fish larvae and adults), an onshore shift in the VICC may increase the density and abundance of these organisms in near-shore waters. High prey density transects were primarily observed when strong southeast and southwest winds followed a period of strong northwest winds. Therefore, northwest winds may have acted to slow the speed of the VICC near the ocean's surface, potentially making it easier for the following onshore winds and ocean currents to drive the VICC, and organisms entrained in the VICC, towards the coastline. This pattern, however, was very noisy, which suggests that there is probably a complex interaction between ocean currents, wind speed and wind direction in this area.

Wind-induced changes in water circulation near the outer Vancouver Island coast are known to result from southeast and onshore wind events (Thomson and Grower 1985), causing distributional changes of plankton biomass and fish along the coast (McFarlane et al. 1997). These wind-driven changes in water circulation appear to act on a temporal scale that is consistent with the fluctuations in prey density and abundance observed in this study. Consequently, it seems likely that changing wind directions associated with the inshore displacement of the VICC and potentially with the relaxation of upwelling may be responsible for the observed prey density and abundance fluctuations. Overall, these episodic wind-induced events appeared to increase prey density and abundance around the Seabird Rocks breeding colony, supplying auklets with abundant prey to feed both themselves and their chicks.

INTERANNUAL VARIABILITY IN FISH SIZE COMPOSITION

Size differences in fish available during chick rearing can affect the breeding success of auklets (Vermeer 1980). Many size differences were observed between 1995 and 1996. First, juvenile sand lance collected at feeding flocks were significantly larger in 1995 than in 1996, however, juvenile herring collected at feeding flocks were significantly smaller in 1995 than in 1996. The difference in sand lance size between years probably resulted from different sampling efforts between years. For instance, sand lance were only sampled once at feeding flocks in late August of 1995, however, in 1996 sand lance were sampled consistently from May to August. Therefore, juvenile sand lance at feeding flocks were probably not actually larger in 1995 than in 1996. In addition, juvenile herring collected at feeding flocks in 1996 were only approximately 2 mm longer than in 1995.

This small size difference, although statistically significantly, probably had little impact on the ability of adults to provision their chicks.

Second, juvenile sand lance and herring collected in meals of chicks at the colony, showed opposite trends in size differences from those collected at feeding flocks, with sand lance in meals of chicks being larger in 1996 and herring being larger in 1995. In addition, salmon were larger in 1996 than in 1995 but surf smelt were smaller in 1995 than in 1996. It is unlikely that large scale changes in oceanic conditions caused these size differences between years, due to the inconsistency of these differences between fish species. For instance, if ocean productivity was much lower in one year, growth rates of juvenile sand lance and herring would likely be affected in a similar manner. In addition, interannual variation in juvenile sizes (≈ 10 mm) appears to be normal in certain areas due to distributional shifts in the rearing areas of juvenile fish between years (D. Hay pers. comm).

The interannual size differences in fish delivered to auklet chicks in this study (10-30 mm) may have had an impact on growth rates of chicks. For instance, the smaller surf smelt individuals delivered in 1996 may have been easier for chicks to swallow, resulting in a lower probability of chick choking to death (Vermeer 1980). For the most part, however, the size differences between years appeared to have little impact on the proportion of each species delivered to chicks by mass (Table 1-1). Consequently, the size differences of each fish species between years probably had little impact on the body conditions of auklets adults and chicks, in comparison to the difference in the number of larger fish species delivered to chicks between years (Table 1-1).

ECOLOGY OF RHINOCEROS AUKLET PREY

Background on the four main prey species of auklets is reviewed in this section to interpret the consistent presence of each species in chick diets and at feeding flocks in both years.

SURF SMELT

Surf smelt were not delivered to auklet chicks in high numbers, but due to their large mass, they made up a substantial percentage of the total fish mass delivered to chicks. Surf smelt spawn along sand beaches in British Columbia in most months of the year (Hart 1973), although populations spawn primarily during mid-late summer (Hay et al. 1989). Spawning sites outside the Strait of Georgia are not well known; however, they apparently spawn in Barkley Sound (e.g. Goose Island) (Hay et al. 1989). Spawning usually occurs intertidally on sheltered, sandy beaches where surf action is minimal and adhesive eggs can be buried in the sand (Hart 1973). Each individual is thought to spawn repeatedly within a season (Hart 1973) and, therefore, individuals generally concentrate in spawning areas for a number of months, where they are vulnerable to predation (Hay et al. 1989). Due to the high content of sheltered, sandy beaches in my study area, this species of smelt may use it as spawning grounds during the summer. This would account for the consistent appearance of surf smelt in meals of chicks during both years of this study.

SALMON SPECIES

Salmon species also made up a high percentage of chick diets, both by number and by mass. Although the species of salmon were not identified in this study, Burger et al. (1993) collected three species of salmon at Seabird Rocks: *Onchorhynchus keta* (chum), *O. tsawytscha* (chinook) and *O. kisutch* (coho). Salmon were identified to species in 2 years of this 3-year study. In one year chinook was the dominant species and in the other year chum predominated, whereas coho were incidental. The other two species of Pacific salmon, pink and sockeye, were not collected in chick diets, probably since pink mainly spawn in northwestern tributaries and sockeye migrate quickly offshore upon entering the ocean (Hay et al. 1992).

Chum migrate immediately to the ocean after emerging from spawning nests (Hart 1973). A major spawning population occurs in Nitinat Lake, just south of the study area. Like chum, chinook generally migrate to sea soon after emerging from nests (Hart 1973) and juveniles generally disperse to sheltered marine nurseries by mid-late June (Hay et al. 1992). Both chum and chinook occupy sheltered nursery habitats until September, at which point they begin their seaward and northward migration with the Vancouver Island Coastal Current (Hay et al. 1992). The presence of these species in sheltered coastal habitats during the summer probably explains their presence in auklet diets.

Unlike chinook and chum, coho salmon usually remain in freshwater streams for approximately one year after emergence from spawning nests (Hart 1973). Juveniles enter the ocean in May of the following year and, similar to sockeye salmon, this species spends little time in sheltered waters (Hay et al. 1992). This probably explains its low presence in auklet diets; however, a major spawning population occurs in Nitinat Lake (Hay et al. 1992) and, thus, they likely travel through the study area on their northward migration during the summer.

HERRING

Juvenile herring generally spend their first summer inshore in shallow, sheltered inlets and bays (Gallego et al. 1995; Hart 1973; Hourston 1958). Hourston (1958) concluded that the primary factor describing the rearing grounds of juvenile herring was a high degree of shelter from wind and waves, rather than temperature or salinity preferences. Even within these sheltered bays, juvenile herring generally concentrated where the surface was less disturbed by winds, the currents were relatively weak and the water was relatively shallow (Hourston 1958). Due to their consistent presence in the study area in both years, these juvenile herring potentially used the study area as rearing grounds. Juvenile herring were not a main prey item in meals of chicks but were one of the two main prey types found at mixed-species feeding flocks. Consequently, they may be an important food source for adult auklets during the breeding season.

In early fall, these juveniles move from their rearing grounds to offshore, where they remain as immature fish until they join the spawning stocks as mature adults, generally in their third year (Grosse and Hay 1988). Older herring remain farther offshore than juveniles, which may explain why larger herring were not collected at feeding flocks in this study because all sampled flocks were inshore (<40 m depth) in prime juvenile rearing habitat (Grosse and Hay 1988). The offshore distribution of older herring also may explain their relatively infrequent appearance in meals of chicks because auklets were generally found diving inshore to collect fish for chicks.

SAND LANCE

Sand lance species are thought to bury into sandy bottom refuges throughout the night and possibly for short periods during the day (Reay 1970; Scott 1972; Winslade 1974; Meyer et al. 1979; Field 1988). Burying behaviour is thought to occur in response to predators and also for rest because sand lance lack swimbladders and are negatively buoyant (Reay 1970; Field 1988). Consequently, sand lance concentrate in shallow waters (<50m, generally < 20m) that contain suitable substrate for burrowing (Reay 1970; Field 1988). Suitable substrates include coarse sand of grain sizes ranging from 1-15 mm that are well washed (Reay 1970; Dick and Warner 1982). Sand lance also have been found distributed near the entrances of rivers and streams or in estuaries (Dick and Warner 1982; Reay 1970; Field 1988), likely due to high current flow keeping bottom sediments well flushed of mud and debris. The study area is a well known Gray Whale foraging area and, thus, has a high content of sandy substrates (Oliver et al. 1984). This probably explains the abundance of sand lance both at feeding flocks and in meals of chicks.

Juvenile sand lance are thought to be found in similar inshore areas as adults, due to their requirements for bottom refuges, but do not form mixed schools (Reay 1970). This may be due to their different swimming speeds and to the tendency for similar-sized fish to form schools. Other evidence suggests that juvenile sand lance behave differently than adults. For instance, juvenile sand lance (30-110 mm) were observed in the water column at night, whereas adults were not, presumably because they were buried in bottom sediments (Winslade 1974). In addition, juvenile and adult sand lance were collected by digging in sediments which became exposed at low tides but only juvenile fish were collected in beach seines (Dick and Warner 1982). Finally, the diets of surface-feeding birds in Shetland contained primarily juvenile sand lance, whereas pursuit diving birds contained a higher proportion of older sand lance (Monaghan et al. 1994). All of this suggests that juvenile sand lance are found closer to the surface and possibly have a more inshore distribution than adults. Behavioural differences between adult and juvenile sand lance may explain why only juvenile sand lance were found at feeding flocks.

CHAPTER TWO

FORAGING BEHAVIOUR AND ACTIVITY ANALYSIS OF BREEDING RHINOCEROS AUKLETS

INTRODUCTION

During moderate declines in prey availability, some seabirds increase the time spent foraging at sea and/or decrease the time spent resting at the colony (Burger and Piatt 1990; Burness et al. 1994; Uttley et al. 1994; Monaghan et al. 1994; Birkhead and Nettleship 1987; Hamer et al. 1991). It is possible that alcids also may alter their foraging strategies when prey availability declines, although this has not been documented. Some pursuit-diving seabirds utilize two main foraging strategies: solitary and socially facilitated foraging (Wittenberger and Hunt 1985). These strategies differ in the types of searching required to locate prey patches. Solitary diving requires exploratory diving, an energetically expensive activity (Gaston 1985), whereas social foraging mainly requires observing the foraging activities of other seabirds. At any one time, seabirds probably employ a combination of the two strategies but may increase the use of one strategy over the other according to varying energetic and time constraints. These constraints primarily arise due to increased foraging activities, which may be related to both reduced prey availability and/or the need to feed chicks.

Social foraging is both less energetically costly and also provides information at a faster rate on prey patch locations and qualities, relative to solitary diving (Wittenberger and Hunt 1985). Thus, social foraging enhances foraging efficiency by decreasing search times for prey (Wittenberger and Hunt 1985). This faster-information gathering may be important for seabirds during moderate prey availability declines, when their rate of energetic intake is dependent on prey encounter rates (Piatt 1990). Therefore, seabirds may use social foraging to a higher degree when prey availability drops and when energetic demands increase (Wittenberger and Hunt 1985).

Another strategy that birds may employ to reduce foraging efforts when faced with variable provisioning demands is the exploitation of spatially and temporally predictable prey patches. For the most part, seabird prey are patchily distributed and patches are constantly changing in both their location and quality. There is evidence, however, that predictable prey concentrations occur near breeding colonies and that seabirds are able to exploit these concentrations efficiently (Schneider et al. 1990; Hunt et al. 1990; Cairns and Schneider 1990; Coyle et al. 1992; Hunt et al. 1988). The predictability of prey concentrations is likely an important factor affecting breeding success because it also may minimize energetically expensive search activities.

The primary goal of this part of the study was to describe the foraging responses of auklets to daily and seasonal fluctuations in prey availability and to changing provisioning demands throughout the breeding season. This tested whether adults have flexible time budgets or whether they are time-limited during the breeding season. This also tested whether auklets shift their foraging strategies under varying conditions and varying provisioning demands. Other behavioural responses to variable prey availability and provisioning demands are reported as well.

METHODS

SCAN DATA

The activities of Rhinoceros Auklets at-sea were measured in 1996 through instantaneous visual scans at a fixed range from land (Martin and Bateson 1986), using a 15-45 power zoom spotting scope. Scans were conducted from the same observation point each day (chapter 1, Fig. 1-1, 'Observation Point'), which was situated on a rocky ledge 7-10 m above sea level. The scanning area covered a foraging area that was frequently used by auklets during the breeding season (A. E. Burger unpublished data).

One-hour observation bouts, separated by at least one hour, were divided into three 20-minute scans, in which three distinct areas were scanned sequentially. During each hour of observation, the first two scan areas were selected at random, to ensure that scans were not conducted in the same order in each hour. An average of 3 one-hour observation bouts were conducted per day (range 1-6).

Each 20-min scan consisted of watching one field of view in the spotting scope for 90 s, then moving the scope to the next field of view. This method was used to obtain an accurate measure of the number of auklets diving solitarily. In each field of view, I recorded the number of adult auklets engaged in each of four activity categories: Foraging, Resting, Swimming and Maintaining. Within each of these categories, the specific activity of each adult was also recorded. Foraging included: solitary diving, flock diving, head dipping and prey capture (swallowing prey). Resting included: sitting on the water (alert resting) and head tucked (nonalert resting). Maintaining included: preening, surface flapping and bathing. Finally, Swimming included swimming on the ocean's surface. During scans, the number of auklets holding fish and flying was recorded. Flying was not included as one of the standard activities because auklets that are flying may be counted more than once during a scan and because they are more conspicuous, resulting in an overestimate of flying birds and an underestimate of auklets engaged in other activities on the water. Group sizes, the total number of auklets and the number of feeding flocks were also recorded, along with the tidal stage, time of day, sea state, wind speed and wind direction.

The numbers of auklets in each activity category during each successive 20-minute scan were summed to get hourly totals. These totals were then used to calculate the percentage of auklets in the surveyed population engaged in each activity in each hour. Percentages were calculated by dividing the number of auklets engaged in each activity during an hour by the total number of auklets observed in that hour. The square root of these proportions were calculated and then arcsine transformed to meet the underlying assumption of normally distributed data for parametric statistical analysis (Zar 1984). The number of auklets and the number of feeding flocks also were summed to get hourly totals. Group sizes were averaged to get mean group sizes of auklets per hour. These hourly values and the transformed proportions were compared between daily categories using multi-factor ANOVAs for unbalanced designs. The statistical program SYSTAT was used. SYSTAT computes unbalanced design ANOVAs by creating dummy variables out of the classifying input variable, in which the sum of the effects estimated for the classifying variable is zero (SYSTAT 1992). Interactions between factors, or categories, also were examined if sufficient data were available, or cells were not missing. Due to the unbalanced design of the ANOVAs in this study, the sum of squares associated with one factor depends on the sum of squares for another (Zar 1984). Therefore, careful interpretation of main factor effects is required when an interaction term is significant and whether the interaction is ordinal or disordinal for the main factors (Krebs 1989; Keppel 1973).

Mean daily percentages were calculated by averaging the untransformed hourly percentages in each activity category. The square root of these proportions were calculated and then arcsine transformed, again to meet the underlying assumption of normally distributed data for parametric analysis (Zar 1984). Daily means of group sizes, the number auklets and the number of feeding flocks also were calculated. These daily means and transformed proportions were then tested for significant differences between seasonal categories using Independent sample t-test, single factor ANOVAs and multi-factor ANOVAs for unbalanced designs. See Appendix 1-2 for detailed descriptions of both seasonal and daily categories.

FOCAL DATA

Dive and inter-dive recovery (pause) durations of auklets were recorded in the study area throughout the three breeding phases in 1996 to obtain a measure of foraging effort. The focal animal sampling technique was used (Martin and Bateson 1986), where in one individual was tracked until it terminated its dive bout, was lost from sight, or was confused with other conspecifics. Termination of a dive bout was assumed if the bird began prolonged preening, surface flapping or bathing (2 standard deviations above the mean pause duration). Dive and pause durations were measured to the nearest second using a stop watch and observations were recorded on a tape recorder.

Rhinoceros Auklets can travel long distances under water during a dive (50 m; Burger et al. 1993) and may emerge their bills only momentarily for breathing (Dewar 1924; L. Paul pers. comm.); thus, it is possible to miss a pause. This can artificially elevate recorded dive durations; thus, dives exceeding 2 standard deviations above the mean were discarded prior to analysis.

RESULTS

During the 1996 breeding season, 147 hours of visual scans were obtained: 41 during incubation, 73 during chick rearing and 33 during post-fledging. Nine hours of visual scans from June 13 to 20 were eliminated from breeding phase analyses because there was a mixture of auklets chick rearing and incubating; thus, a particular breeding phase could not be defined. During visual scans, 360 feeding flocks were observed and the dive and pause durations of 113 auklets were recorded.

SCAN DATA - SEASONAL

BREEDING PHASE

Over the three breeding phases, the percentage of auklets Resting (24-46%) was significantly higher in incubation than in chick rearing and post-fledging (Table 2-1; Appendix 2-1). The number of auklets flying also was significantly higher in incubation than in the other two phases. In contrast, the percentage of auklets Swimming (26-49%) was significantly lower in incubation, compared to chick rearing and post-fledging. The percentage of auklets Maintaining (14-20%) differed significantly over the three breeding phases, being lower in chick rearing compared to the other two phases. The percentage of auklets Foraging (9-21%), however, did not differ significantly among the three breeding phases but the percentage of auklets flock diving was higher in chick rearing and the percentage of auklets diving solitarily declined from incubation to post-fledging (Fig. 2-1).

PREY AVAILABILITY

During periods of low prey density and abundance, a significantly higher percentage of auklets were foraging solitarily compared to periods of high prey density and abundance (Fig. 2-2; Appendix 2-2). The percentages of auklets Foraging and flock diving, however, remained relatively constant.

Between June 13-20, when juvenile herring were frequently observed schooling in surface waters (high prey accessibility period), the percentage of auklets Foraging increased significantly, relative to all other sampling dates, primarily due to a significantly

Table 2-1. The percentage of Rhinoceros Auklets engaged in the four activity categories (± SD) and the mean number of auklet flying per seasonal category (± SD) in the 1996 breeding season. The sample size (n) is the number of scan days

	Percentages (%)				Numbers	
Category	Foraging	Resting	Maintaining	Swimming	Flying Birds	n
Breeding Phase						
Incubation	8.9 ± 7.0	46.1 ± 15.0	19.6 ± 9.0	26.2 ± 14.0	65.8 ± 30.2	20
Chick Rearing	10.6 ± 7.0	27.6 ± 15.0	13.6 ± 7.0	49.2 ± 15.0	45.1 ± 21.2	23
Post-fledging	9.8 ± 7.0	25.7 ± 9.0	19.1 ± 7.0	46.2 ± 17.0	11.8 ± 11.7	11
Prey Density						
High	11.6 ± 8.0	31.4 ± 17.0	17.4 ± 9.0	41.4 ± 19.0	51.1 ± 35.9	9
Low	9.1 ± 9.0	33.0 ± 10.0	15.4 ± 5.0	42.3 ± 13.0	61.2 ± 86.8	45
Wind Speed						
High	11.4 ± 8.0	32.9 ± 15.2	17.8 ± 9.0	39.0 ± 16.7	52.0 ± 50.6	16
Low	10.7 ± 8.9	29.0 ± 18.9	14.2 ± 5.7	47.6 ± 20.8	76.3 ± 39.1	38
Wind Direction						
Northwest	12.4 ± 8.0	29.7 ± 17.1	15.9 ± 8.0	43.5 ± 21.0	56.7 ± 56.6	33
Southeast	9.2 ± 8.0	35.0 ± 15.0	18.0 ± 8.0	38.5 ± 12.0	46.6 ± 24.9	21
Prey Accessibility						
High	21.2 ± 10.0	24.0 ± 14.0	17.9 ± 10.0	37.8 ± 17.0	127.1 ± 88.5	48
Low	9.9 ± 7.0	32.7 ± 16.0	16.6 ± 8.0	42.1 ± 19.0	43.5 ± 29.6	6

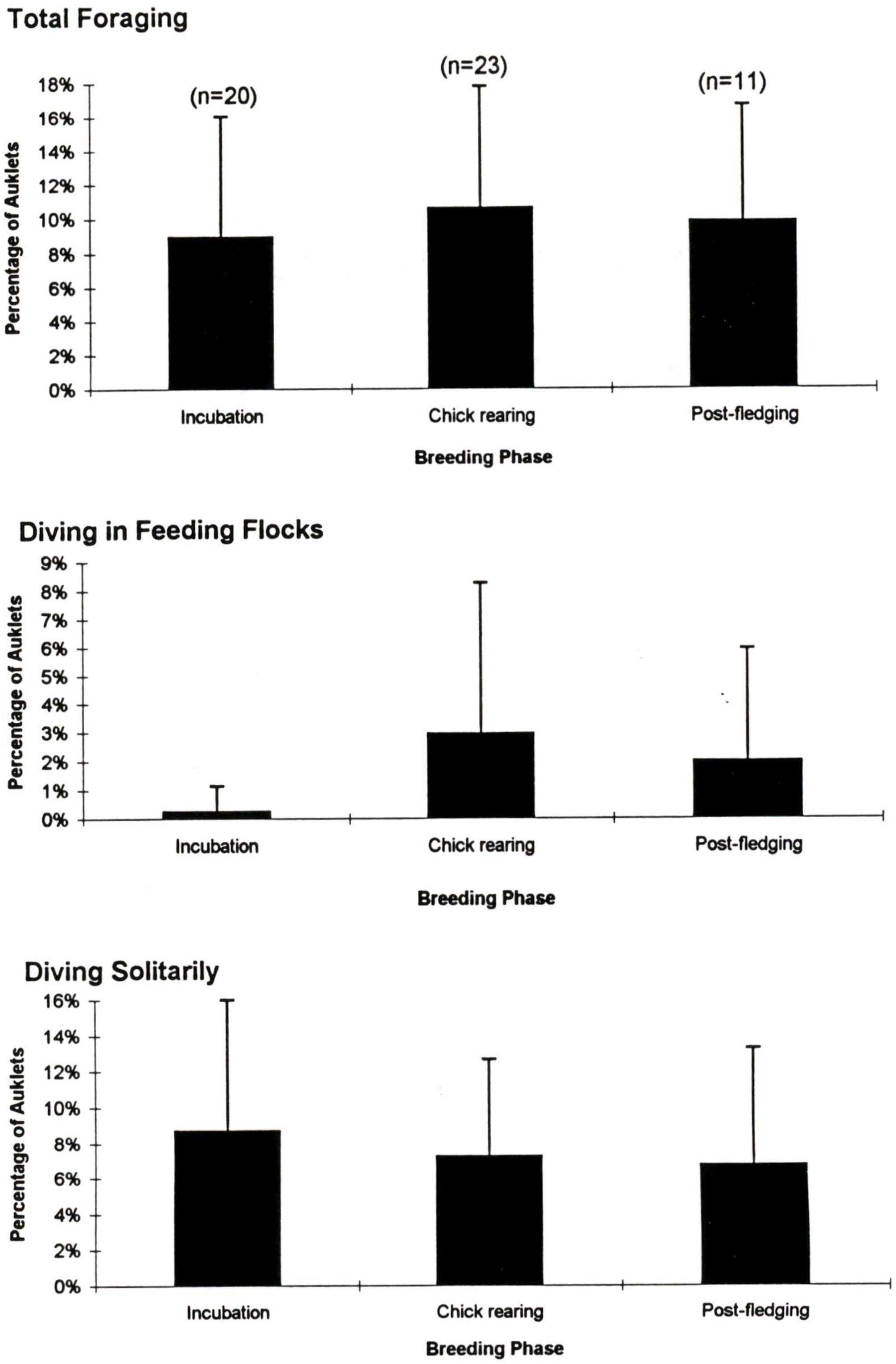


Fig. 2-1. The mean percentages of Rhinoceros Auklets foraging per day (+ SD) in each breeding phase during the 1996 auklet breeding season. The sample size (n) is the number of days.

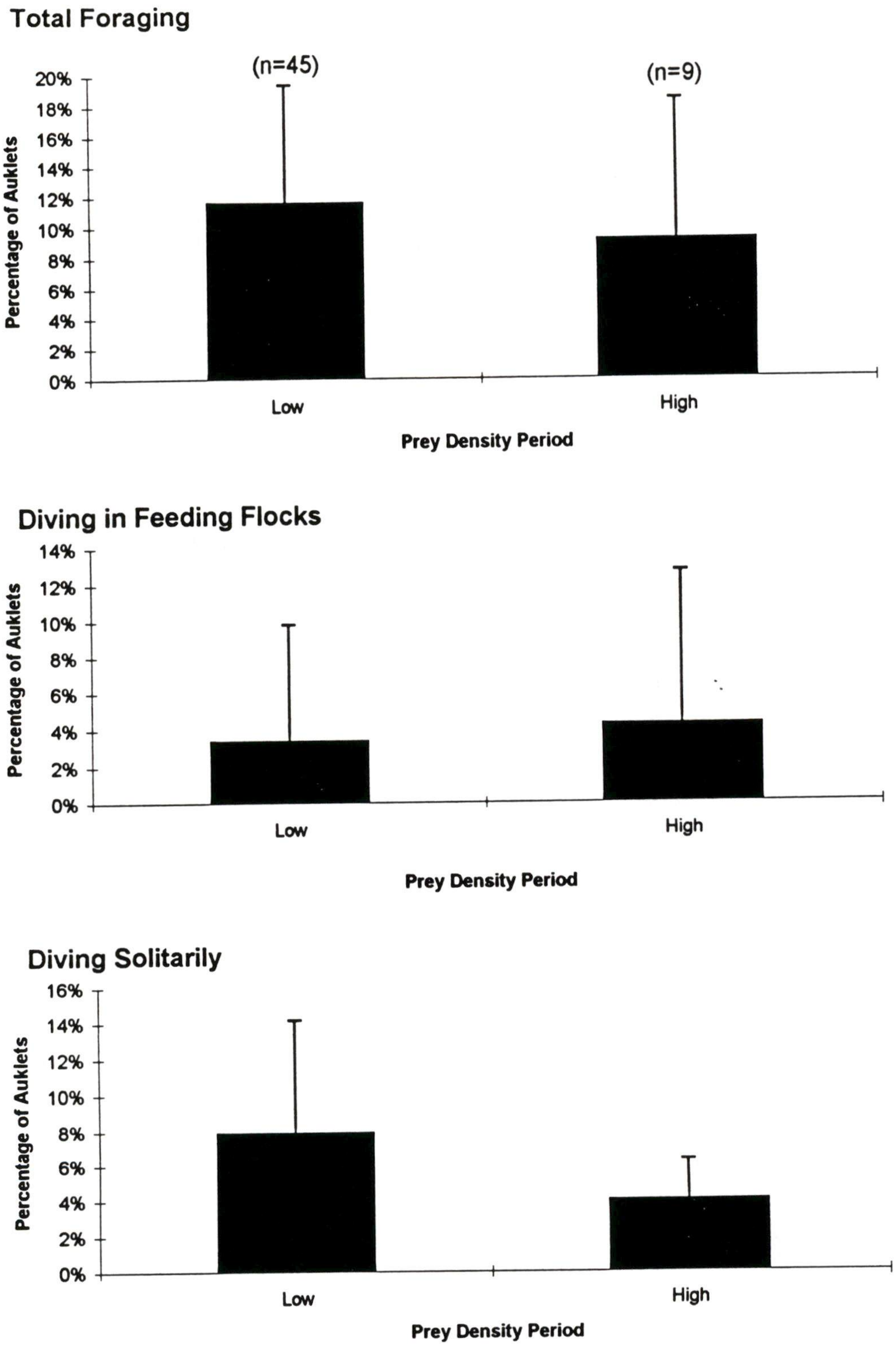


Fig. 2-2. The mean percentages of Rhinoceros Auklets foraging per day (+ SD) in each prey density period during the 1996 auklet breeding season. The sample size (n) is the number of days.

higher percentage of auklets flock diving (Fig. 2-3; Appendix 2-3). The number of feeding flocks also increased significantly during this period (Fig. 2-4).

WEATHER

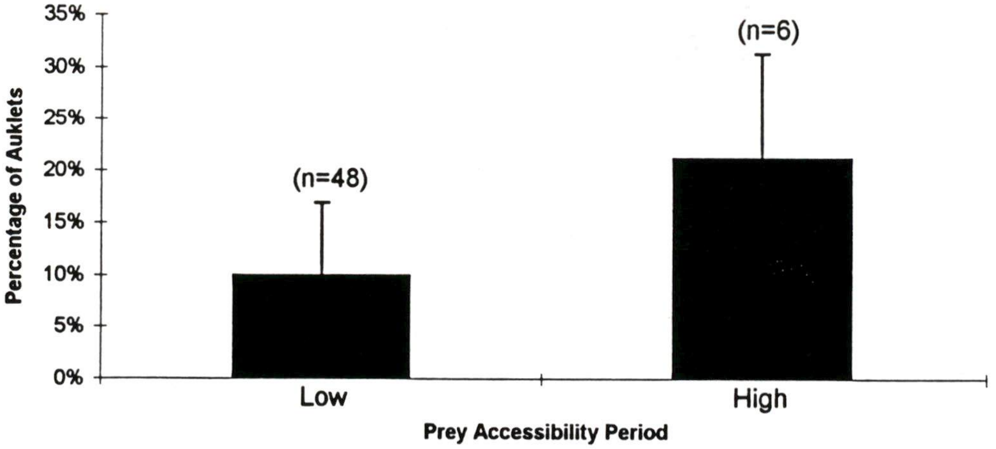
The percentage of auklets engaged in each activity did not change with wind direction or wind speed (Table 2-1; Appendix 2-3). The number of auklets flying, however, was significantly higher during high wind speed periods, relative to low wind speed periods, and was significantly higher during northwest wind periods, relative to southeast wind periods. In addition, there was a significant interaction among prey accessibility and wind speed and among prey accessibility and wind direction for the number of auklets flying. Both of these interactions were disordinal for both factors, showing that the number of auklets flying is influenced by a combination of these three factors.

SCAN DATA - DAILY

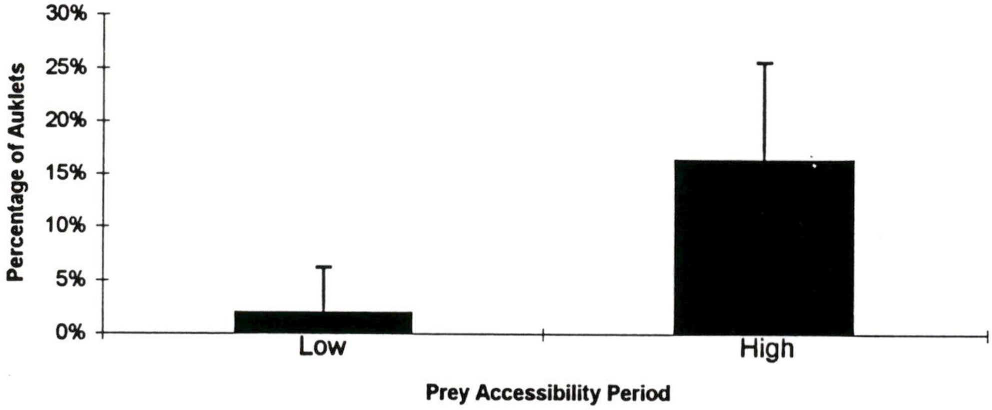
TIME OF DAY

During incubation, the percentage of auklets Foraging differed significantly between the time of day categories, being highest in the evening, compared to earlier in the day (Table 2-2; Appendix 2-4). This increase in auklets Foraging in the evening was primarily due to a significantly higher percentage of auklets diving solitarily, whereas flock diving was low throughout the day and peaked in the afternoon (Fig. 2-5).

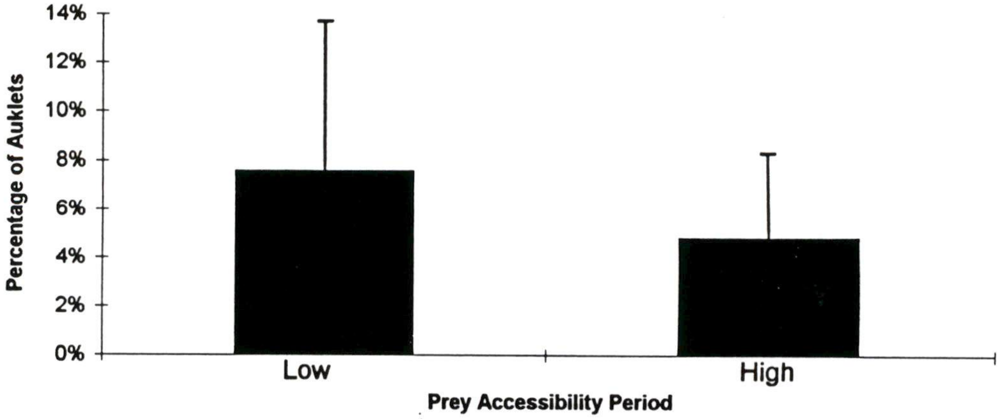
During chick rearing, the percentage of auklets Foraging also differed significantly between the time of day categories, being higher in the afternoon and evening categories (Table 2-2). This increase in auklets Foraging later in the day was again due to a significantly higher percentage of solitary diving, whereas flock diving decreased throughout the day (Fig. 2-6). The number of adults holding fish, presumably for delivery to chicks, also increased significantly during this evening category (Fig. 2-7). The number of auklets flying was significantly lower during this evening category, as were the total number of auklets on the water and the mean group sizes of auklets (Fig. 2-8; Appendix 2-4).



Total Foraging



Diving in Feeding Flocks



Diving Solitarily

Fig. 2-3. The mean percentages of Rhinoceros Auklets foraging per day (+ SD) in each prey accessibility period during the 1996 auklet breeding season. The sample size (n) is the number of days.

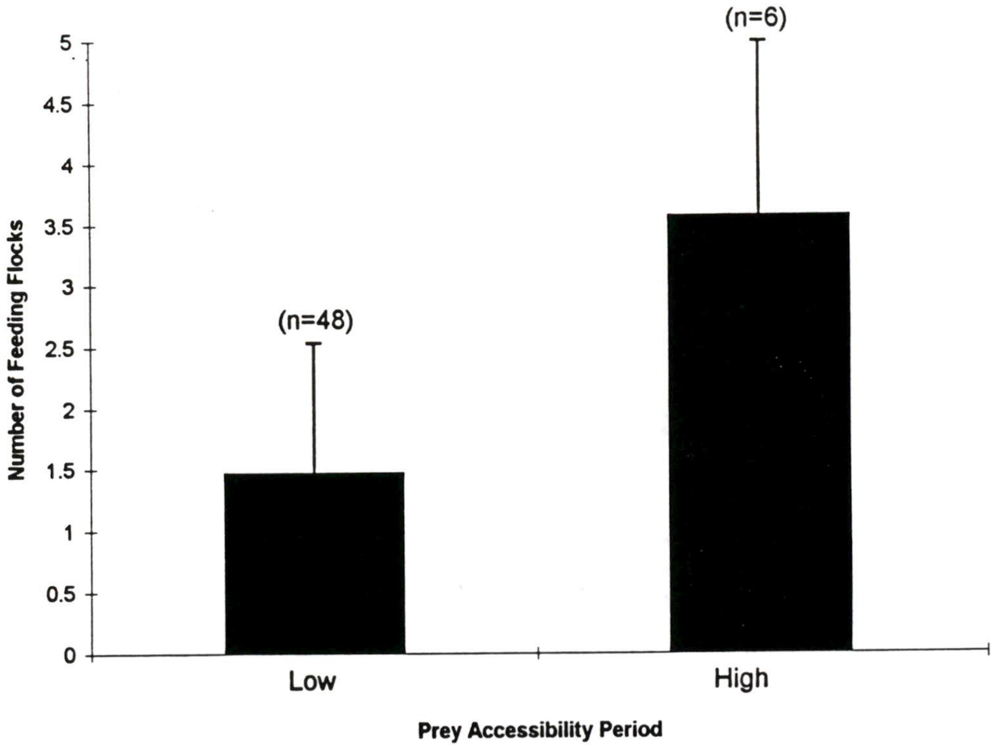


Fig. 2-4. Mean number feeding flocks containing Rhinoceros Auklets per day (+ SD) in each prey accessibility period during the 1996 chick rearing phase. Sample size (n) is the number of days.

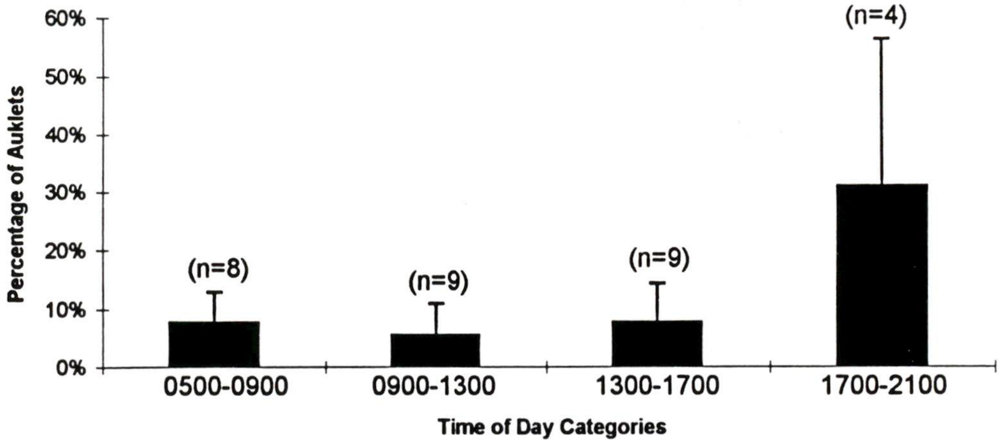
Table 2-2. The percentage of Rhinoceros Auklets engaged in the four activity categories (± SD) and the mean number of auklet flying in each breeding phase per daily category (± SD) in the 1996 breeding season. Sample size (n) is the number of hourly scans

	Percentages (%)				Numbers	
Category	Foraging	Resting	Maintaining	Swimming	Flying Birds	n
Incubation						
Time of Day						
0500-900	7.6 ± 5.0	47.5 ± 21.0	24.0 ± 9.0	22.5 ± 16.0	74.9 ± 31.8	8
0900-1300	5.4 ± 5.0	48.8 ± 19.0	23.0 ± 9.0	24.8 ± 24.0	91.3 ± 50.9	9
1300-1700	7.7 ± 7.0	49.5 ± 19.0	13.2 ± 6.0	30.7 ± 16.0	51.7 ± 31.6	9
1700-2100	30.9 ± 25.0	22.3 ± 21.0	25.1 ± 15.0	23.2 ± 11.3	25.0 ± 13.7	4
Tidal Stage						
Low	12.4 ± 12.0	48.6 ± 21.0	20.5 ± 10.0	19.7 ± 13.0	90.0 ± 60.7	7
Flood	10.7 ± 8.0	42.4 ± 21.0	18.0 ± 9.0	30.2 ± 17.0	52.5 ± 29.1	9
High	4.4 ± 4.0	55.7 ± 20.0	21.6 ± 12.0	19.7 ± 19.0	81.7 ± 36.4	6
Ebb	11.8 ± 10.0	37.5 ± 24.0	22.9 ± 12.0	30.5 ± 27.0	49.3 ± 33.4	8
Sea state						
1	6.3 ± 5.0	35.5 ± 19.0	28.4 ± 13.0	30.5 ± 12.0	69.7 ± 45.0	3
2	7.6 ± 7.0	52.5 ± 19.0	19.2 ± 13.0	21.4 ± 5.0	46.0 ± 20.8	3
3	9.7 ± 9.0	48.1 ± 25.0	22.7 ± 10.0	21.9 ± 20.0	94.6 ± 53.5	9
4	10.0 ± 5.0	45.2 ± 17.0	19.1 ± 11.0	27.4 ± 19.0	55.8 ± 31.5	12
5	18.4 ± 6.0	39.2 ± 26.0	14.2 ± 1.0	29.9 ± 27.0	39.7 ± 32.3	3
Chick Rearing						
Time of Day						
0500-900	3.8 ± 3.0	38.9 ± 23.0	10.5 ± 7.0	49.6 ± 28.0	43.0 ± 34.6	9
0900-1300	3.8 ± 3.0	35.9 ± 19.0	20.4 ± 20.0	42.4 ± 19.0	61.9 ± 48.8	15
1300-1700	10.4 ± 10.0	28.4 ± 22.0	14.0 ± 13.0	49.6 ± 22.0	64.2 ± 43.5	24
1700-2100	18.0 ± 14.0	24.2 ± 20.0	10.9 ± 10.0	49.3 ± 25.0	25.5 ± 13.2	25
Tidal Stage						
Low	5.5 ± 5.0	28.4 ± 22.0	12.6 ± 9.0	56.9 ± 32.0	42.7 ± 22.9	11
Flood	14.5 ± 14.0	29.3 ± 20.0	13.0 ± 12.0	44.8 ± 16.0	45.2 ± 41.0	26
High	7.3 ± 7.0	30.7 ± 20.0	16.0 ± 10.0	47.9 ± 22.0	61.1 ± 54.0	14
Ebb	11.5 ± 10.0	30.5 ± 23.0	14.1 ± 14.0	47.3 ± 26.0	45.0 ± 34.2	22
Sea state						
1	7.9 ± 7.0	33.7 ± 23.0	24.8 ± 24.0	37.3 ± 24.0	59.7 ± 59.6	10
2	7.2 ± 7.0	37.7 ± 23.0	9.4 ± 7.0	47.5 ± 19.0	65.6 ± 53.8	14
3	9.8 ± 9.0	31.5 ± 21.0	15.0 ± 14.0	46.1 ± 23.0	47.0 ± 26.0	17
4	11.5 ± 10.0	27.7 ± 20.0	12.6 ± 9.0	50.4 ± 24.0	39.0 ± 27.4	19
5	17.4 ± 16.0	18.9 ± 16.0	10.3 ± 8.0	55.4 ± 23.0	33.6 ± 25.1	13

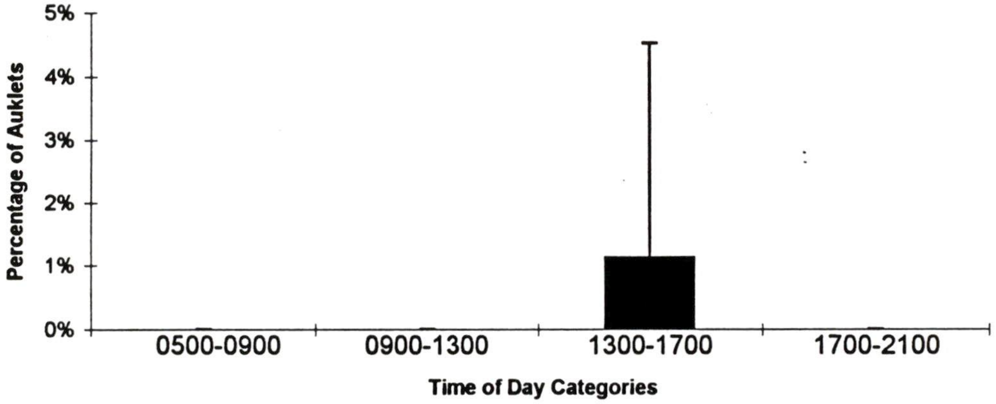
Table 2-2 continued

Category	Percentages (%) Foraging	Resting	Maintaining	Swimming	Numbers Flying Birds	n
Post-fledging						
Time of Day						
0500-900	24.6 ± 19.0	20.8 ± 12.0	23.9 ± 23.0	32.4 ± 15.0	10.6 ± 8.9	5
0900-1300	10.2 ± 7.0	21.1 ± 14.0	19.3 ± 10.0	50.3 ± 16.0	11.8 ± 11.7	13
1300-1700	4.5 ± 4.0	29.6 ± 18.0	19.8 ± 8.0	47.9 ± 24.0	12.8 ± 11.1	9
1700-2100	7.1 ± 7.0	36.5 ± 16.0	19.3 ± 7.0	38.6 ± 25.0	13.3 ± 14.9	6
Tidal Stage						
Low	16.6 ± 16.0	30.3 ± 20.0	16.5 ± 5.0	38.0 ± 18.0	16.6 ± 16.5	8
Flood	8.0 ± 7.0	19.3 ± 14.0	25.4 ± 17.0	49.4 ± 23.0	10.1 ± 9.8	12
High	9.7 ± 7.0	25.3 ± 10.0	18.4 ± 11.0	47.6 ± 20.0	12.2 ± 8.7	6
Ebb	7.7 ± 7.0	34.0 ± 15.0	16.8 ± 5.0	42.5 ± 19.0	10.7 ± 10.6	7
Sea state						
1	11.6 ± 7.0	29.0 ± 17.0	20.0 ± 6.0	40.4 ± 17.0	20.7 ± 17.1	12
2	12.6 ± 7.0	19.9 ± 18.0	18.9 ± 9.0	49.8 ± 20.0	12.8 ± 8.2	5
3	12.3 ± 12.0	25.2 ± 15.0	21.6 ± 19.0	43.1 ± 22.0	5.9 ± 4.5	10
4	2.4 ± 2.0	27.6 ± 15.0	19.1 ± 11.0	52.5 ± 24.0	5.2 ± 4.6	6
5	-	-	-	-	-	0

Total Foraging



Diving in Feeding Flocks



Diving Solitarily

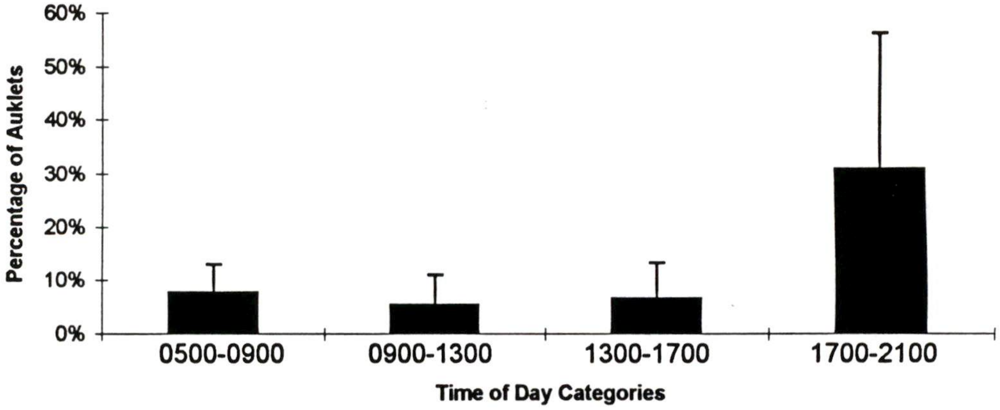


Fig. 2-5. The mean percentages of Rhinoceros Auklets foraging (+ SD) in each time of day category during the 1996 incubation phase. Sample size (n) is the number of hourly scans.

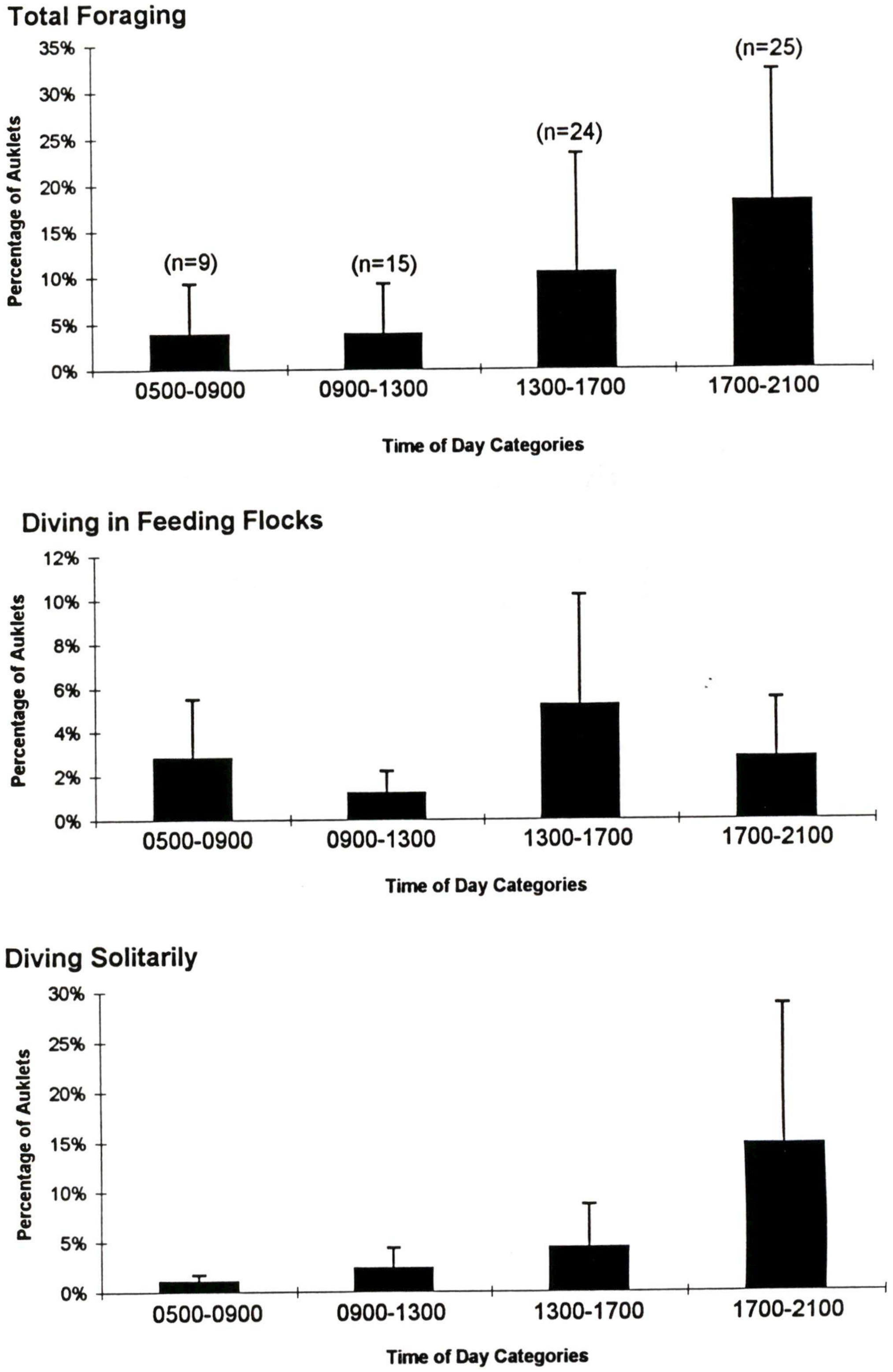


Fig. 2-6. The mean percentages of Rhinoceros Auklets foraging (+ SD) in each time of day category during the 1996 chick rearing phase. Sample size (n) is the number of hourly scans.

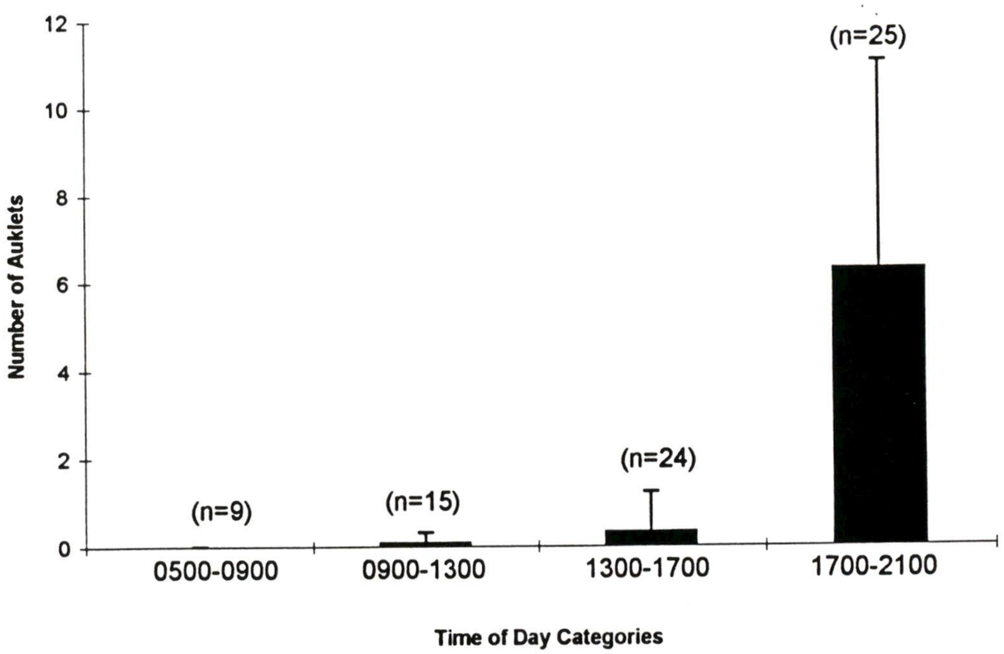
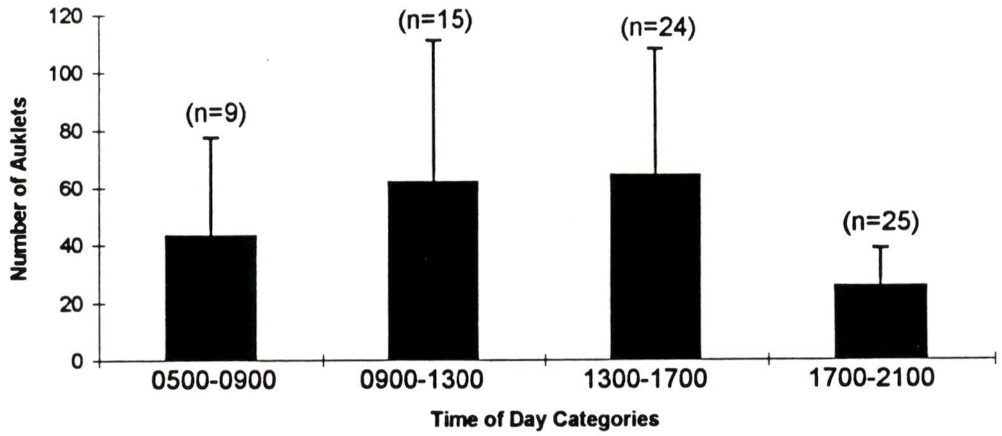
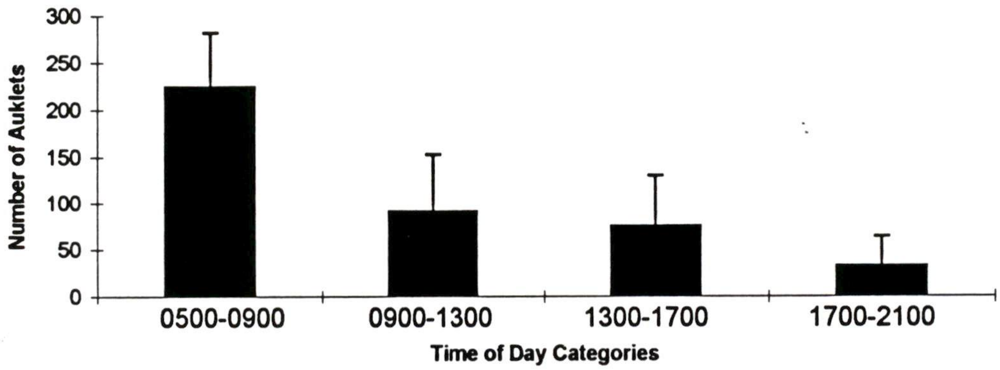


Fig. 2-7. Mean number of Rhinoceros Auklets holding fish (+ SD) in each time of day category during the 1996 chick rearing phase (ANOVA, F=26.030, n=72, P<0.0001). Sample size (n) is the number of hourly scans.

Number of Auklets Flying



Number of Auklets on the Water



Group Size of Auklets

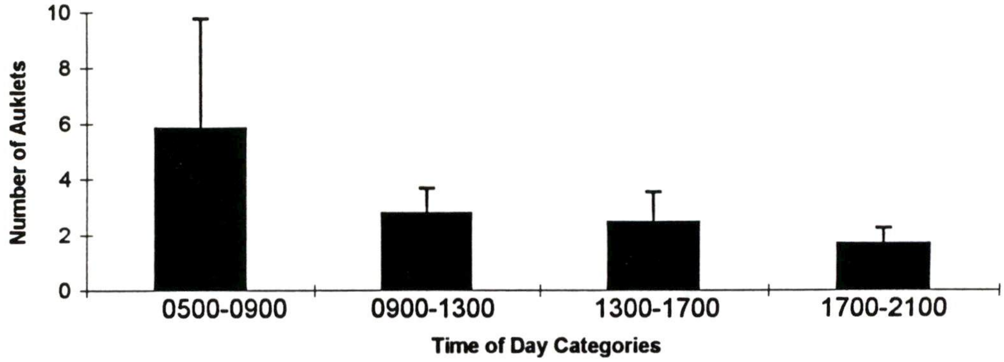


Fig. 2-8. The mean number of Rhinoceros Auklets (+ SD) in each time of day category during the 1996 chick rearing phase. Sample size (n) is the number of hourly scans.

During post-fledging, the percentage of auklets Foraging also differed significantly between the time of day categories, being highest in the early morning category, compared to later in the day (Table 2-2). This decrease in auklets Foraging throughout the day was primarily due to both lower percentages of auklets solitary and flock diving (Fig. 2-9). There was, however, a significant interaction among time of day and tidal stage for solitary diving. This interaction was ordinal for both factors, suggesting that the main factors effects can be interpreted separately (Keppel 1973).

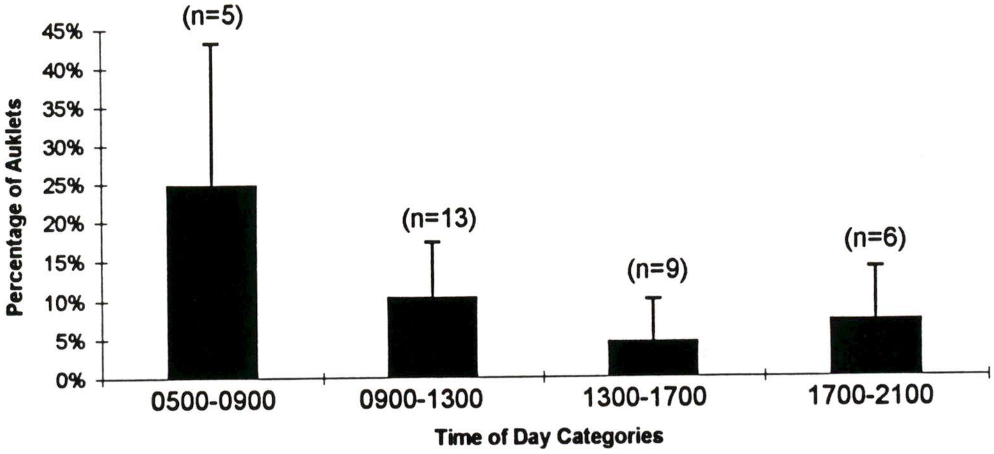
TIDAL STAGE

During incubation, percentages of auklets engaged in each activity did not change with tidal stages (Table 2-2; Appendix 2-4). During chick rearing, however, the percentage of auklets Foraging was significantly higher during flood and ebb tidal stages, primarily due to a significant increase in the percentage of auklets flock diving, compared to the high and low tidal stages (Fig. 2-10). Solitary diving showed a similar trend. The number of feeding flocks being formed in the study area was significantly higher at the flood tidal stage, compared to other stages (Fig. 2-11). There were also significant interactions among tidal stage and time of day for both the percentage of auklets Resting and Swimming. During post-fledging, a significant interaction among tidal stage and time of day was also observed for the percentage of auklets Maintaining. All of these interactions for each factor were disordinal, suggesting that the combination of time of day and tidal stage has a significant effect on these activities and, thus, these factors should not be interpreted separately.

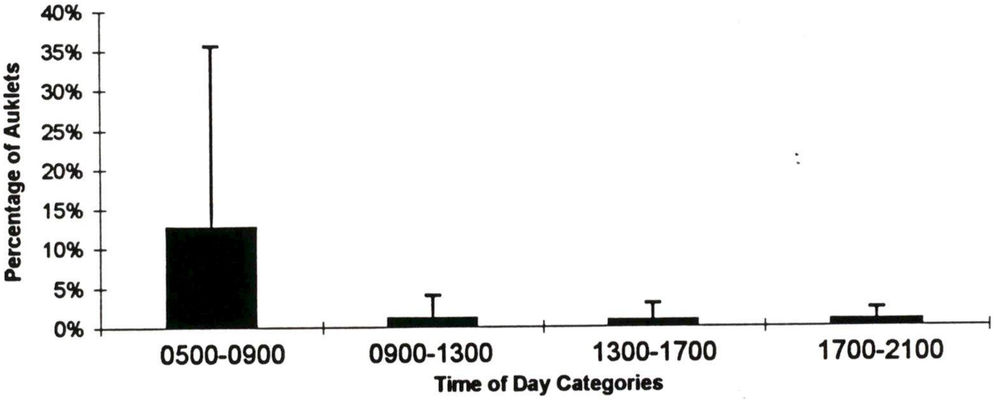
SEA STATE

During incubation, percentages of auklets engaged in each activity did not change with sea state (Table 2-2; Appendix 2-4). During chick rearing, however, the percentage of auklets Foraging was higher at the highest sea state (5 on Beaufort scale 0-9), primarily due to a significantly higher percentage of auklets flock diving at high sea states, than at lower sea states (Fig. 2-12). The total number of auklets observed on the water declined

Total Foraging



Diving in Feeding Flocks



Diving Solitarily

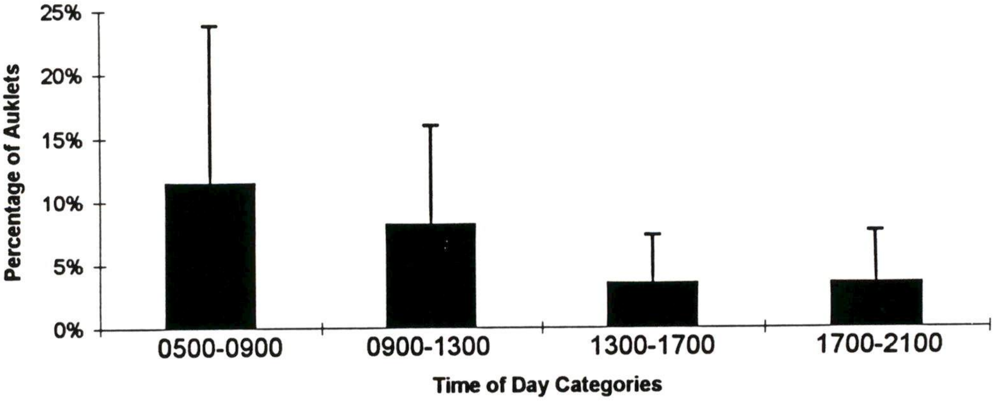


Fig. 2-9. The mean percentages of Rhinoceros Auklets foraging (+ SD) in each time of day category during the 1996 post-fledging phase. Sample size (n) is the number of hourly scans.

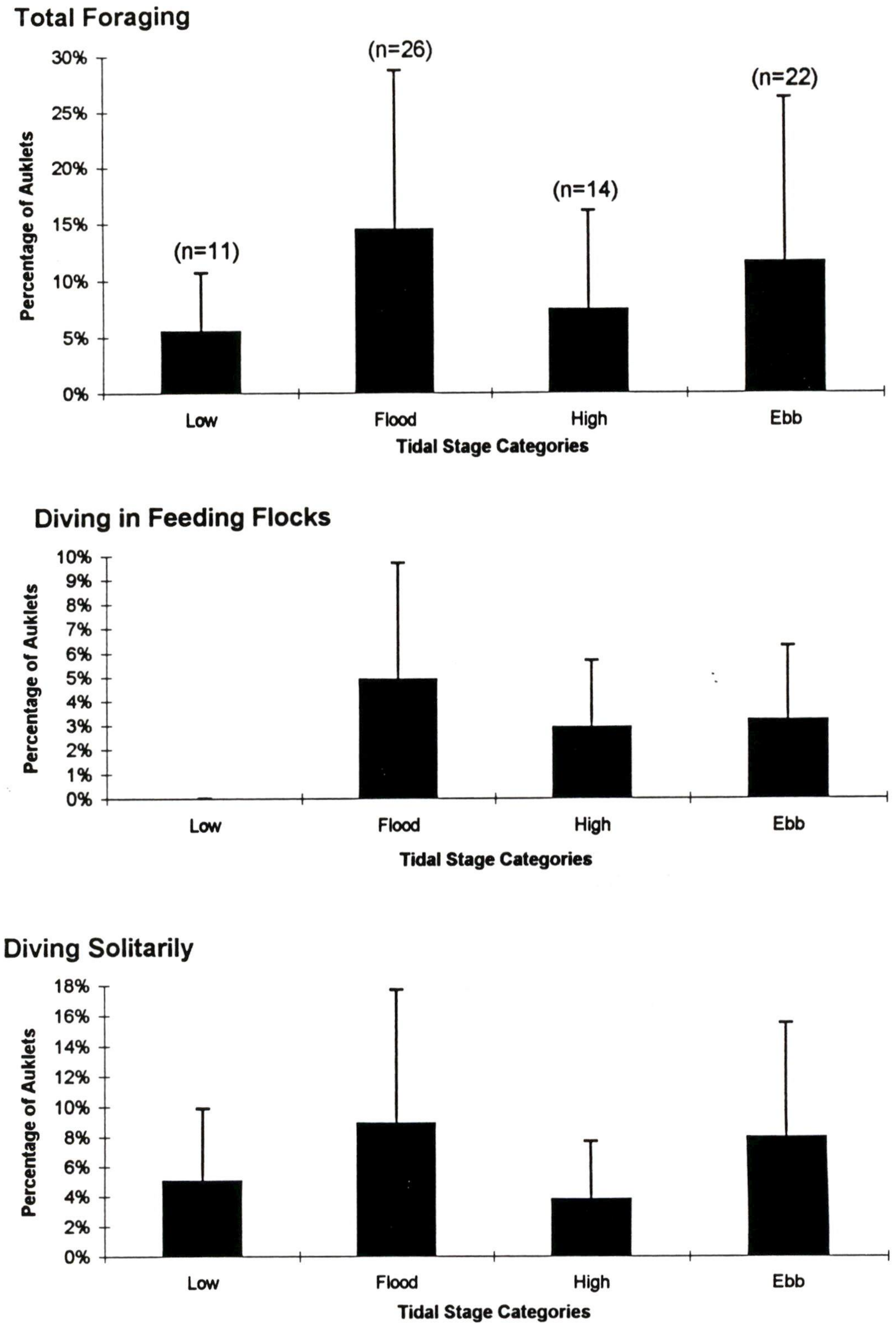


Fig. 2-10. The mean percentages of Rhinoceros Auklets foraging (+ SD) in each tidal stage category during the 1996 chick rearing phase. Sample size (n) is the number of hourly scans.

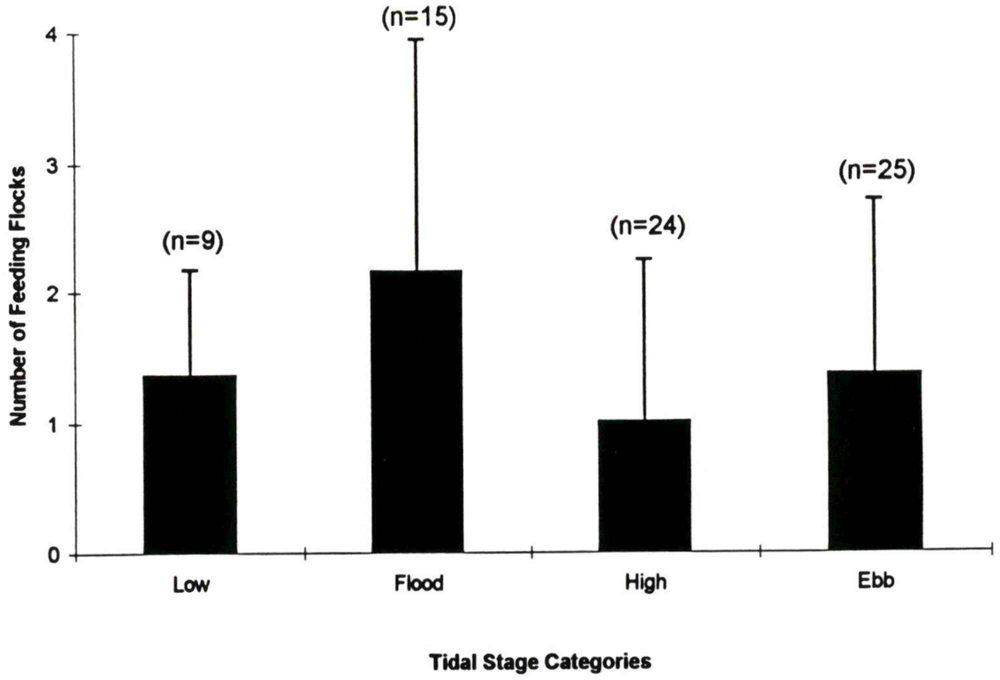


Fig. 2-11. Mean number feeding flocks containing Rhinoceros Auklets (+ SD) in each tdial stage category during the 1996 chick rearing phase. Sample size (n) is the number of hourly scans.

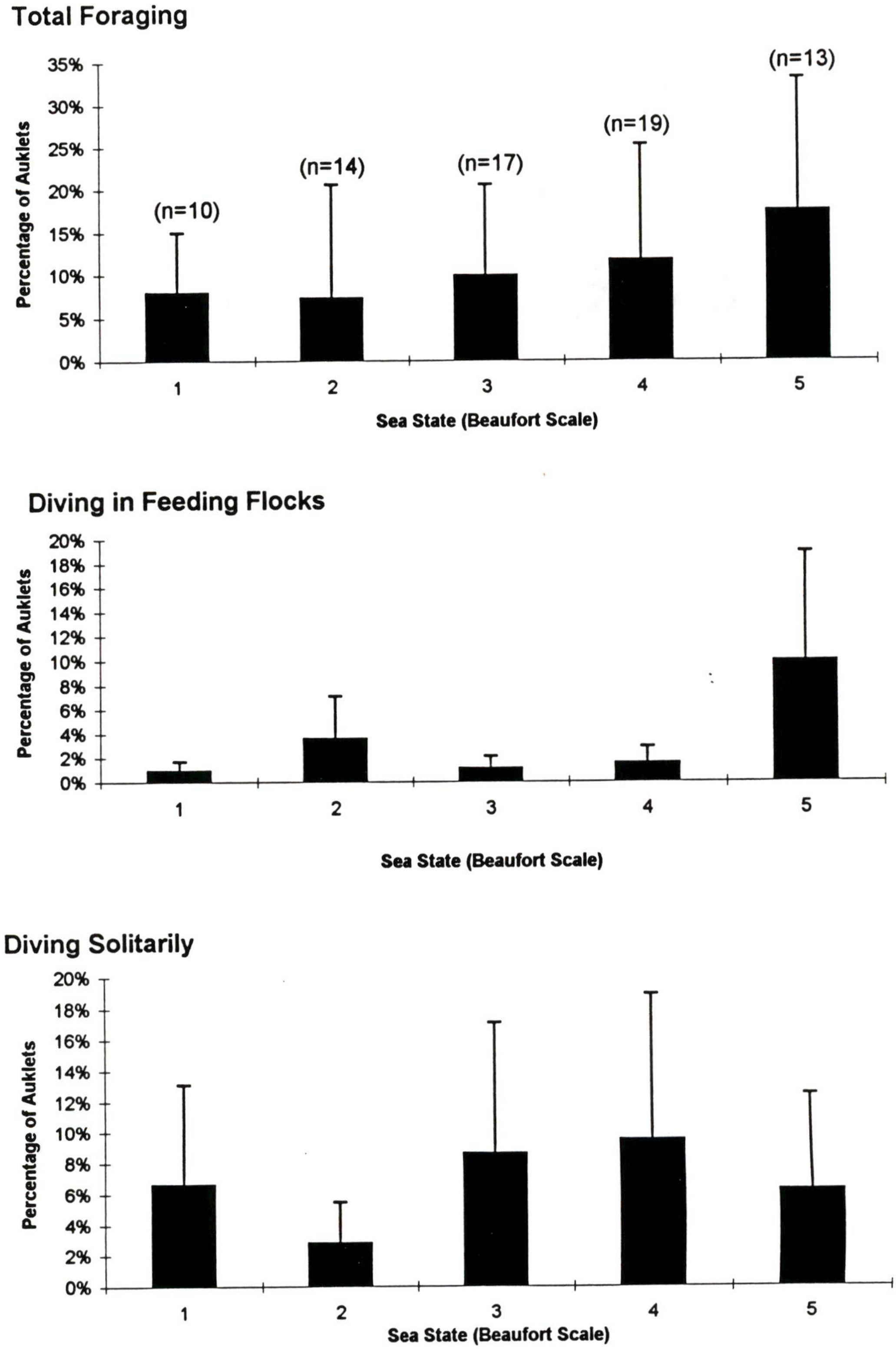


Fig. 2-12. The mean percentages of Rhinoceros Auklets foraging (+ SD) in each sea state category during the 1996 chick rearing phase. Sample size (n) is the number of hourly scans.

with increasing sea state. During post-fledging, percentages of auklets Foraging, flock diving and solitary diving were lowest at high sea states (Fig. 2-13).

FOCAL DATA

The durations of dives did not differ significantly between seasons or days (Table 2-3; Appendix 2-5). In contrast, the durations of pauses were highest at high sea states (Beaufort 5). The durations of pauses also differed significantly among the three breeding phases, being higher during incubation than during chick rearing and post-fledging (Table 2-3).

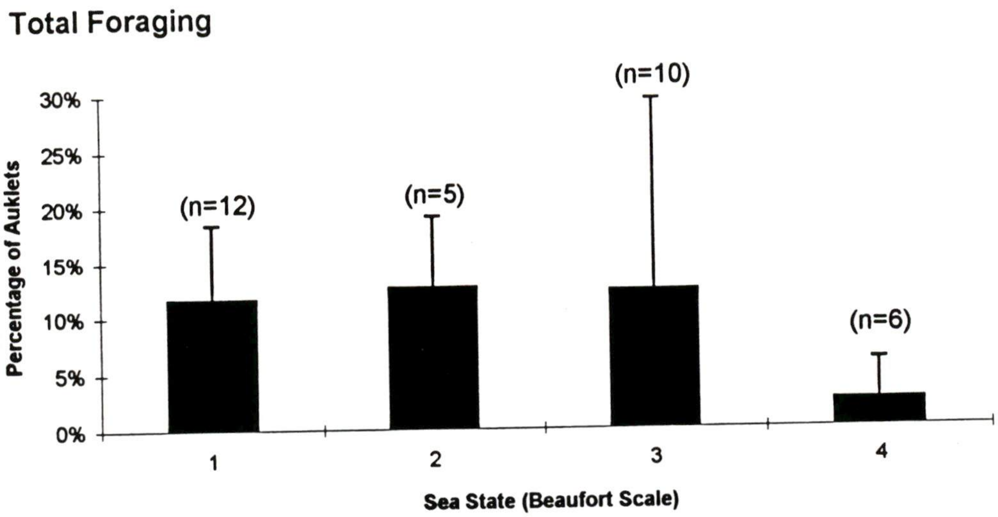
DISCUSSION

SEASONAL

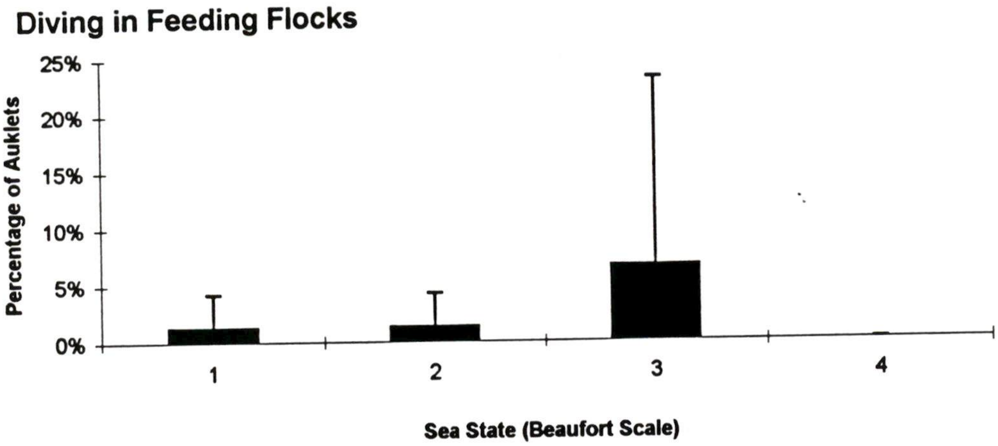
EFFECTS OF BREEDING PHASE

Auklets must collect prey items for both themselves and their chicks during chick rearing; thus the percentage of auklets Foraging was generally expected to increase during chick rearing. The percentage of auklets Foraging, however, did not increase. Instead a higher percentage of auklets were flock diving during chick rearing, relative to the two other breeding phases. These auklets and other seabirds are known to forage in feeding flocks to a high degree during chick rearing. For instance, Burger et al. (1993) reported that Rhinoceros Auklets rearing chicks spent 90% of their underwater time in the top 10 m of the water column. The high use of feeding flock is reflected by auklets foraging primarily in surface waters because feeding flocks form where fish are concentrated at the ocean's surface (Porter and Sealy 1982; Hoffman et al. 1981). In addition, Hoffman et al. (1981) observed flock diving to be frequent in coastal areas during chick rearing, with both breeding and nonbreeding birds of several different species participating regularly in flocks.

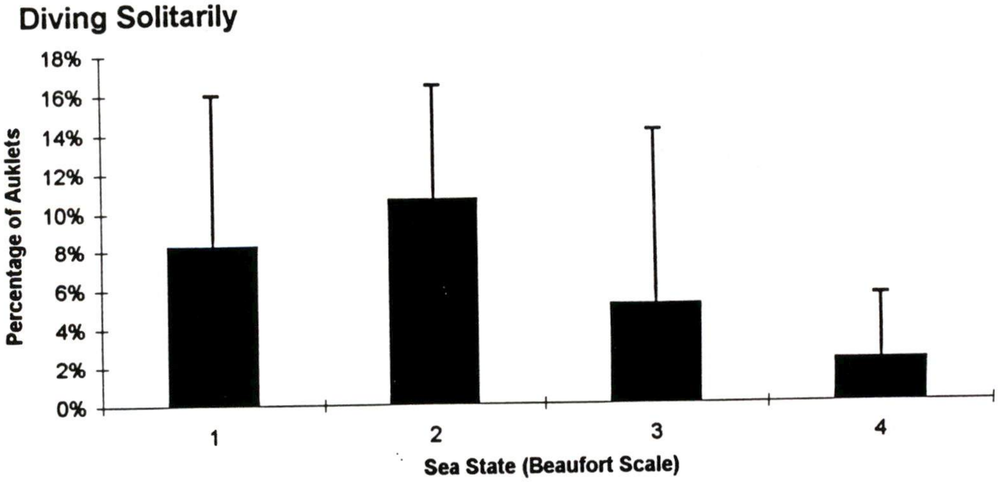
Many seabird species cue to the foraging activities of others ('local enhancement'; Wittenberger and Hunt 1985) because prey patches are unpredictably distributed and birds are unable to deplete prey numbers within fish schools (Hoffman et al. 1981; Porter and



Total Foraging



Diving in Feeding Flocks



Diving Solitarily

Fig. 2-13. The mean percentages of Rhinoceros Auklets foraging (+ SD) in each sea state category during the 1996 post-fledging phase. Sample size (n) is the number of hourly scans.

Table 2-3. Mean dive and inter-dive recovery (pause) durations (± SD) of Rhinoceros Auklets in different breeding phases, life history stages and prey density periods during the 1996 breeding season. Sample size (n) is the number of individual auklets observed diving

Category	Mean Dive Duration (s)	Mean Pause Duration (s)	n
Seasonal Categories			
Breeding Phase			
Incubation	41.6 ± 17.0	21.2 ± 21.1	41
Chick Rearing	35.2 ± 12.3	8.0 ± 5.5	56
Post-fledging	37.6 ± 13.5	7.3 ± 3.7	16
Breeding Stage			
Adults - without fish	38.8 ± 14.8	14.8 ± 14.7	80
Adults - with fish	35.1 ± 13.7	7.7 ± 5.3	29
Juveniles	39.5 ± 14.8	6.5 ± 4.3	4
Prey Density			
High	35.9 ± 6.2	14.3 ± 14.2	15
Low	38.2 ± 15.4	12.4 ± 12.3	98
Wind Direction			
Northwest	38.5 ± 15.8	12.7 ± 12.6	79
Southeast	36.5 ± 11.1	12.5 ± 12.4	34
Prey Accessibility			
High	43.9 ± 17.1	10.5 ± 7.2	7
Low	37.5 ± 14.3	12.8 ± 19.1	106
Daily Categories			
Time of Day			
0500-900	33.8 ± 12.0	6.7 ± 3.3	6
0900-1300	39.3 ± 15.8	18.8 ± 18.7	29
1300-1700	39.0 ± 15.8	10.8 ± 7.7	17
1700-2100	37.3 ± 14.0	10.9 ± 15.1	61
Tidal Stage			
Low	38.4 ± 14.2	9.8 ± 6.3	20
Flood	36.8 ± 14.7	15.3 ± 15.2	44
High	43.7 ± 13.7	12.6 ± 12.5	21
Ebb	34.8 ± 14.6	10.6 ± 10.5	28
Sea state			
1	38.8 ± 7.4	7.4 ± 4.7	17
2	36.2 ± 13.7	7.7 ± 5.8	31
3	33.5 ± 14.7	22.8 ± 22.7	27
4	41.6 ± 18.6	9.5 ± 9.4	26
5	42.5 ± 12.2	17.1 ± 14.0	12

Sealy 1982; Greene 1987; Burger 1997; Evans 1983). This allows the exploitation of readily accessible prey. The combination of both a number of different food-finding techniques of various seabird species and a higher number of birds searching for prey may act together to increase each individual's probability of locating a prey patch (Horn 1968; Perrins and Birkhead 1983; Clark and Mangel 1984). Searching activities of auklets (e.g. diving and flying) are energetically expensive (Gaston 1985); thus, higher flock diving during chick rearing may effectively reduce the amount of time and energy required to locate prey patches, allowing more resource allocation to provisioning. Thus, although auklets were collecting prey items for both themselves and their chicks, by increasing the use of mixed-species feeding flocks, the percentage of auklets Foraging remained at levels consistent with the other breeding phases.

EFFECTS OF PREY AVAILABILITY

During periods of low prey density and abundance, it is presumably more difficult to locate prey patches; thus, the time spent engaged in foraging-related activities should increase (Kramer and Weary 1991). In this study, a significantly higher percentage of auklets was engaged in solitary diving when prey densities were low, relative to high prey density periods, but the percentage of auklets flock diving did not change among prey density periods. This suggests that auklets are capable of increasing the time spent foraging under varying levels of prey density and abundance.

During periods of low prey density, the percentage of auklets flock diving remained consistent with high prey density periods. In contrast, I expected flock diving to increase in response to higher energetic demands during periods of low prey density because flock diving is less energetically expensive and provides information about patch locations and qualities at a faster rate. Fish schools exploited at feeding flocks were, however, initially found by an individual diving solitarily and prey patches were presumably harder to locate during low prey density periods; thus, more solitary diving was probably required to locate prey during periods of low prey density and abundance. In contrast, significantly more flock diving occurred during periods when fish schools were observed in surface waters (the high prey accessibility period). This suggests that flocking behaviour may be driven by the accessibility of prey schools at the ocean's surface, rather than in response to increased energetic demands imposed by decreased prey density and abundance in an area. Overall, this suggests that auklets shift their foraging strategies according to the accessibility of their prey. Auklets, however, may not be able to shift to flock diving during periods of low prey density and abundance and must increase the time spent foraging because infrequent encounters with surface schools result in the formation of fewer feeding flocks.

DAILY

EFFECTS OF TIME OF DAY

A diurnal shift in foraging patterns was exhibited during chick rearing: auklets mainly foraged in feeding flocks during the day (0600-1700) and then shifted to solitary diving in the late afternoon (1700-dusk). This shift in foraging strategies probably is not associated with diurnal fluctuations in prey density and abundance (chapter 1) but instead with the nocturnal provisioning behaviour of auklets. This is likely because the number of auklets holding fish on the water, presumably for delivery to chicks, increased after the shift to solitary diving. In addition, those auklets holding fish were observed to dive only solitarily. Consequently, adults mainly collected fish for chicks by diving solitarily in the evening, whereas adults mainly fed themselves by diving in mixed-species feeding flocks earlier in the day.

Auklets may not have collected meals of chicks by diving in mixed-species feeding flocks for a number of reasons. First, prey found at feeding flocks may be unsuitable for meals of chicks. In support, only juvenile fish were found at feeding flocks; therefore, if auklets selected larger fish for delivery to chicks, they may have been forced to dive solitarily. Second, solitary diving may be preferred when adults have to hold fish in their beaks to avoid kleptoparasitism by gulls. Rhinoceros Auklets and other alcids have rarely been observed to surface with fish in their bills while foraging in mixed-species feeding flocks (Mahon et al. 1992; Grover and Olla 1983; Sealy 1973) and those which surfaced with fish were subject to kleptoparasitic attacks by gulls (Hoffman et al. 1981). When collecting meals of chicks, requiring fish to be held in bills, murres tended to surface further from the center of the flocks (Hoffman et al. 1981). Similarly, other alcids do not dive in feeding flocks to collect meals of chicks (e.g. Marbled Murrelets, Mahon et al. 1992). Kleptoparasitism on auklets was not observed in this study but auklets may have avoided this by swallowing prey underwater. Overall, it is likely that these two factors (e.g. kleptoparasitism and unsuitable prey) affected the choice of foraging strategies when collecting meals of chicks.

Diurnal foraging behaviours of auklets during incubation and chick rearing were similar, with most auklets foraging at the end of the day. In contrast, during post-fledging, the percentage of auklets Foraging peaked at dawn and then decreased throughout the day. This change in auklet behaviour observed in post-fledging may be due to a combination of factors. First, the time constraints and provisioning demands on auklets changed from incubation and chick rearing to post-fledging. For instance, during post-fledging, auklets were no longer highly active at night since they were not returning to the colony. This may have allowed them to be more active in the morning, compared to the two previous breeding phases. Second, herring did not appear to be present in the study area during post-fledging, leaving sand lance as the primary feeding flock species (chapter 1). Sand lance are thought to be most vulnerable during the dawn transition, when they move to the water column from their sandy bottom refuges (Hobson 1986). This vulnerability is thought to be due to smaller school sizes, since some fish are still buried, and due to the partial emergence of fish from the sand, a position from which they can be flushed easily from sediments (Hobson 1986; Girsa and Danilov 1978). Evidence of this vulnerability has been shown by higher sand lance catches in the morning (this study; Burger and Piatt 1990, in Newfoundland). Thus, auklets may have been concentrating their foraging efforts during the morning to take advantage of this predictable prey source.

EFFECTS OF SEA STATE

Although most of the significant changes in auklet behaviour with sea state can be attributed to the low visibility of auklets in rough sea conditions, the increased percentage of auklets flock diving at high sea states can not be attributed to this because mixed-species feeding flocks are highly conspicuous. The conspicuous nature of feeding flocks may have lead, however, to an overestimate of the percentage of auklets engaged in flock diving because all other nonconspicuous activities on the water were probably underestimated. Nonetheless, small scale temporal changes in prey availability have been reported with changing sea state conditions. During storms, zooplankton and fish are thought to be forced down farther in the water column, making them less accessible (Jangaard 1974; Meyer et al. 1979), resulting in lower prey capture rates in some seabirds (e.g. Dunn 1973). Under turbulent conditions, however, juvenile herring schools were found to be more concentrated in sheltered waters (Hourston 1958). Therefore, even though prey patches may have been more difficult to locate, once a patch was found it may have been large and highly concentrated. This again suggests that flock diving behaviour was driven primarily by the concentration of prey.

EFFECTS OF TIDAL STAGE

The percentage of auklets flock diving and the number of feeding flocks formed were highest during flood and ebb tides, but primarily during flood. Other seabird studies have shown high feeding rates during these tidal stages (e.g. Slater 1976). In addition, a study conducted in Alaska showed that the highest catches of sand lance were made during periods of the strongest tidal current flow, primarily during flood tides (Dick and Warner 1982). High activity and accessibility of fish during flood tides may be associated with the prey of these fish being brought into feeding areas, resulting in increased foraging activity of fish (Reay 1970). In support, mixed schools of juvenile sand lance and herring in Alaska were observed foraging during flood tides, at which time they were found near the ocean's surface (Hobson 1986). Fish schools are generally more dispersed when feeding, compared to when resting (Patridge 1982), and there is less time spent vigilant; thus, fish schools may be more vulnerable to predation when foraging. Consequently, the predictable nature of this increased vulnerability of foraging juvenile sand lance and herring may explain the more intense predatory behaviour of auklets at these stages.

SUMMARY

Overall, most environmental variables had relatively minor effects on the percentages of auklets engaged in each activity and also had little effect on the dive and pause durations of auklets. Flock diving seemed to increase in response to the size, density, accessibility and predictability of prey schools rather than in response to higher energetic demands imposed by low prey density and abundance in the study area. Auklets, however, appeared to increase flock diving during chick rearing, possibly to minimize energetic output during this phase. Solitary diving appeared to be driven by prey density and abundance in the study area, increasing as density decreased. Overall, this suggests that auklets have flexible time budgets and are able to shift foraging strategies to minimize provisioning demands and to take advantage of highly concentrated prey schools.

Flock diving appeared to be the main foraging strategy used to collect fish for self-feeding. Auklets switched from flock to solitary diving later in the day, reflecting a preference for solitary diving to collect fish for chicks or a preference for prey not normally found at feeding flocks. This is the first study to document different foraging strategies used by adults for self-feeding compared to chick provisioning in seabirds.

CHAPTER THREE

PREY-TRACKING BEHAVIOUR AND PATCH SCALES OF BREEDING RHINOCEROS AUKLETS

INTRODUCTION

Previous studies using standard marine transects showed that seabirds are patchily distributed at sea (Haney and Solow 1992). However, there has been variable success at determining the factors causing this distribution (Haney and Solow 1992). Many researchers believe it is a result of the patchy distribution of their prey but studies have shown a range from no correlations to strong correlations between seabird and prey densities at sea (Haney and Solow 1992). This variable strength of correlation of seabirds and prey densities is not surprising for a number of reasons. On a large scale, foraging habitats during the breeding season are generally restricted to areas around breeding colonies; thus seabirds may not show preferences for high prey density patches on a large scale. There is also evidence that breeding seabirds are capable of depleting local prey stocks surrounding breeding colonies, also causing weak positive correlations between seabirds and prey densities at larger scales (Ashmole 1963; Birt et al. 1987).

On a finer scale, seabirds may have problems maintaining current information on all prey patches in an area because they generally feed on patchily distributed prey, which change constantly in location and quality (Shettleworth et al. 1988; McNamara and Houston 1985). To deal with this problem, seabirds presumably must sample patches on a regular basis (Shettleworth et al. 1988) and, thus, are not always likely to be located with patches of high prey density (Clark and Mangel 1984; Hunt et al. 1990). Even if seabirds have a complete knowledge of the available prey patches in an area, it is unlikely that they would be correlated with prey when they were not actively tracking prey (e.g. resting) (Au and Pitman 1986). In support, diving seabirds spend generally less than 30% of their time at sea diving (e.g. Cairns et al. 1987; this study, chapter 2); therefore, transects conducted when seabirds are resting may not measure strong correlations between seabird and prey densities. In addition, variable correlation strength may result from errors associated with transect methods (e.g. echosounder beam width being smaller than observational transect width, inappropriate transect lengths) and analysis methods (e.g. not conducting a scale analysis) (Piatt 1990; Haney and Solow 1992; Schneider and Piatt 1986).

Due to the varied success transect methods have had in determining the factors causing seabird distributions, researchers began observing and describing foraging aggregations of seabirds at sea and the reasons for these concentrations. Studies have primarily focused on the role of each species in an assemblage (Chilton and Sealy 1987; Hoffman et al. 1981; Harrison et al. 1991; Hunt et al. 1988; Porter and Sealy 1981, 1982; Mahon et al. 1992), the benefits of flock diving (e.g. Gotmark et al. 1986) and both the biological and physical mechanisms responsible for concentrating prey (Grover and Olla 1983; Harrison et al. 1991; Hunt et al. 1988). Differences in foraging behaviour of seabirds in mixed-species feeding flocks over periods of fluctuating prey availability, however, have not been examined.

The first objective of this study was to test whether the association of auklets and prey at sea were scale-dependent. The second objective was to test whether auklet and prey associations would change with varying behaviour of auklets at sea and with fluctuating prey availability. The third objective was to test whether the foraging behaviour of seabirds in mixed-species feeding flocks varied in response to changing prey availability and varying provisioning demands.

METHODS

Two types of transects were conducted to describe the behavioural responses of Rhinoceros Auklets to fluctuating prey availability in the study area. First, route-focused transects were conducted to examine the magnitude of association and spatial overlap of auklets and prey at different spatial scales. Route-focused transects also were used to describe the variability in aggregation intensity of auklets and prey schools separately at different spatial scales. Second, flock-focused transects were conducted to examine seabird behaviour (e.g. total numbers, foraging intensity and persistence in flocks) in mixed-species feeding flocks. Descriptions of the sampling methods for route and flock-focused transects were described in chapter 1.

For each route-focused transect, the magnitude of association between auklet densities and prey densities was measured by calculating the Pearson product-moment correlation coefficient (r). Spatial overlap was measured by computing a ratio (Ro) of the total number of time blocks containing both auklets and prey schools divided by the total number of time blocks containing prey in each route-focused transect. Consequently, the resulting spatial overlap ratio illustrates the proportion of time in each route-focused transect in which auklets were located with prey out of the total number of opportunities to be located with prey. Variability in the aggregation intensity of auklets and prey was measured separately by computing variance-to-mean ratios (I') for each route-focused transect (Schneider and Piatt 1986; Cairns and Schneider 1990; Piatt 1990). The interpretation that I' describes the distribution of auklets and prey as aggregated, random and uniform is based on the null hypothesis of a Poisson distribution (Pielou 1969). Recently, researchers have suggested that this interpretation is not reliable and, therefore, the I' values in this study are used only as an index of variability in the numerical abundance of auklets and prey with increasing frame sizes rather than to describe their distributions (D. Schneider pers. comm.).

The variability of r, Ro and I' at increasing time/spatial scales (frame sizes) was determined for each route-focused transect (Schneider and Piatt 1986; Cairns and Schneider 1990; Piatt 1990). Auklet and prey densities were integrated into larger frame sizes by successively summing the auklet numbers and prey density scores within adjacent 20 s blocks at 7 frame sizes (20 s, 40 s, 1 min, 2 min, 3 min, 5 min and 10 min). Measurement intervals were scaled in seconds and minutes of each transect ($\approx$100 m traveled per 20 seconds of transect; vessel speed ca. 18 km/hr). Correlations between auklet and prey densities were also computed at these 7 frame sizes. The tracking scale of auklets to prey for each transect was defined as the frame size corresponding to the maximum value of r (Schneider and Piatt 1986). The patch scales of both auklets and prey for each transect were defined as the frame size corresponding to the maximum value of I' (Schneider and Piatt 1986; Pielou 1977).

Variability in the patch scales of auklets and prey were compared between seasonal categories, using chi-squared tests on the number of transects were I' values corresponded to the defined patch scale and those transects were I' values deviated from the defined patch scale. The values of r and Ro at the defined tracking scale were then compared between seasonal and daily categories using multi-factor ANOVAs for unbalanced designs. The statistical program SYSTAT was used. SYSTAT computes unbalanced design ANOVAs by creating dummy variables out of the classifying input variable, in which the sum of the effects estimated for the classifying variable is zero (SYSTAT 1992). Interactions between factors, or categories, also were examined if sufficient data were available, or cells were not missing. Due to the unbalanced design of the ANOVAs in this study, the sum of squares associated with one factor depends on the sum of squares for another (Zar 1984). Therefore, careful interpretation of main factor effects is required when an interaction term is significant and whether the interaction is ordinal or disordinal for the main factors (Krebs 1989; Keppel 1973). The seasonal and daily categories were defined in Appendix 1-2.

For each flock-focused transect, I recorded the foraging intensity of all seabirds, the fish school size observed and the persistence of seabirds at the feeding flock, after passage by the boat, on a scale of 0 to 5 (see Appendix 1-1). These index values then were compared between seasonal and daily categories using multi-factor ANOVAs for unbalanced designs, as described above. In addition, these indices were also compared between flock-focused transects containing different prey species using paired sample t-tests.

RESULTS

SCALE-DEPENDENCY

The magnitude of association (r) values between auklet and prey densities were all positive and peaked at the 1-minute frame size; thus this was defined as the primary tracking scale of auklets to their prey (Fig. 3-1 and 3-2). Sample size decreased with increasing frame size, causing r values required for significant correlations to increase with

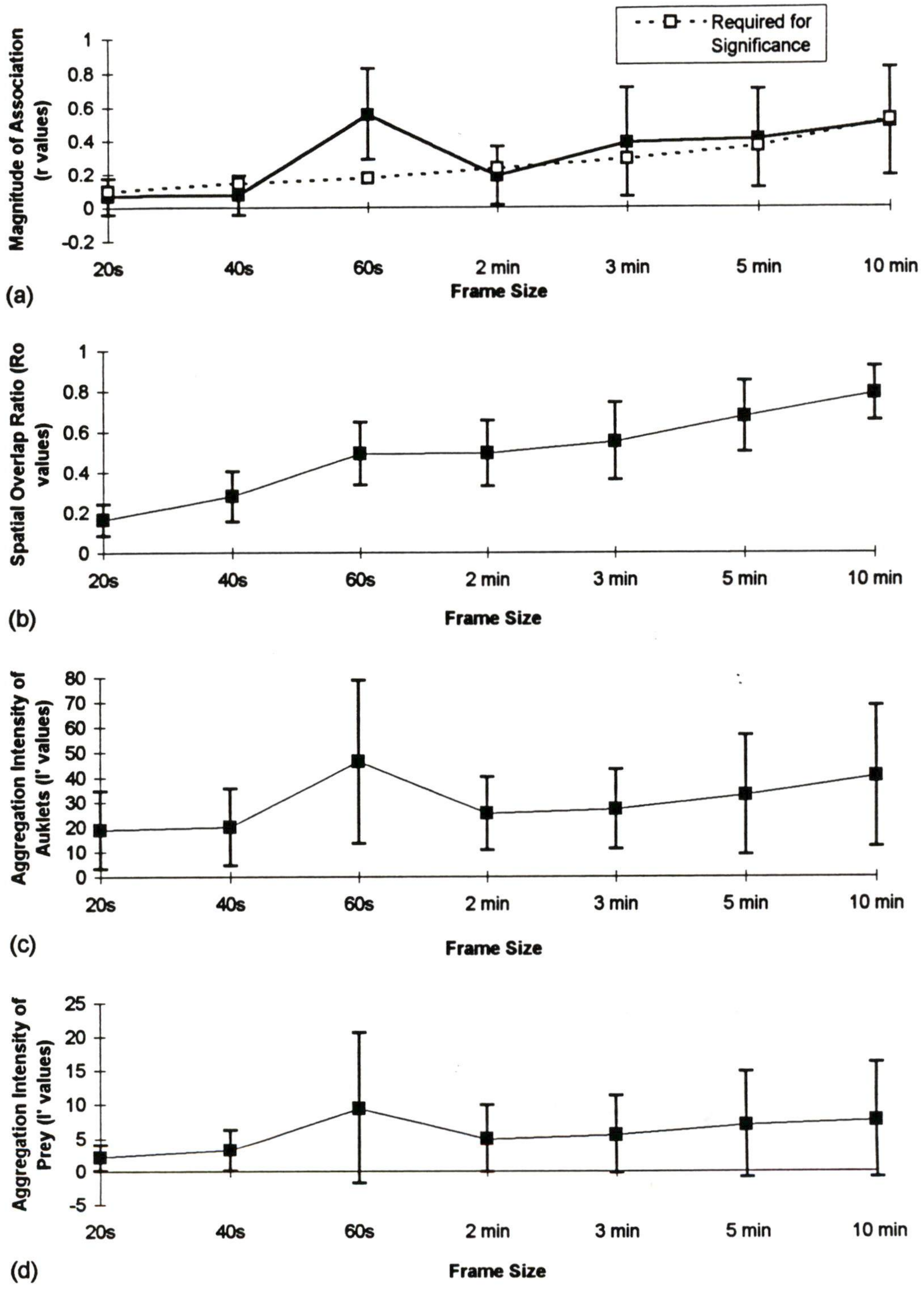


Fig. 3-1. The mean index values (+/- SD) in route-focused transects in 1995 (n=10); (a) magnitude of association between auklets and prey (r); (b) spatial overlap Ro; (c) aggregation intensity of Auklets (I' auklet) and (d) aggregation intensity of Prey (I' prey).

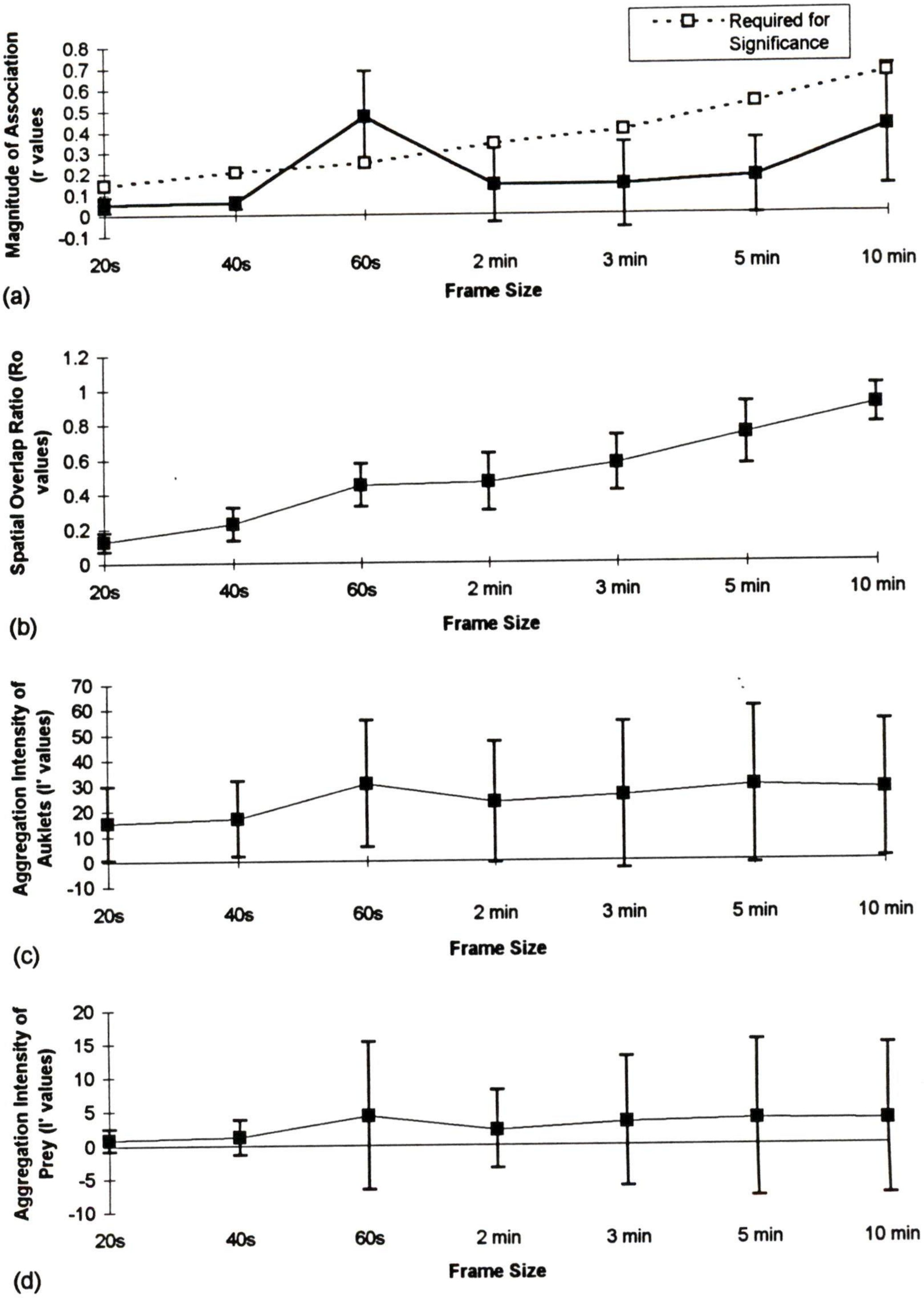


Fig. 3-2. The mean index values (+/- SD) in route-focused transects in 1996 (n=23); (a) magnitude of association between auklets and prey (r); (b) spatial overlap Ro; (c) aggregation intensity of Auklets (I' auklet) and (d) aggregation intensity of Prey (I' prey).

increasing frame size. Therefore, the r values required for significance are shown in Fig. 3-1 and 3-2, indicating that the 1- and 10-minute frame sizes contained the highest percentage of transects with significant correlations (Table 3-1). The I' values of auklets and prey also peaked at the 1-minute frame size; thus this was defined as the primary patch scale for both auklets and prey. The spatial overlap ratio (Ro) of auklets and prey was highest at the largest frame size (10 minutes) but increased little after 1 minute (Fig. 3-1 and 3-2). Consequently, the most appropriate spatial/time scale for further analysis was 1 minute (≈ 300 m).

ASSOCIATIVE BEHAVIOUR OF AUKLETS AND PREY

In both years, the magnitude of association between auklet and prey densities (r values) did not differ significantly between seasons or days (Appendix 3-1). Auklets, however, had a significantly higher magnitude of association with prey densities in evening transects than in morning transects in 1996 (Table 3-2). In addition, the tracking scale of auklets to prey increased beyond the 1-minute frame size during the period of high prey accessibility, which was also the only period when auklet and prey densities were not significantly correlated at the 1-minute frame size.

In both years, the spatial overlap of auklets and prey (Ro values) also did not differ significantly between seasons or days (Appendix 3-1). There was, however, a significantly higher spatial overlap in low prey density periods than in high prey density periods in 1995 (Table 3-2). In 1995, the spatial overlap of auklets and prey was also significantly higher in post-fledging, compared to chick rearing.

Significant differences were not found between years for the spatial overlap of auklets and prey schools during chick rearing (independent sample t-test, t=0.585, df=11.8, P=0.570) and during post-fledging (t=-0.263, df=3.9, P=0.806). Significant differences also were not found between years for the magnitude of association of auklets and prey schools during chick rearing (t=-0.337, df=12.0, P=0.742) and during post-fledging (t=-0.311, df=2.5, P=0.780).

Table 3-1. Percentage of maximum r, Ro, I' auklet and I' prey values in each frame size, derived from route-focused transects, in 1995 (n=10) and 1996 (n=23). The percentage of transects showing significant correlations between auklet and prey school densities within each frame size in 1995 and 1996

		Frame Size						
Index	Year	20 s (100m)	40 s (200m)	1 min (300m)	2 min (900m)	3 min (1200m)	5 min (1500m)	10 min (3000m)
Magnitude of Association (r)	1995	0	0	50	0	0	10	40
	1996	0	0	56.5	0	0	0	43.5
Spatial Overlap Ratio (Ro)	1995	0	0	50	10	10	0	30
	1996	0	0	52	4	0	4	40
Aggregation Intensity of Auklets (I')	1995	0	0	40	0	10	20	30
	1996	0	0	78	4	4	4	10
Aggregation Intensity of Prey (I')	1995	0	0	80	0	0	0	20
	1996	0	0	52	4	13	18	13
Significant Correlations (r)	1995	10	10	90	30	50	40	50
	1996	0	0	82	4	9	4	17

Table 3-2. Mean association indices (± SD) of Rhinoceros Auklets and their prey (r and Ro) for both daily and seasonal categories in the 1995 and 1996 auklet breeding season. The sample size (n) is the number of route-focused transects

Category	Magnitude of Association (r)		Spatial Overlap Ratio (Ro)		n	
	1995	1996	1995	1996	1995	1996
Prey Density						
High	0.304 ± 0.270	0.422 ± 0.140	0.312 ± 0.060	0.441 ± 0.140	3	5
Low	0.662 ± 0.200	0.485 ± 0.240	0.566 ± 0.110	0.470 ± 0.050	7	18
Breeding Phase						
Incubation	-	0.426 ± 0.210	-	0.397 ± 0.100	0	12
Chick Rearing	0.496 ± 0.300	0.491 ± 0.210	0.423 ± 0.120	0.457 ± 0.100	7	8
Post-fledging	0.692 ± 0.090	0.600 ± 0.290	0.646 ± 0.100	0.622 ± 0.120	3	3
Wind Direction						
Southeast	0.391 ± 0.390	0.425 ± 0.180	0.469 ± 0.160	0.441 ± 0.090	3	11
Northwest	0.625 ± 0.170	0.522 ± 0.250	0.499 ± 0.170	0.454 ± 0.160	7	12
Prey Accessibility						
Low	-	0.452 ± 0.208	-	0.440 ± 0.124	0	4
High	-	0.560 ± 0.277	-	0.481 ± 0.138	0	19
Tidal Stage						
Low	0.684	0.377 ± 0.210	0.517	0.397 ± 0.090	1	6
Flood	0.535 ± 0.270	0.490 ± 0.290	0.466 ± 0.180	0.466 ± 0.110	5	6
High	-	-	-	-	0	0
Ebb	0.560 ± 0.430	0.512 ± 0.180	0.559 ± 0.040	0.465 ± 0.150	2	11
Time of Day						
Morning	0.555 ± 0.268	0.438 ± 0.210	0.490 ± 0.155	0.380 ± 0.070	10	20
Afternoon - Evening	-	0.693 ± 0.200	-	0.457 ± 0.130	0	3

PATCH SCALE OF AUKLETS AND PREY

Deviations from the defined patch scales of auklets and prey (1 minute) may suggest that both auklets and prey are behaving differently from normal. Deviations from the 1-minute frame size were always larger, rather than smaller patch scales (Table 3-3 and 3-4). In 1995, few transects showed larger patch scales of auklets (20%), however, many transects showed larger patch scales of prey (60%). In 1996, the opposite was observed, with more transects showing larger patch scales of auklets (48%) than those of prey (22%). The number of transects showing larger patch scales of auklets did not differ significantly between years; however, the number of transects showing larger patch scales of prey was significantly higher in 1995 than in 1996 (Appendix 3-2).

There were also two periods in 1996 where larger patch scales of both auklets and prey were observed. First, in 1996, the number of transects showing larger patch scales of auklets was significantly higher during chick rearing than during incubation and post-fledging (Table 3-3; Appendix 3-2). A similar trend was shown in 1995, however, the difference was not significant. Second, during the period of high prey accessibility, the number of transects showing larger patch scales of prey was significantly higher than when prey was less accessible (Table 3-4). The number of transects showing larger patch scales of auklets was also higher during this period but did not differ significantly relative to periods when prey was less accessible.

SEABIRD BEHAVIOUR IN MIXED-SPECIES FEEDING FLOCKS

In both years, the foraging intensity, persistence and school size indices did not differ significantly between seasons or days (Table 3-5; Appendix 3-3). In 1996, the total number of birds observed participating in feeding flocks during flock-focused transects, however, increased significantly in post-fledging, compared to both incubation and chick rearing. The birds associated with feeding flocks containing known prey species did not differ significantly in foraging intensity, persistence and in total numbers (Appendix 3-5). The formation of feeding flocks and the behaviour of birds at feeding flocks is described in the discussion.

Table 3-3. The variance to mean ratio (I') values for the numerical abundance of Rhinoceros Auklets at each frame size during the route-focused transects in 1995 and 1996. The underlined values represent the patch scale, or maximum I' values in each transect

			Frame Size				
DATE	20 s (100m)	40 s (200m)	1 min (300m)	2 min (900m)	3 min (1200m)	5 min (1500m)	10 min (3000m)
1995							
21-Jul	60.266	59.629	126.532	57.703	57.370	82.206	81.348
22-Jul	9.872	10.200	18.060	15.670	16.260	15.680	14.290
23-Jul	16.260	16.685	55.432	29.915	36.412	48.308	80.679
27-Jul	10.701	12.283	28.454	12.969	15.562	16.466	25.339
28-Jul	20.906	23.166	57.234	32.141	43.937	59.773	69.538
1-Aug	21.730	21.942	62.722	27.753	29.101	29.403	52.064
2-Aug	19.490	19.320	32.690	30.580	29.190	30.490	28.360
21-Aug	6.157	5.952	20.349	7.361	8.584	6.922	9.705
22-Aug	4.975	6.257	19.310	10.860	7.497	11.080	12.130
23-Aug	18.291	25.738	41.677	29.867	26.991	28.291	29.700
1996							
24-May	2.167	2.103	4.107	3.440	3.256	2.930	2.292
31-May	7.780	7.774	9.209	7.175	7.004	7.140	4.492
1-Jun	11.451	12.091	16.502	12.753	11.070	10.344	16.205
2-Jun	11.790	11.533	13.946	10.60	14.205	9.964	8.722
5-Juna	16.637	25.664	45.433	40.054	41.066	43.369	42.967
5-Junb	3.956	3.861	8.323	4.270	4.900	5.833	7.111
6-Jun	1.731	1.737	6.874	1.841	3.079	2.606	2.865
11-Jun	12.907	17.610	49.479	22.884	31.254	58.041	60.312
16-Jun	17.562	20.406	37.085	30.479	23.713	32.866	34.541
18-Jun	13.928	14.949	42.129	26.303	32.212	54.262	50.248
19-Jun	13.101	13.336	24.700	15.230	14.506	14.000	27.425
20-Jun	20.167	19.856	25.414	19.488	22.743	19.757	18.238
4-Jul	25.262	26.673	35.107	27.124	30.545	36.995	30.494
10-Jul	2.220	2.226	6.400	2.028	2.442	1.860	2.091
12-Jul	38.415	38.259	45.081	39.961	39.323	47.747	43.609
21-Jul	10.497	11.793	26.600	14.182	25.226	22.400	26.817
22-Jul	68.695	67.727	109.600	111.177	141.603	135.820	119.575
23-Jul	20.117	26.101	32.609	36.929	36.267	34.017	29.477
28-Jul	19.598	29.134	79.596	50.725	49.636	75.437	58.799
2-Aug	17.755	18.161	36.712	31.292	33.047	36.920	30.129
21-Aug	7.030	8.121	21.187	13.629	11.647	9.320	7.082
24-Aug	3.388	3.813	12.288	4.519	5.246	9.106	7.676
3-Sep	4.843	5.636	13.459	5.614	6.667	8.433	9.682

Table 3-4. The variance to mean ratio (I') values for prey at each frame size during the route-focused transects in 1995 and 1996. The underlined values represent the patch scale, or maximum I' values in each transect

			Frame Size				
DATE	20 s (100m)	40 s (200m)	1 min (300m)	2 min (900m)	3 min (1200m)	5 min (1500m)	10 min (3000m)
1995							
21-Jul	3.702	6.153	29.322	11.915	13.130	12.959	15.215
22-Jul	3.997	5.402	16.601	9.414	9.747	9.448	10.397
23-Jul	4.525	7.101	26.178	11.826	15.282	22.356	24.857
27-Jul	0.139	0.159	0.491	0.271	0.259	0.294	0.502
28-Jul	4.864	7.66	13.172	8.95	8.885	16.008	15.975
1-Aug	1.486	1.633	2.555	1.942	1.93	2.045	3.070
2-Aug	0.018	0.033	0.171	0.083	0.111	0.099	0.160
21-Aug	0.544	0.644	0.945	0.629	0.666	0.984	0.854
22-Aug	1.066	2.094	2.406	2.108	2.608	2.580	2.506
23-Aug	0.397	0.674	2.221	1.858	2.100	2.244	2.730
1996							
24-May	0.028	0.051	0.757	0.149	0.201	0.312	0.273
31-May	0.002	0.003	0.234	0.006	0.010	0.013	0.009
1-Jun	2.572	3.032	10.802	4.098	5.330	9.829	11.464
2-Jun	0.397	0.704	1.252	0.735	0.927	0.750	0.693
5-Juna	0.009	0.012	0.053	0.020	0.027	0.037	0.0253
5-Junb	0.901	0.948	1.218	0.939	0.938	0.907	0.923
6-Jun	0.031	0.053	0.422	0.142	0.148	0.168	0.343
11-Jun	0.590	0.594	0.663	0.589	0.571	0.600	0.568
16-Jun	0.064	0.089	0.308	0.206	0.200	0.354	0.361
18-Jun	0.082	0.087	0.164	0.094	0.093	0.104	0.105
19-Jun	6.952	11.509	51.249	26.823	45.152	55.831	53.320
20-Jun	0.423	0.480	0.459	0.507	0.457	0.438	0.359
4-Jul	0.267	0.300	1.064	0.507	0.451	0.494	0.648
10-Jul	0.041	0.044	0.313	0.059	0.064	0.071	0.035
12-Jul	0.139	0.186	0.398	0.302	0.200	0.330	0.291
21-Jul	0.382	0.531	1.348	0.902	0.957	1.059	1.109
22-Jul	0.013	0.019	0.089	0.034	0.027	0.052	0.054
23-Jul	0.028	0.029	0.081	0.028	0.026	0.042	0.022
28-Jul	3.175	4.885	16.503	9.536	13.551	8.092	5.432
2-Aug	0.324	0.548	5.841	1.240	1.895	2.256	1.821
21-Aug	3.045	3.048	3.183	3.058	2.926	2.817	2.353
24-Aug	0.157	0.273	1.132	0.637	1.146	0.748	0.646
3-Sep	0.194	0.204	0.495	0.199	0.185	0.260	0.338

Table 3-5. Mean number of birds, foraging intensity, persistence and school size indices (± SD) in mixed-species feeding flocks containing Rhinoceros Auklets in the 1995 and 1996 auklet breeding seasons. Sample size (n) is the number of flock-focused transects

Category	Total Number of Birds		Foraging Intensity Index		Persistence Index	School Size Index	n	
	1995	1996	1995	1996	1996	1996	1995	1996
Prey Density								
Low	71.0 ± 26.0	36.0 ± 27.1	2.3 ± 0.7	1.9 ± 0.6	1.6 ± 0.9	1.2 ± 1.1	10	18
High	-	55.6 ± 19.5	-	2.4 ± 0.2	1.8 ± 1.3	1.8 ± 1.7	0	4
Breeding Phase								
Incubation	-	31.0 ± 8.1	-	1.7 ± 0.6	1.6 ± 1.5	1.7 ± 1.5	0	3
Chick Rearing	73.8 ± 17.3	30.2 ± 24.2	2.2 ± 0.7	2.2 ± 0.6	1.5 ± 0.9	1.2 ± 1.1	6	14
Post-fledging	66.7 ± 38.5	69.2 ± 38.9	2.6 ± 0.7	2.0 ± 0.3	2.1 ± 1.2	1.0 ± 0.7	4	5
Wind Direction								
Northwest	82.2 ± 4.7	39.3 ± 23.1	2.2 ± 1.0	1.9 ± 0.5	1.3 ± 1.1	1.7 ± 1.2	7	16
Southeast	66.1 ± 30.2	39.7 ± 30.8	2.4 ± 0.6	2.1 ± 0.7	1.8 ± 1.0	1.1 ± 1.0	3	6
Prey Accessibility								
Low	-	41.4 ± 26.9	-	2.1 ± 0.4	1.7 ± 1.2	1.5 ± 1.4	0	4
High	-	31.4 ± 19.9	-	1.9 ± 1.0	1.3 ± 0.8	0.2 ± 0.1	0	18
Tidal Stage								
Low	61.3 ± 17.0	26.3 ± 10.3	2.3 ± 1.0	1.9 ± 0.2	1.7 ± 1.6	2.2 ± 1.5	4	5
Flood	75.7 ± 38.5	48.7 ± 41.1	2.2 ± 0.5	1.9 ± 1.1	1.6 ± 0.4	0.8 ± 0.7	4	5
High	-	43.7 ± 28.6	-	2.1 ± 0.4	1.2 ± 1.0	1.4 ± 1.3	0	6
Ebb	80.8 ± 9.7	39.0 ± 15.0	2.9 ± 0.2	2.1 ± 0.3	2.1 ± 1.1	0.8 ± 0.7	2	6
Time of Day								
Morning	76.7 ± 25.3	36.9 ± 21.5	2.1 ± 0.7	1.9 ± 0.5	1.7 ± 1.3	1.2 ± 1.1	5	14
Afternoon - Evening	65.2 ± 28.2	44.2 ± 32.7	2.6 ± 0.8	2.3 ± 0.6	1.6 ± 0.8	1.5 ± 1.4	5	8

DISCUSSION

SCALE-DEPENDENCY

Many studies have shown scale-dependent correlations between seabirds and their prey (zooplankton and fish) (Schneider and Piatt 1986; Piatt 1990; Erikstad et al. 1990; Hunt et al. 1990). In this study, auklets tracked prey schools in a scale-dependent manner, primarily at the 1-minute (300 m) frame size and secondarily at the 10-minute (3 km) frame size. The 1-minute tracking scale was similar to the patch scale of both auklets and prey. Auklets did not track prey schools at very small (20-40s or 0.1-0.2 km) or intermediate frame sizes (2-5 min. or 0.6-1.5 km). This may be due to predator avoidance behaviour of prey, to auklets losing contact with prey between dives or upon termination of a dive bout and/or to the locomotory differences of auklets and fish (Schneider and Piatt 1986).

Other seabird studies showed prey-tracking scales of 2-6 km for Common Murres and Atlantic Puffins (Schneider and Piatt 1986), 8-144 km for Common Murres (Erikstad et al. 1990) and 9-12 km for Least Auklets (Hunt et al. 1990). These are larger than the tracking scales found in this study (0.3-3 km). This is probably due to longer transect lengths and higher densities of birds and prey encountered during these other studies, compared to this study. For instance, Schneider and Piatt (1986) conducted their study in an area where several hundred thousand pairs of murres and puffins breed, along with large spawning populations of their principal prey species, capelin.

ASSOCIATIVE BEHAVIOUR OF AUKLETS AND PREY

The magnitude of association between seabirds and prey schools (r values) was observed to vary from survey to survey, with 1-82% of the variation in auklet density being explained by the density of prey schools. This variability also was observed in a number of other studies (Piatt 1990; Schneider and Piatt 1986; Hunt et al. 1900; Erikstad et al. 1990) and is probably due to the varying behaviours and foraging strategies of auklets (chapter 2, Table 2-1 and 2-2). The only period when auklets were not correlated with prey at the 1-minute frame size was in 1996 during the period of high prey accessibility. Therefore, during this period, high auklet densities were found associated with both low and high patch densities, rather than just with high patch densities.

This may be interpreted in a number of ways. First, when fish schools were observed frequently in surface waters, auklets were mainly flock diving. Auklets may have had an incomplete knowledge of prey patch locations and qualities, because they were primarily cueing to the foraging activities of other seabirds. This may have resulted in the exploitation of lower patch densities relative to those that were available. In addition, since auklets were not actively seeking prey schools, if transects did not go directly through an active feeding flock, there is a high probability that auklets were mainly resting, again resulting in the weak correlations or the observed higher tracking scales of auklets to prey. In support, the magnitude of association between auklet and prey (r values) was significantly lower during morning transects when auklets were resting, compared to evening transects, when they were significantly more dispersed and actively collecting fish for their chicks (chapter 2, Fig. 2-6 and 2-8).

Second, auklets also may detect prey density in a threshold manner, as shown for other alcids (e.g. Common Murres and Atlantic Puffins; Piatt 1990). For instance, when prey are highly accessible, seabirds may be able to obtain enough food in small prey aggregations and, therefore, do not unnecessarily expend extra energy searching out peak concentrations (Woodby 1984; Hunt et al. 1990). Consequently, auklets may have exploited the nearest available surface schools, regardless of their prey densities, because they were readily accessible.

The spatial overlap of auklets and prey schools (Ro values) increased during low prey density periods, relative to high prey density periods. This result may be interpreted in two ways. First, when prey densities are low, there were fewer prey patches for the same number of auklets to choose from, thus resulting in a higher probability that all prey patches were exploited. Second, auklets may have attempted to stay in contact with known patches because prey schools were more scarce. This may have allowed auklets to maintain current information on patch locations and qualities and may have allowed them to maximize their energetic intake by selecting higher density patches. In support, more auklets were primarily diving solitarily during periods of low prey density (chapter 2; Fig. 2-2) and the magnitude of association between auklets and prey schools was also higher during these periods.

Auklets and prey schools also had a higher spatial overlap during post-fledging relative to other breeding phases. This may have resulted from increased numbers of auklets on the water, due to the influx of fledglings from the colony. In support, there was a significantly higher number of birds participating in feeding flocks during post-fledging, compared to both chick rearing and incubation. With more auklets on the water, more extensive searching could be conducted, resulting in a higher probability of more patches being discovered and exploited. Therefore, the higher number of auklets on the water effectively simulated a decrease in prey density and abundance because the auklet to prey school ratio increased in a similar manner.

PATCH SCALE OF AUKLETS AND PREY

The patch scale of prey was larger in 1995 than in 1996. This suggests that prey generally formed larger patches in 1995 and, therefore, it may have been easier for auklets to locate or maintain contact with prey in 1995, compared to 1996. This may explain why a higher percentage of the transects in 1995 showed significant correlations between auklet and prey densities at each frame size, compared to 1996 (Table 3-1).

Deviations from the 1-minute patch scale were observed in 1996 during the period of high prey accessibility and during chick rearing. During these two periods, the patch scales of auklets increased beyond 1 minute to 2-5 minutes. During chick rearing, transects were primarily conducted in the morning, which was when auklets were primarily resting in large rafts on the water (chapter 2). Consequently, the larger patch scale of auklets during this breeding phase may be explained by the higher mean group size of auklets in the morning (chapter 2, Fig. 2-6) and the higher percentage of auklets Resting in the morning, compared to the rest of the day (chapter 2, Table 2-2).

The larger aggregations of auklets when fish were highly accessible and concentrated in surface-waters may be due to the high flock foraging behaviour during this period (chapter 2). First, larger aggregations of auklets may have resulted from individuals attempting to maintain visual contact with other birds, in order to cue to their foraging activities. Second, large resting groups of auklets formed after birds finished foraging in a feeding flock (see next section). Third, larger numbers of auklets may have aggregated over each prey patch to take advantage of the high accessibility of prey. Finally, auklets may have been responding to the significantly larger patch scales of prey during this period. Therefore, larger patches of auklets were forming over larger patches of prey.

SEABIRD BEHAVIOUR IN MIXED-SPECIES FEEDING FLOCKS

I generally saw Type I flocks, as described in Hoffman et al. (1981). The feeding flocks in this study were similar to those observed by Grover and Olla (1983), Hoffman et al. (1981), Chilton and Sealy (1987), Harrison et al. (1991), Mahon et al. (1992), Porter and Sealy (1981, 1982) and Sealy (1973). For the most part, these feeding flocks were initiated by underwater predators, mainly pursuit-diving birds, the majority of which were Rhinoceros Auklets. Consequently, this study, along with Mahon et al. (1992), emphasizes the important role that diving birds play in initiating and maintaining mixed-species feeding flocks of seabirds, in comparison to gulls and other surface-feeding seabirds (Porter and Sealy 1981, 1982; Chilton and Sealy 1987).

Once a feeding flock was initiated, there was a rapid increase in the number of seabirds joining the flock. High foraging activity was maintained while in contact with fish schools and this activity lasted from 1 to several minutes. Auklets generally conducted several short dives in rapid succession, with little time spent on the water between dives, and gulls mainly fluttered, vocalized and seized fish at the ocean's surface. Once birds lost contact with fish schools, or finished foraging, all birds began resting on the water (this study; Grover and Olla 1983). During this resting period, auklets and other species slowly began to disperse from the feeding flock location (Mahon et al. 1992; this study), generally forming large rafts of birds which were resting and preening.

Kleptoparasitism was observed between gulls in feeding flocks. Gulls in the center of feeding flocks obtained large numbers of fish and then generally flew to the periphery of the flock to swallow them (this study; Porter and Sealy 1982). These gulls were often chased by conspecifics and sometimes were attacked, resulting in the loss of some or all of their fish (this study; Porter and Sealy 1982). Kleptoparasitism was, however, not observed between gulls and auklets. Auklets surfaced on the periphery of feeding flocks, even without fish in their bills, and it was suggested that they may be responding to the threat of kleptoparasitism by gulls in this way (Chilton and Sealy 1987; Hoffman et al. 1981).

In the vicinity of the breeding colony, two levels of information transfer seemed to be occurring. First, the rapid dives made in succession by Rhinoceros Auklets and other diving bird species (e.g. Common Murres) seemed to attract other diving and surface-feeding seabirds ('network foraging'; Wittenberger and Hunt 1985; Grover and Olla 1983). Second, in some instances, the majority of the gulls foraging in mixed-species feeding flocks would fly off the water and circle high above the feeding flock for 30 seconds to a minute, before setting down again to resume foraging at similar rates. This more active signaling behaviour also attracted many birds to feeding flocks ('local enhancement'; Wittenberger and Hunt 1985).

Auklet behaviour in feeding flocks did not change over varying environmental conditions and because prey densities at feeding flocks also did not change with varying environmental conditions for the most part (chapter 1), this result was not surprising. At feeding flocks of known prey species composition, auklets did not show any preference for sand lance or herring. This is also not surprising because prey densities did not differ between schools of the two species (chapter 1). The foraging intensity and persistence of auklets at feeding flocks did not change over prey density periods, prey accessibility periods, nor during chick rearing, when provisioning demands on auklets were the highest. This suggests that auklets forage in an opportunistic manner at feeding flocks, regardless of the prey availability around the breeding colony and current varying provisioning demands.

The one difference that was noted in feeding flocks was that there were a significantly higher number of birds in feeding flocks during the post-fledging phase. This was probably due to the high number of juvenile seabirds in the area. Juvenile birds are probably less skilled at locating and capturing prey and, thus, they may compensate for this inexperience by cueing to the foraging activity of other seabirds and flock foraging (Porter and Sealy 1982). Therefore, mixed-species feeding flocks may provide an important food source for recently fledged seabirds and may ultimately increase their chances for survival.

CHAPTER FOUR

INTERANNUAL CHANGES IN REPRODUCTIVE EFFORT OF BREEDING RHINOCEROS AUKLETS

INTRODUCTION

Interannual variation in seabird breeding success has been attributed to changes in prey availability near breeding colonies (Bertram et al. 1991; Vermeer 1980; Monaghan et al. 1991; Anderson et al. 1982; Hamer et al. 1991; Hodder and Graybill 1985; Martin 1989; Murphy et al. 1984; Springer et al. 1986; Safina et al. 1988). Many seabirds are able to adjust reproductive effort when prey availability changes by such things as altering clutch sizes (Birkhead and Nettleship 1984). For those species that lay only a single-egg clutch (e.g. most alcids), other parameters may be adjusted because clutch size can not be changed (Birkhead and Nettleship 1982; Hatchwell and Pellat 1990).

Low prey availability during chick rearing may result in reduced provisioning loads delivered to chicks, causing reduced growth rates of chicks (Bertram et al. 1991; Ricklefs 1983). An extreme example of this was shown for young chickens, which remained at the body mass of a 10 day old chick for months when fed diets that were reduced to a level just sufficient to fill maintenance requirements (McCance 1960; Dickerson and McCance 1960). When diets were restored to normal levels, growth and development were restored with little effect on adult body size and reproductive capacity (McRoberts 1965). For seabirds breeding in colonies, however, it may be important for chicks to fledge within a particular time frame. This would increase breeding synchrony, resulting in higher safety for chicks and provisioning parents, and potentially would maximize the temporal overlap of chick rearing with high prey densities (Wittenberger and Hunt 1985; Safina and Burger 1985). Due to the growth rates of chicks affecting the time of fledging, some seabirds are able to increase provisioning efforts, thereby elevating growth rates and allowing chicks to develop at time periods consistent with other years (Gaston and Nettleship 1981; O'Connor 1975).

Low prey availability during the egg formation period may result in reduced egg and hatchling size (Birkhead and Nettleship 1982; Hatchwell and Pellatt 1990); thus also requiring increased growth rates for chicks to reach fledging in a time period similar to other years. The cost of egg formation, however, is not thought to be high compared to other birds because alcids lay only a single age clutch (Birkhead and Nettleship 1984). Therefore, egg production is not thought to be very sensitive to declines in prey availability. Another parameter that appears to be affected by lowered prey availability is the timing of breeding (Drent and Daan 1980; Birkhead and Nettleship 1982; Birkhead and Nettleship 1984), possibly due to the increased time required for yolk deposition (Hatchwell and Pellat 1990).

The objective of this study was to describe interannual differences in chick provisioning and growth rates of Rhinoceros Auklet chicks and to relate those differences to variations in prey availability. This tests whether auklets are able to adjust chick provisioning and buffer the negative effects of lower prey availability on chick growth.

METHODS

Growth rates of chicks were estimated and food loads delivered to chicks were collected in 1995 and 1996 to determine if these variables were affected by fluctuations in prey availability. Trips were made to the Seabird Rocks breeding colony approximately every ten days during the chick rearing phase of Rhinoceros Auklets in both years. Four trips were made to the colony in 1995 and three were made in 1996. Visits to the colony were planned as single-night visits but lasted up to 4 nights during some trips due to unfavorable weather conditions. During each visit, chick growth measurements were collected in the afternoon and meals of chicks were collected after dusk. Chick growth measurements and meals of chicks were collected in completely separate areas of the colony to minimize the disturbance of chicks in the growth study. When colony visits were extended for a second night, meals of chicks were sampled again in a third area.

PROVISIONING

Meals of chicks were collected by blocking the entrances of 35-40 auklet burrows, to prevent fish-carrying parents from entering, following Hatch (1982). Screens of galvanized hardware cloth (1.25 cm mesh) sized appropriately for auklet burrows (ca. 18 x 18 cm) were used to block entrances. The tussock grass next to screened burrows was marked with white flagging tape for easy relocation.

Burrows were usually screened one hour before dusk, or before auklets began circling the colony (ca. 2000 hrs). Screens were left in burrow entrances for the entire night and were checked every 30 minutes during the peak arrival time of auklets (2200 to 0200 hrs). During these checks, screened burrows and surrounding areas were searched for fish. Fish found were placed in a labeled bag and samples collected from each screen were kept separate. Fish were then washed with salt water to remove dirt, identified to species, weighed and measured (chapter 1). The food loads found at each screen were recorded separately to determine the total mass of fish per screen. It was impossible to determine whether each sample represented the effort of one or more parental visits and, thus, these loads were referred to as 'burrow loads' (Hatch 1984).

Meals of chicks also were collected by capturing parents returning to the colony at night with fish for their chicks. Auklets regularly landed on strips of land containing no vegetation or rock ('runway') when returning to the colony. Sitting near a run way would allow easy capture of adults. Samples from individual adults were placed into separate labeled bags and called 'bill loads'. Fish were then cleaned and measured, as mentioned above.

Burrow loads were compared for interannual differences in mean mass, as were bill loads, using independent sample t-tests. Interannual comparisons were conducted for the mean mass of fish, mean length of fish, number of fish and the number of species in bill and burrow loads, using independent sample t-tests. Interannual comparisons were made between the number of each age class of sand lance delivered to chicks using a chi-squared test. A similar comparison was made for the age classes of herring delivered to chicks.

GROWTH

Chicks that were accessible from burrow entrances (ca. 1m) were measured for estimates of chick growth rates. Four measurements were collected from each chick: mass, with a 300 g or a 1000 g Pesola spring balance to the nearest 1g; culmen and tarsus (tarsometatarsus) lengths, with Venier calipers to the nearest 0.1 mm; and flattened wing chord length, with a wing rule, to the nearest 1 cm.

Growth rates of chicks were estimated in two ways. First, a composite growth curve was constructed, following the methods in Ricklefs and White (1975). For this, chicks encompassing a range of developmental stages were measured in early July and then 10 days later. Therefore, estimate from this method reflects only growth during early chick rearing. The ages of various wing lengths were estimated, assuming that each hatchling (age 0) had an average wing length of 21 mm (D. Bertram unpublished data). The slope of the regression of mass on estimated age for the entire data set in each year was then used as an estimate of the rate of chick growth for all chicks in that year. This method assumes that wing length grows constantly throughout the rearing phase and is not sensitive to the nutritional status of the chick (Ricklefs and White 1975).

Rodway (1997), however, found that wing growth, in a closely related species the Atlantic Puffin (*Fratercula arctica*), is influenced by nutritional status and, thus, wing length will vary with age depending on the growth rate of chicks in any year. Consequently, if chicks grow was slower in a particular year, a given wing length may correspond to an older age, resulting in an underestimate of chick age when assuming that the growth of wing length is independent of nutritional status. Due to the error surrounding the estimation of chick age for wing length, I violated one of the underlying assumptions of the standard linear regression theory, that the independent (X) variable is measured without error (Krebs 1989). Consequently, I conducted a geometric mean regression, which computes the slope by dividing the slope from the standard regression line (b) by the correlation coefficient (r) (Krebs 1989). The slopes of the geometric mean regression lines, or growth rates of chicks, in each year were then compared using an independent sample t-test, in a manner that is analogous to testing the differences between two population means (Zar 1984, pg. 292). The data used to compute the slope, or growth rate of chicks, in each year consisted of two measurements of the same chick at two intervals, resulting in data points that were not independent within each year. This violates an underlying assumption of the t-test and causes the degrees of freedom to become inflated and a higher probability of rejecting the null hypothesis when it is in fact true (Type I error; Zar 1984). Thus, the t-test results should be interpreted with caution.

Second, sequential growth rates were calculated. For this, each individual chick was measured at least three times throughout the chick rearing period. Therefore, this estimate represents the growth rate of chicks throughout the entire chick rearing phase. A measure of the growth rate for each individual chick was estimated by the slope of the regression of mass on wing length for each chick. The estimated growth rates for chicks were then compared between years using an independent sample t-test. The sequential method again assumes that wing growth is not sensitive to the nutritional status of the chick and again involves repeated measures of chicks; thus the t-test results should again be interpreted with caution. The composite and sequential growth rate estimates in each year were compared qualitatively.

UPWELLING INDEX

Bakun upwelling index values were obtained from the Pacific Fisheries Environmental Group for the 48°N 125°W station, which is most likely to reflect the conditions near Barkley Sound (D. Mackas pers. comm.). This index depicts the intensity of large-scale, wind-induced coastal upwelling and the calculation is based on the mass transport of surface water (upper 50-100 m) due to wind stress (Bakun 1990). Positive values indicate upwelling, whereas negative values indicate downwelling. Mean daily values were obtained and these values represent the period from midnight to midnight for each day.

RESULTS

PROVISIONING

No significant differences were found in mean burrow load mass between years; however, mean bill load mass was significantly higher in 1996 compared to 1995 (Table 4-1; Appendix 4-1). A higher frequency of larger bill loads also was found in 1996, compared to 1995 (Fig. 4-1). The larger food loads were primarily due to larger fish being delivered to chicks, rather than an increase in the number of fish per burrow and bill load (Appendix 4-1). The larger size of fish delivered to chicks in 1996, compared to 1995, resulted from a higher percentage of age class 1+ sand lance and herring (Table 4-2) and a higher percentage of larger fish species (salmon and surf smelt; chapter 1, Table 1-1).

GROWTH

Based on the composite growth rate estimates, growth rates of chicks during early chick rearing were significantly higher in 1995 than in 1996 (Table 4-3). In addition, the age-specific chick mass appeared to be higher in 1995 than in 1996 during early chick rearing (Fig. 4-2). Based on the sequential growth rate estimates, mean growth rates of chicks were significantly higher throughout chick rearing in 1996 than in 1995 (Table 4-3). Therefore, during early chick rearing, chicks grew slower in 1996 than in 1995; however, over the entire chick rearing period, chicks grew faster in 1996 than in 1995.

DISCUSSION

COMPARISONS WITH LITERATURE ON RHINOCEROS AUKLETS

CHICK DIETS

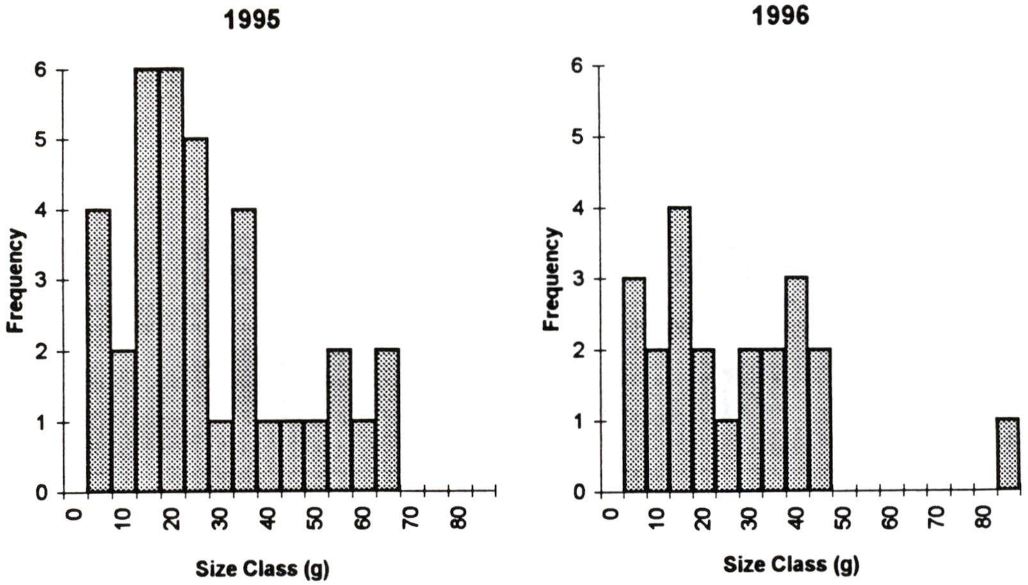
The diets of auklet chicks were similar to a previous study at this colony (Burger et al. 1993) and with other colonies throughout British Columbia, Alaska, Washington and Oregon (Wilson and Manuwal 1986; Burger et al. 1993; Bertram and Kaiser 1993; Vermeer and Westrheim 1984; Harfenist 1991; Hatch 1984). The primary prey species in diets of auklet nestlings in most years is sand lance (Gaston and Dechesne 1996). Other

Table 4-1. Summary of bill loads and burrow loads delivered to chicks of Rhinoceros Auklets during chick rearing in 1995 and 1996 at the Seabird Rocks breeding colony. The sample size (n) is the number of bill loads and burrow loads collected and the standard deviation from the means are reported

Category	1995					1996			
	July 4-5	July 14-15	July 24-25	August 3-4	Total	July 7-10	July 17-18	July 30-31	Total
Bill Load									
Mass (g)	-	26.2 ± 6.6	30.8 ± 9.3	-	30.7 ± 11.4	43.8 ± 19.5	45.4 ± 11.6	44.8 ± 8.5	44.7 ± 13.1
Range (g)	-	14.3 - 29.8	20.5 - 38.5	-	14.3 - 56.6	21.0 - 67.3	36.5 - 65.8	38.8 - 50.8	21.0 - 67.3
Number of Fish per Load	-	5.0 ± 4.9	8.7 ± 4.9	-	6.1 ± 4.7	3.8 ± 2.3	7.0 ± 2.7	4.5 ± 0.7	4.8 ± 3.0
Number of Species per Load	-	1.7 ± 0.8	1.7 ± 1.2	-	1.7 ± 0.8	1.5 ± 0.7	2.0 ± 1.3	2.4 ± 0.7	1.8 ± 1.0
n	0	6	3	0	10	4	6	2	12
Burrow Load									
Mass (g)	35.0 ± 19.9	31.6 ± 13.0	25.1 ± 20.8	18.8 ± 2.1	31.5 ± 21.8	29.4 ± 22.8	26.7 ± 16.1	46.6 ± 0.2	28.8 ± 19.4
Range (g)	8.5 - 65.3	17.5 - 55.3	9.3 - 68	17.3 - 20.3	8.5 - 68	5.3 - 89.0	8.3 - 52.5	46.5 46.8	5.3 - 89
Number of Fish per Load	3.6 ± 2.3	2.5 ± 2.0	5.0 ± 3.9	6.0 ± 5.9	5.0 ± 4.1	4.0 ± 2.3	4.4 ± 2.9	3.0	4.0 ± 2.3
Number of Species per Load	1.6 ± 0.8	1.3 ± 0.5	1.6 ± 0.7	1.0 ± 0	3.9 ± 3.8	1.4 ± 0.5	1.9 ± 1.1	2.5 ± 0.7	1.8 ± 0.9
n	9	6	9	2	33	12	7	2	21
Total Number of Fish	23	45	71	12	151	59	62	15	136
Mean Fish Mass (g)*	9.3 ± 6.8	7.1 ± 7.0	4.5 ± 4.4	3.1 ± 3.0	2.1 ± 2.0	8.4 ± 8.3	6.8 ± 6.4	11.6 ± 10.2	8.0 ± 7.9
Mean Fish Length (mm)*	107.9 ± 20.4	91.6 ± 27.8	73.1 ± 6.2	73.1 ± 6.2	90.7 ± 22.6	90.7 ± 22.6	105.1 ± 19.9	96.3 ± 25.5	102.3 ± 23.7

* all fish species combined

Burrow Loads



Bill Loads

Fig. 4-1. The histogram of all Rhinoceros Auklet burrow loads collected in 1995 (n=33) and 1996 (n=21) and bill loads collected in 1995 (n=10) and 1996 (n=12) at the Seabird Rocks breeding colony, grouped into 5 g size classes.

Table 4-2. Percentage of total number of fish age classes within sand lance and within herring delivered to chicks of Rhinoceros Auklets in each visit at the Seabird Rocks breeding colony in 1995 and 1996

Date	Sand lance		Herring	
	0 +	1 +	0 +	1 +
Colony 1995				
July 4-5	8	92	0	0
July 14-15	80	20	100	0
July 24-25	98	2	50	50
August 3-4	100	0	0	0
Total *	72	28	75	25
Colony 1996				
July 7-8	54	46	100	0
July 17-18	41	59	50	50
July 30-31	100	0	50	50
Total *	65	35	67	33

* Chi-squared test for differences in age class composition between years (Sand lance: X^2=1.131, df=1, P=0.288; Herring: X^2=0.140, df=1, P=0.708).

Table 4-3. Interannual comparisons of growth rates (g/day) of Rhinoceros Auklet chicks estimated via the composite growth curve method and mean growth rates (± SD) based on sequential measurements of chicks in the 1995 and 1996 chick rearing phases at the Seabird Rocks colony. Independent sample t-test results are also presented

	Year				
Growth Rate Estimate Method	1995	1996	t statistic	df	P value
Composite Growth Rate (1995: July 4-14; 1996: July 7-17)	8.3	7.2	2.726	42	0.004
Number of chicks measured	11	12			
Sequential Growth Rate (1995: July 4-24; 1996: July 7-31)	3.7 ± 0.8	4.8 ± 1.1	2.527	17	0.022
Number of chicks measured	9	10			

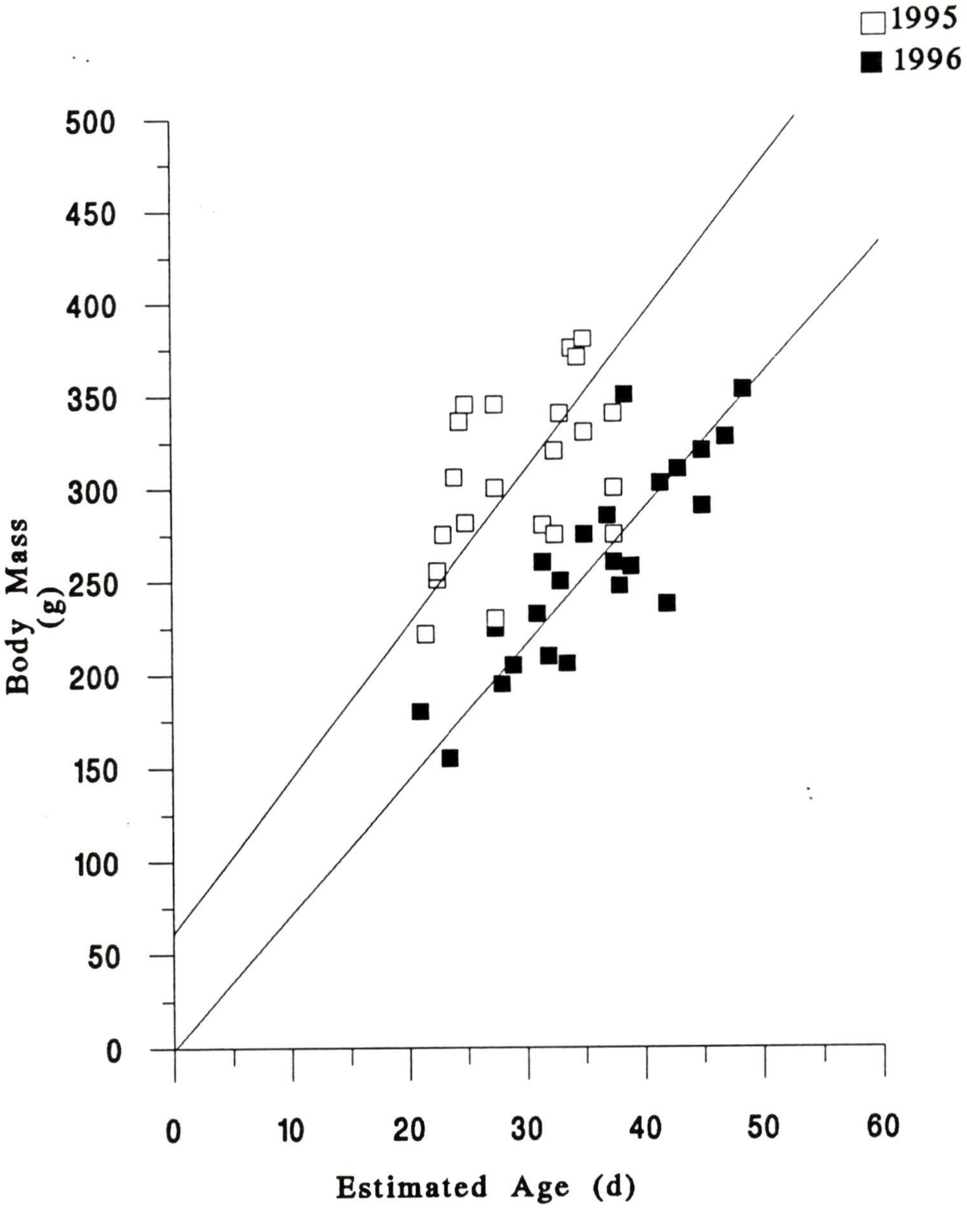


Fig. 4-2. The composite growth curve for Rhinoceros Auklet chicks from Seabird Rocks in 1995 (n=22) and 1996 (n=24) at two visits (visit 1=July 4-7; visit 2=July 14-17).

species that make up significant parts of nestling diets include salmon, herring, Pacific saury, northern anchovy and rockfish (Gaston and Dechesne 1996). Pacific saury and rockfish are generally important prey species at oceanic breeding colonies (e.g. Triangle and Destruction Islands; Vermeer et al. 1987) and, therefore, were not expected at this colony. Seabird Rocks was the only colony where surf smelt appeared in auklet diets, possibly due to suitable spawning habitat in the study area. Most fish delivered in meals of chicks also fell within the normal size range reported in other studies for these auklets (50-120 mm; Gaston and Dechesne 1996).

PROVISIONING AND GROWTH

Mean bill loads in British Columbia ranged between 23.8-33.9 g (8 colony years, Bertram and Kaiser 1993) and in Washington ranged between 19.0-33.9 g (12 colony years, Wilson and Manuwal 1986). The mean bill load mass of 44.7 ± 13.1 g collected in 1996 of this study is higher than other reported averages, the highest of which was 39.6 ± 16.5 g (standard deviation) at Semidi Island in Alaska (n=68; Hatch 1984). Bill loads are the primary measure of food loads in most studies; therefore, there are few records of burrow loads. Hatch (1982) reported that burrow loads ranged between 9.9-81.3 g (mean 39.6 g) for Rhinoceros Auklets in one year and 6.5-80.5 g (mean 36.4 g) in another year, using the screening technique. These were similar to my results but my mean values were lower.

As do most seabirds, Rhinoceros Auklets have sigmoidal growth curves; thus, growth rates vary with chick age (Bertram et al. 1991). Growth rates of chicks of Rhinoceros Auklets reported in the literature ranged from 3.8-7.4 g/d, with the majority falling within 5.0-6.0 g/d (Leschner 1976; Wilson and Manuwal 1986; Bertram et al. 1991; Harfenist and Ydenberg 1995; Gaston and Dechesne 1996). Growth rate estimates of the chicks in this study generally fell within these ranges. Both sequential and composite methods were used to estimate growth rates for Rhinoceros Auklet chicks in one other study (Bertram et al. 1991). Growth rates estimated by the sequential method were much lower than composite growth estimates in both this study and Bertram et al. (1991). Bertram et al. (1991), however, observed a similar interannual trend in growth rates of chicks using the two methods, whereas I found a difference in interannual trends using these two methods.

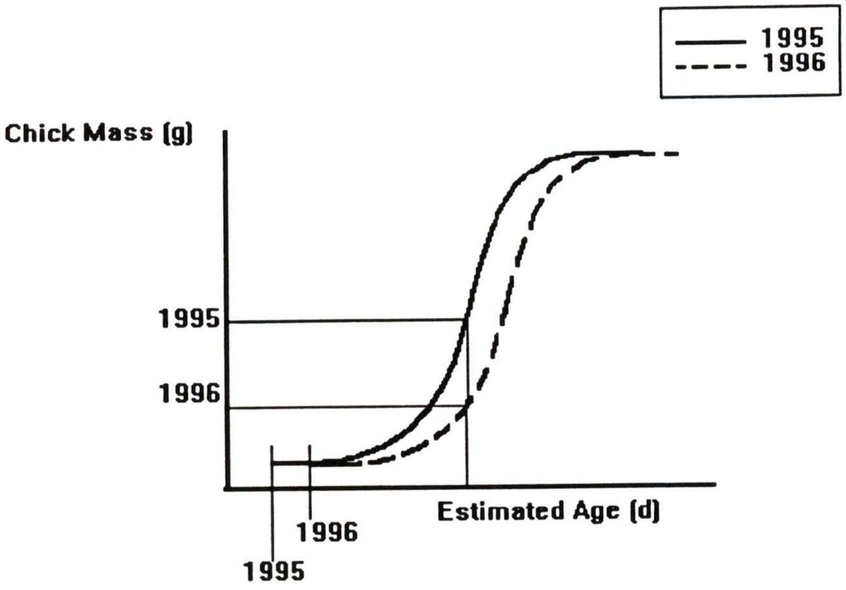
INTERANNUAL DIFFERENCES IN REPRODUCTIVE EFFORT

Chick provisioning was significantly higher in 1996 than in 1995, shown by heavier bill loads. Heavier burrow loads were not observed in 1996 potentially due to the errors surrounding the screening technique. For instance, fish may be lost either by parents eating fish when they can not deliver them to their chicks or by not collecting fish that were scattered farther away from screens. Growth rates of chicks were higher throughout the chick rearing phase than in 1996 than in 1995 but growth rates were higher in early chick rearing in 1995 than in 1996. In addition, chick mass appeared to be heavier during early chick rearing in 1995 than in 1996.

These results may be interpreted in a number of ways. First, auklets may have delayed breeding in 1996, which would result in measuring chicks at different points along their sigmoidal growth curves (Fig. 4-3a). This would explain the lower growth rates and lighter mass of chicks observed during early chick rearing in 1996, relative to 1995. Delayed breeding in 1996, however, does not explain the significantly higher food loads delivered to chicks in 1996 over 1995, which exceeded food load sizes reported in all other studies on this auklet. In addition, this does not explain the higher growth rates of chicks over the entire chick rearing period in 1996 over 1995.

An alternative explanation is based on two results: chicks were smaller and growth rates of chicks were lower during early chick rearing in 1996 than in 1995. The smaller chick sizes in early chick rearing in 1996, compared to 1995, may have resulted from the lower growth rates in early chick rearing in 1996. Parents may have delivered larger food loads to chicks throughout the rest of chick rearing (Table 4-1) to compensate for both the lower initial growth rates and chick sizes in 1996, compared to 1995 (Fig. 4-3b). Lower chick mass early in chick rearing is known to influence chick growth for only a few days, after which parents are able to increase growth rates, thereby compensating for any differences in size by the time chicks fledge (Gaston and Nettleship 1981; O'Connor 1975). Therefore, lowered chick masses in early chick rearing may have caused

Delayed Breeding in 1996



Lower Initial Chick Sizes in 1996

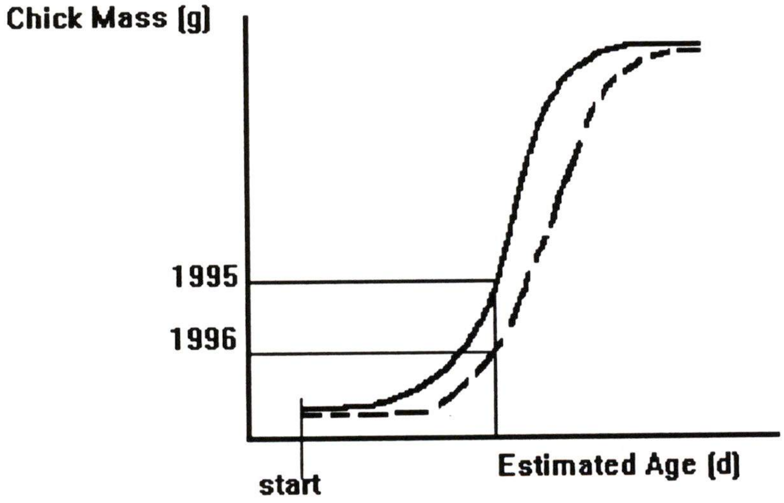


Fig. 4-3. Hypothetical sigmoidal chick growth curves showing changes in chick growth rates and chick mass between years when sampling at the same dates due to delayed breeding in 1996 relative to 1995 and lower initial chick mass in 1996 relative to 1995.

adults to increase chick provisioning, which resulted in a higher growth rate of chicks throughout chick rearing in 1996 compared to 1995 (Fig. 4-3b).

These smaller chick sizes may have resulted from lower prey availability during the egg-forming period and during early chick rearing (late June - early July). Lower prey availability during early chick rearing may also explain the lower initial chick growth rates. Unfortunately, prey abundance and density of both route and flock-focused transects could not be compared between years during these periods, due to the late sampling period in 1995 (chapter 1, Fig. 1-3). Reduced prey availability during egg formation in 1996, however, may have occurred due to the late establishment of coastal upwelling in 1996 compared 1995 (Fig. 4-4). Since nutrients were not being upwelled into the surface layers until at least two weeks later in 1996, the burst in primary productivity was probably delayed, leading to a temporal delay in the spring/summer peaks in zooplankton biomass (Mackas 1992; Denman et al. 1989). This would subsequently cause a temporal delay in the transport of plankton biomass towards the Strait of Juan de Fuca, via the Juan de Fuca canyon, which would subsequently delay the northward transport of biomass into my study area, via the Vancouver Island Coastal Current (Thomson et al. 1989; McFarlane et al. 1995). Continued southeast winds, or downwelling-favorable winds, would also increase the northward dispersal of plankton biomass via the VICC, probably resulting in reduced fish densities in my study area, since fish would likely follow the dispersal of their prey. Other studies have also linked the timing and abruptness of upwelling establishment and subsequent strength of the VICC to changes in the distribution and abundance of fish larvae, fish adults and invertebrate larvae (McFarlane et al. 1995; Ware and McFarlane 1995; Jamieson et al. 1989).

Overall these results show that auklets were able to increase chick provisioning. This shows that they are able to adjust provisioning during the breeding season and that they may be able to buffer the negative effects of lowered prey availability, or other adverse conditions, on breeding success.

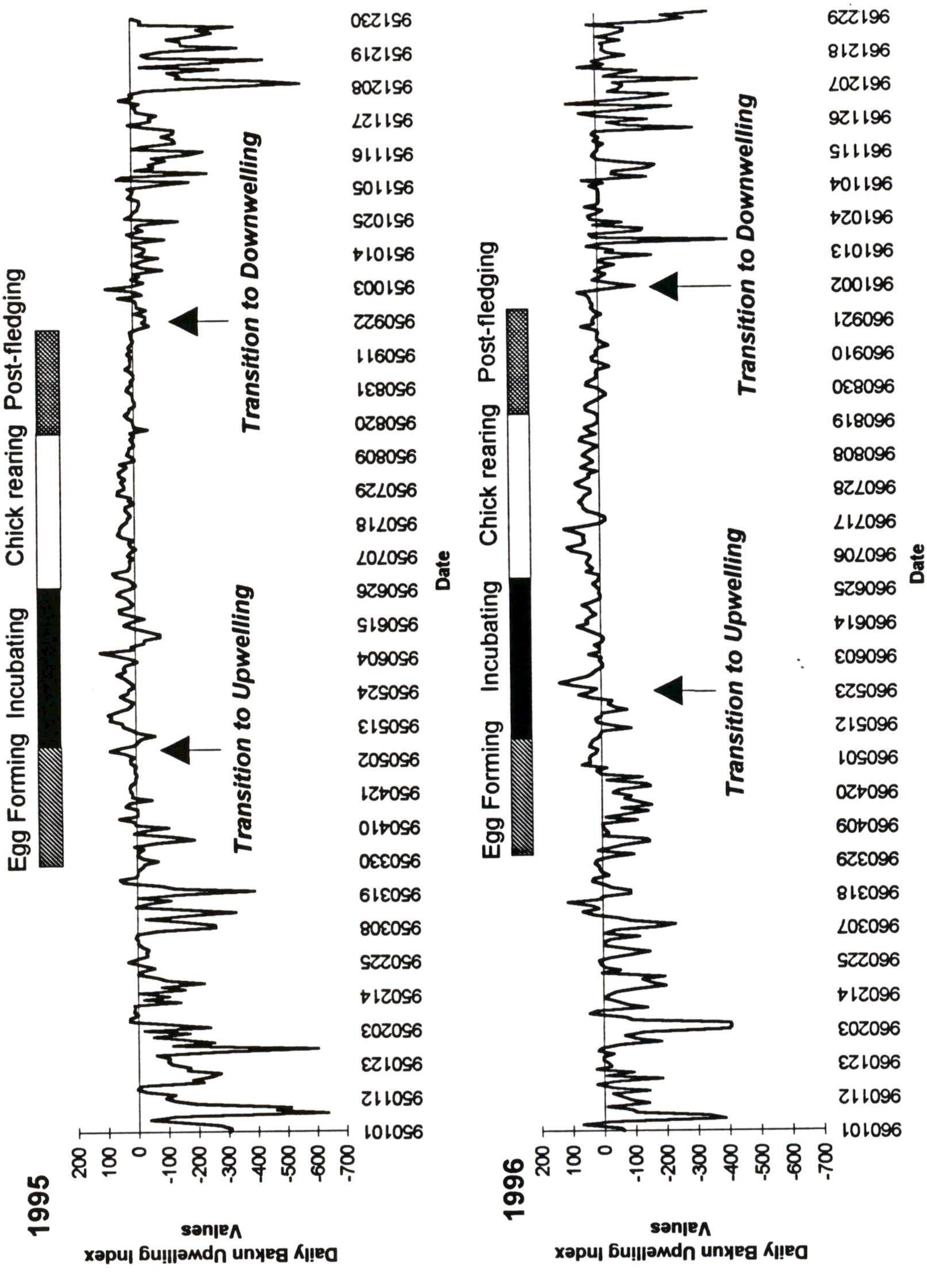


Fig. 4-4. Daily Bakun upwelling index values for 1995 and 1996, indicating breeding phases and the transitions to upwelling (+) and downwelling (-).

SYNTHESIS DISCUSSION

This study was the first to simultaneously record ocean-based and colony-based measures of foraging and provisioning, along with at-sea time budget information for a pursuit-diving seabird. This approach allowed greater insight into the prey base dynamics surrounding the breeding colony and the oceanographic processes that influence prey availability. This study was also the first to describe time budgets of Rhinoceros Auklets at sea, including both provisioning and self-feeding behaviours. Time budgets of pelagic seabirds are generally not well known.

The major findings of this study were threefold. First, auklets made a consistent switch between both foraging strategies and prey preferences when self-feeding in comparison to when collecting meals of chicks. Second, auklets showed great plasticity in their foraging strategies and prey-tracking behaviours and showed flexibility in their time budgets and provisioning behaviour when faced with varying prey availability and varying provisioning demands. Third, sampling of nestling and adult diets reflected both diurnal behaviours and seasonal habitat preferences of auklet prey species. The latter two results suggest that these auklets may be reasonable indicators of prey availability and prevailing ocean conditions.

SELF-FEEDING VERSUS CHICK PROVISIONING BEHAVIOUR

During chick rearing, auklets collected meals of chicks only in the late afternoon and evening. This may have been due to higher prey availability at this time but is more likely related to the nocturnal provisioning behaviour of these auklets. Nocturnal provisioning is thought to be a response to the threat of predation (e.g. by Peregrine Falcons) and kleptoparasitism (e.g by large gulls) at breeding colonies (Watanuki 1990; Paine et al. 1990). These threats also may explain why each parent usually only makes one trip to the colony each night, rather than many trips per night. In addition, auklets probably wait until the evening to collect fish for chicks to minimize the constraints of holding fish in their bills and this also may reduce dehydration of fish delivered to chicks. Montevecchi and Piatt (1987) showed that small fish can lose up to 12% of their body mass per hour when exposed to winds similar to those during flight in the bill of a bird. Dehydration of fish may be important because fish are presumably a major source of water for nestlings.

Fish collected for chicks were significantly larger than those collected at feeding flocks. Researchers have observed such prey size selectivity for chick meals in other seabird species (Mahon et al. 1992; Vermeer et al. 1987; Bradstreet and Brown 1985). For instance, Marbled Murrelets foraged extensively in feeding flocks during chick rearing; however, they never collected the juvenile sand lance found in these feeding flocks for their chicks (Mahon et al. 1992). Instead, larger sand lance (age class 1+), herring and shiner perch were collected for chicks (Mahon et al. 1992). Other studies have shown that seabirds feeding primarily on zooplankton as adults brought back primarily fish to their chicks (Vermeer et al. 1987; Bradstreet and Brown 1985). In addition, adult diets of piscivorous seabirds may contain a wide variety of lower quality fish (e.g. less energetic value), whereas chick diets primarily contain only fish of high caloric value (Cairns 1984; Piatt 1987). This type of prey selectivity is a function of food delivery in bills because adults that regurgitate prey to their chicks are not constrained by the number of prey items that they can collect.

Central-place foraging theory predicts that foragers/provisioners should increase the amount of energy gained at a prey patch when travel times to the patch from the central place increase (Orians and Pearson 1979). However, auklets only provision their chicks once a day and, thus, do not act as ‘classical’ central-place foragers/provisioners, which provision their chicks a number of times a day. For instance, as travel times increase, food loads delivered to chicks do not necessarily increase because with only one chance to provision chicks each day, auklets should always maximize food loads. Maximizing food loads is probably very important to the breeding success of auklets because the food load size that parents deliver to chicks each night determines the growth rates of chicks. Consequently, this may cause auklets to be more selective of both the prey items and foraging strategies used when collecting meals for chicks. For instance, even with an unlimited supply of small fish, adults may never be able to collect a sufficient mass of these small fish for chick meals. To illustrate, 30 fish is the maximum number of fish known to be delivered to chicks of Rhinoceros Auklets (Gaston and Dechesne 1996). The fish found at feeding flocks in my study were on average 0.95 ± 0.3 g. Therefore, the maximum load of small fish that a parent could bring back has a theoretical range between 28.5 - 37.5 g. In comparison, bill loads containing larger fish in this study (i.e. surf smelt and 1+ herring), were on average 48.4 ± 13.7 g. This suggests that parents were able to maximize food loads delivered to chicks by selecting larger prey items.

Time also may be a constraint for these auklets, because they must collect fish for chicks all at once in the evening, which again differs from the 'classical' central-place foraging/provisioning scenario. Many factors may elevate the time spent collecting fish in feeding flocks, compared to diving solitarily, because adults must hold fish in their bills for delivery to chicks. For instance, because small fish were found only at feeding flocks, the time spent collecting fish at a feeding flock should increase as the number of fish in the bill increase, due to the parent's inability to handle a large number of prey items ('loading effect'; Pyke 1984). In addition, the time spent collecting fish at a feeding flocks also will increase if parents lose previously collected prey items, due to kleptoparasitic attacks by gulls. Consequently, it may be more time efficient to collect a few large fish for chicks by solitary diving, than collecting a large number of small fish by flock diving. In contrast, when self-feeding, auklets are not faced with these constraints because they swallow fish soon after capturing them; thus the time required to capture and handle prey is negligible. Consequently, it may be more efficient to collect a few small fish that are abundant and highly accessible for self-feeding, especially because little time and energy was probably expended in locating the patch initially.

Overall, auklets selected different fish sizes and foraging strategies for self-feeding than for collecting chick meals. Although several studies have documented different adult and chick diets, this is the first study to document different foraging strategies used in adult and chick provisioning. This shows that auklet parents make different foraging decisions when collecting fish for their chicks than when self-feeding, as predicted by Ydenberg (1994).

RESPONSES OF FORAGING BEHAVIOUR TO VARIABLE PREY AVAILABILITY AND PROVISIONING DEMANDS

Overall, auklets showed flexibility in their time budgets and foraging strategies when faced with varying prey availability and provisioning demands. During periods of low prey density and abundance, auklets appeared to increase solitary diving, thereby increasing search activities and possibly maintaining contact with prey patches. Flexibility in daily time budgets has been shown for many other seabirds, by decreased resting times at the colony or increased durations of foraging trips, when food supplies were reduced (Burger and Piatt 1990; Burness et al. 1994; Uttley et al. 1994; Monaghan et al. 1994; Birkhead and Nettleship 1987; Hamer et al. 1991). Auklets were also able to adjust chick provisioning, resulting in increased growth rates of chicks, compared to other years of this study. Flexible provisioning efforts of seabirds also have been demonstrated in other studies (e.g. Bertram et al. 1991; Bertram and Kaiser 1993). The ability to adjust foraging and chick provisioning suggests that these auklets were not working at maximum capacity during the breeding season. This also is supported by the fact that one quarter to one half of the total surveyed population of auklets was resting at any given time (chapter 2, Table 2-1 and 2-2). Other studies have confirmed a high percentage of resting in the daily time budgets of other alcids species (e.g. Common Murres; Cairns et al. 1987; Cairns et al. 1990).

Auklets also showed great plasticity in their foraging strategies. During chick rearing, auklets appeared to be able to offset increased provisioning demands by increased flock diving. This appeared to allow auklets to maintain foraging activities at levels consistent with other breeding phases, despite the need to collect fish for both themselves and their chicks. In addition, auklets may have minimized energetic expenditure during chick rearing by concentrating foraging efforts at temporally predictable prey concentrations. This use of predictable prey concentrations during the breeding season appears to be a commonly used strategy in seabirds (Schneider et al. 1990; Hunt et al. 1990; Cairns and Schneider 1990; Coyle et al. 1992; Hunt et al. 1988).

Flock diving behaviour, on the other hand, appeared to increase primarily in response to the size, density, accessibility and predictability of prey schools, rather than in response to higher energetic demands imposed by low prey density and abundance in the study area. To illustrate, when prey density and abundance was low but schools were not large and concentrated, auklets did not shift to increased flock diving. In support, auklets foraged in feeding flocks with the same intensity and persistence regardless of provisioning demands and the level of prey availability.

The use of different foraging strategies, predictable prey concentrations and ultimately the ability to increase the time spent foraging and provisioning are probably important characteristics of seabird life history because prey availability appeared to be highly variable during the breeding season (chapter 1; Fig. 1-3). The flexibility described for Rhinoceros Auklets in this study suggests that parents are capable of buffering the negative effects of low prey availability on breeding success and potentially on their own survival. Overall, by increasing reproductive success and the probability of survival in any one breeding season, these auklets may maximize the number of offspring produced per lifetime ('lifetime reproductive success'; Newton 1989).

Despite all of these mechanisms to compensate for fluctuations in prey availability during the breeding season, these auklets still have large ranges in the duration of chick rearing, growth rates of chicks and body mass at fledging (Vermeer and Cullen 1979; Wilson and Manuwal 1986; Harfenist 1991; Harfenist 1995; Ydenberg et al. 1995). This may be explained by the parent-offspring conflict regarding when to fledge, which appears to depend on trade-offs between higher safety in the nest and higher growth rates at sea (Harfenist 1991; Harfenist 1995; Ydenberg et al. 1995). In addition, this may reflect differences in parent quality (Newton 1989) and/or reflect the highly unpredictable nature of prey availability around seabird colonies (Gaston 1985; Vermeer and Cullen 1979).

AUKLET DIETS REFLECT THE DISTRIBUTION AND BEHAVIOUR OF THEIR PREY

Fish populations in inshore areas are difficult to sample using conventional fishery methods and, therefore, little is known of their distribution and behaviour (Hay et al. 1992; Hart 1973). Traditional fisheries surveys, using hydroacoustical techniques, are often capable of determining the biomass of fish in an area, however, it is impossible to reliably determine the composition of fish species, even with the most sophisticated technology available. Generally 'ground-truthing' is required to determine which species comprise the fish biomass sampled hydroacoustically. Many fisheries scientists do this by towing various types of nets behind large research vessels, with high operating costs. Many nets used to sample fish are highly selective and the majority of them are not able to sample fish in the top 20 m of the ocean (Cairns 1992). Due to these problems, scientists have begun exploring different methods of monitoring fish populations.

Many researchers have suggested that the diets of certain seabird nestlings provide a means of sampling fish populations (Vermeer 1980: Vermeer and Westrheim 1984; Bertram and Kaiser 1993; Burger et al. 1993; Hatch 1982; Hatch and Sanger 1992). Rhinoceros Auklets collect a variety of fish species and year classes (50-120 mm) for their chicks and, thus, are thought to be good samplers of the prey in proximity to colonies during the breeding season (Bertram and Kaiser 1993). Rhinoceros Auklets also are able to switch between different prey species when fish populations fluctuate between years and, thus, are not thought to be highly selective. For instance, when sand lance were in short supply around the Triangle Island breeding colony in one year, adult Rhinoceros Auklets were able to deliver a higher proportion of Pacific saury to their chicks and, thus, maintained growth rates of chicks (Vermeer et al. 1979). In contrast, Tufted Puffins, breeding in this colony, were apparently unable to switch to Pacific saury during this year, resulting in massive breeding failure (Vermeer et al. 1979). In addition, the diets of Rhinoceros Auklets nestlings have reflected significant changes in year class strength of sand lance between successive breeding seasons (Bertram and Kaiser 1993; Bertram et al. 1991). Overall, it appears that Rhinoceros Auklets are not highly selective and thus may act as adequate samplers of the composition of fish species in an area.

In support, nestling diets of auklets in this study contained a wide variety of fish species and age classes within species. By simply collecting fish at feeding flocks, an inaccurate account of the species composition in the area would have resulted. In addition, nestling diets in this study appeared to document the habitat preferences of auklet prey. For instance, the consistency of juvenile herring, sand lance and salmon in chick diets suggests that the study area acted as rearing or nursery grounds for these fish. The consistent presence of surf smelt in chicks diets also suggests that the study area may be an important spawning area for these fish. Burger et al. (1993) also found a consistent presence of surf smelt at Seabird Rocks, but studies at other colonies in British Columbia and Washington did not find surf smelt in chick diets (Gaston and Dechescne 1996).

In addition, sampling fish delivered to chicks and sampling fish at feeding flocks documented the diurnal behaviour of certain juvenile fish species and reflected behavioural differences of fish in the study area. First, only juvenile sand lance and herring were collected at feeding flocks, possibly reflecting differences in schooling behaviour or preferences for vertical positions in the water column both between age classes within species (e.g. adult versus juvenile herring) and also between different fish species (e.g. juvenile herring versus juvenile salmon). Despite the importance of juvenile fish to recruitment into commercial stocks, very little is known of their behaviour. Even less is known about the behaviour of commercially unexploited species (e.g. sand lance) that constitute a large proportion of the diets of commercially important species. Juvenile behaviour also may be important in determining age-specific mortality due to predation both by birds and other marine predators, which may be substantial when fish concentrate in rearing habitats (Hay et al. 1992). Clearly, further investigation of juvenile fish behaviour is required.

CONCLUSIONS

Time budgets, foraging strategies, prey-tracking behaviour, chick provisioning and chick growth rates of auklets appeared to be sensitive to fluctuations in prey availability. The role of flock diving as a buffer against increased energetic expenditure, however, was unclear. Adult and nestling diets of auklets also reflected both the diurnal behaviour and habitat preferences of prey species. The wide variety of fish species found in nestling diets supports the idea that auklets are reasonable samplers of the species composition of fish in that area surrounding breeding colonies. All of this information suggests that auklets may act as reasonable monitors or indicators of prevailing ocean conditions. Due to the complexity of behavioural adjustments to prey availability, however, scientists will have to carefully chose the seabird parameters used to monitor changing ocean conditions. For instance, the time budgets of auklets appeared to be more sensitive to fluctuations in prey availability, compared to chick growth rates, as previously suggested for other seabird species (Cairns 1987; Burger and Piatt 1990). This emphasizes the importance of examining the buffering capabilities of seabirds when designing experiments to test their ability to indicate changes in the ocean environment. In addition, correlations between auklet and prey densities were weaker during periods when auklets were not actively foraging. This is an important consideration when designing future studies employing transect methods to explain seabird distributions at sea.

In addition, seabird and fisheries managers must remember that there are limits to which auklets can indicate changing prey availability. For instance, these auklets primarily feed in surface waters and thus they are likely to be useful indicators of changing prey availability only in the top 60 m (Burger et al. 1993). They also are confined to monitoring programs during the summer breeding seasons and to areas surrounding breeding colonies. There is also the problem of distinguishing between the three components of prey availability: abundance, density and accessibility. For instance, if fisheries managers wanted to compare the abundance of juvenile herring between years, changing auklet diets may reflect only the accessibility of these fish (e.g. vertical distribution in the water column), rather than their abundance. Conducting independent, non bird-biased, estimates of fish (e.g. hydroacoustic surveys) in the area of concern in conjunction with auklet diet sampling and time budget observations appeared to reduce this problem.

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Appendix 1-1. Index definitions for the foraging intensity of auklets in feeding flocks, the persistence of auklets at feeding flocks and the prey school size observed at feeding flocks.

Index	Category Values	Definition
Foraging Intensity Index of Auklets	0	**All Resting**
	1	**Most Resting** (mostly scattered with 10% diving)
	2	**Moderate Foraging** (50% diving; gulls are starting to vocalize and hover)
	3	**Most Foraging** (over 50% diving; gulls are vocalizing and hovering)
	4	**Frenzy** (100% diving; gulls are vocalizing, hovering and fighting for the center of the flock)
Persistence Index of Auklets at Feeding Flocks (after passage with boat)	0	**No Birds Returned** after passage with boat
	1	**Scattered Birds, Not Foraging**
	2	**Reassembled 1** - 20% are back, some foraging
	3	**Reassembled 2** - 50% are back, heavy foraging
	4	**Reassembled 3** - all came back, same as original
	5	**Reassembled 4** - more birds than the original
Fish School Size Index	0	**No Fish Observed**
	1	**Small School** (scattered, < 0.5 m)
	2	**Filled dipnet 1/8** (concentrated, 0.5 m)
	3	**Filled dipnet 1/4** (concentrated, 1.0 m)
	4	**Fill dipnet 1/2** (concentrated, 1.5 m)
	5	**Huge School** (concentrated, > 2 m)

Appendix 1-2. Seasonal and daily category definitions for all four chapters.

Environmental Variable	Category	Definition
Seasonal Categories		
Breeding Phase	Incubation	May 24 - June 12
	Chick Rearing	July 3 - August 5
	Post-fledging	August 20 - September 3
Prey Density (defined by route- focused transects)	Low	Below a prey density score of 0.01
	High	A prey density score of 0.01 and above
Wind Direction	Northwest	Northwest and Other
	Southeast	Only Southeast
Wind Speed	Low	< 20 km/hr (below 3 ft moderate seas)
	High	> 20 km/hr (3 ft moderate seas and above)
Prey Accessibility	High	When juvenile herring were concentrated in surface waters (June 13 - 20)
	Low	All other sampling dates
Daily Categories		
Time of Day - 1 (for transect data)	Morning	before 900 am
	Afternoon - Evening	after 900 am
Time of Day - 2 (for time budget data)	Morning	0500 to 08:59
	Mid-Morning to Early Afternoon	0900 to 12:59
	Mid to Late Afternoon	1300 to 16:59
	Evening	1700 to 2100
Tidal Stage	Low	3 hours surrounding low tide
	Flood	3 hours between low and high tide
	High	3 hours surrounding high tide
	Ebb	3 hours between high and low tide
Sea State (Beaufort Scale)	0	Calm -ocean glassy
	1	Calm - ocean is rippled
	2	One foot chop
	3	Two foot chop - white caps beginning to form
	4	Frequent white caps
	5	Three foot moderate seas
	6 - 10	Gale - greater than three foot moderate seas

Appendix 1-3. Statistical results of multi-factor ANOVAs comparing mean prey density scores within seasonal categories for route and flock-focused transects.

Seasonal Variability	Mean Square	df	F Ratio	P value
Route-focused				
1995				
Breeding Phase	0.000	1	0.057	0.821
Prey Density	0.012	1	21.342	0.006
Wind Direction	0.000	1	0.225	0.655
Wind Direction * Prey Density	0.000	1	0.433	0.540
Error	0.001	5		
1996				
Breeding Phase	0.000	2	1.892	0.187
Prey Density	0.006	1	67.868	<0.0001
Wind Direction	0.000	1	0.719	0.411
Prey Accessibility	0.001	1	13.650	0.002
Wind Direction * Prey Density	0.000	1	0.977	0.340
Prey Accessibility * Wind Direction	0.000	1	0.006	0.939
Prey Accessibility * Prey Density	0.001	1	14.472	0.002
Error	0.000	14		
Flock-focused				
1995				
Flock Areas				
Breeding Phase	0.819	1	1.875	0.220
Wind Direction	0.757	1	1.733	0.236
Wind Direction * Breeding Phase	0.727	1	1.655	0.244
Error	0.423	6		
Post Flock Areas				
Breeding Phase	0	1	0.056	0.821
Wind Direction	0	1	0.015	0.907
Wind Direction * Breeding Phase	0.006	1	1.135	0.328
Error	0.005	6		
1996				
Flock Areas				
Breeding Phase	0.337	2	1.269	0.310
Prey Density	0.713	1	2.684	0.122
Wind Direction	0.782	1	2.940	0.107
Prey Accessibility	0.023	1	0.086	0.774
Wind Direction * Prey Density	1.599	1	6.016	0.027
Error	0.266	15		
Post Flock Areas				
Breeding Phase	0.342	2	1.358	0.287
Prey Density	0.542	1	2.149	0.163
Wind Direction	0.005	1	0.020	0.888
Prey Accessibility	0.093	1	0.370	0.552
Wind Direction * Prey Density	0.040	1	0.160	0.694
Error	0.252	15		

Appendix 1-4. Statistical results of independent sample t-tests comparing mean prey density scores of flock and post-flock areas in flock-focused transects within seasonal categories.

Category	df	t statistic	P value
1995			
Breeding Phase			
Chick rearing	10	2.310	0.053
Post-fledging	6	1.863	0.112
Wind Direction			
Northwest	14	1.827	0.089
Southeast	2	0.598	0.611
1996			
Breeding Phase			
Incubation	4	0.117	0.913
Chick Rearing	26	1.477	0.152
Post-fledging	8	1.743	0.120
Wind Direction			
Northwest	30	1.185	0.246
Southeast	10	1.428	0.184
Prey Density			
Low	34	1.631	0.113
High	6	1.098	0.314
Prey Accessibility			
Low	34	1.642	0.110
High	6	0.761	0.475

Appendix 1-5. Statistical results of single and two-factor ANOVAs comparing mean prey density scores within day categories for route and flock-focused transects.

Within Day Variability	Mean Square	df	F Ratio	P value
Route-focused				
1995				
Tidal Stage	0.002	2	0.690	0.533
Error	0.002	7		
1996				
Tidal Stage	0.000	2	0.024	0.976
Time of Day	0.000	1	0.332	0.572
Tidal Stage * Time of Day	0.000	2	0.055	0.946
Error	0.000	17		
Flock-focused				
1995				
Flock Areas				
Tidal Stage	0.096	2	0.111	0.897
Time of Day	0.344	1	0.400	0.550
Error	0.860	6		
Post Flock Areas				
Tidal Stage	0.004	2	0.795	0.494
Time of Day	0.000	1	0.061	0.814
Error	0.005	6		
1996				
Flock Areas				
Tidal Stage	0.257	3	0.548	0.656
Time of Day	0.041	1	0.087	0.771
Error	0.468	17		
Post Flock Areas				
Tidal Stage	0.134	3	0.499	0.688
Time of Day	0.246	1	0.916	0.352
Error	0.269	17		

Appendix 1-6. Statistical results of paired sample t-tests comparing mean prey density scores, time of day and tidal height between feeding flocks containing herring and those containing sand lance.

Category	df	t statistic	P value
Prey Density - Flock Areas	13	0.260	0.800
Prey Density- Post-flock Areas	13	1.245	0.250
Tidal Height	13	1.592	0.139
Time of Day	13	0.053	0.959

Appendix 1-7. Statistical results of independent sample t-tests comparing fish standard lengths collected both in chick meals and at feeding flocks between years.

Category	df	t statistic	P value
Chick Meals			
0+ sand lance	113	6.457	<0.0001
1+ sand lance	49	1.682	0.098
0+ herring	25	3.1.38	0.006
1+ herring	10	0.138	0.898
salmon	46	3.097	0.003
surf smelt	22	1.644	0.121
Feeding Flocks			
0 + sand lance	201	8.314	<0.0001
0+ herring	338	2.258	0.025

Appendix 2-1. Statistical results of one-factor ANOVAs comparing the percentage of Rhinoceros Auklets in each activity category between breeding phases.

Activity Category	Mean Squares	df	F Ratio	P value
Flock Foraging	13.539	2	0.910	0.409
Solitary Foraging	0.733	2	0.06	0.941
Total Foraging	11.801	2	0.538	0.587
Resting	380.443	2	4.978	0.011
Maintaining	67.120	2	3.269	0.046
Swimming	852.457	2	10.285	<0.0001
Flying	19780.591	2	12.918	<0.0001
Number of Auklets	4312.585	2	20.19	0.143
Group Size of Auklets	0.344	2	0.402	0.671
Number of Feeding Flocks	3.266	2	2.070	0.139

Appendix 2-2. Statistical results of independent sample t-tests comparing the percentage of Rhinoceros Auklets in each activity category between prey density periods.

Activity Category	df	t statistic	P value
Flock Foraging	52	-0.294	0.775
Solitary Foraging	52	3.235	0.003
Total Foraging	52	0.745	0.473
Resting	52	-0.576	0.571
Maintaining	52	0.778	0.445
Swimming	52	-0.187	0.854
Flying	52	-0.344	0.739
Number of Auklets	52	-0.131	0.898
Group Size of Auklets	52	1.519	0.141
Number of Feeding Flocks	52	1.348	0.199

Appendix 2-3. Statistical results of multi-factor ANOVAs comparing the percentage of Rhinoceros Auklets in each activity category and the number of auklets, feeding flocks, auklets flying and the auklet group sizes between seasonal categories.

Activity Category	Mean Squares	df	F Ratio	P value
Flock Foraging				
Wind Speed	11.228	1	1.337	0.254
Wind Direction	0.064	1	0.008	0.931
Prey Accessibility	175.579	1	20.913	<0.0001
Wind Speed * Wind Direction	3.551	1	0.423	0.519
Prey Accessibility * Wind Speed	10.045	1	1.196	0.280
Prey Accessibility * Wind Direction	0.457	1	0.054	0.718
Error	8.396	44		
Solitary Foraging				
Wind Speed	0.000	1	0.000	0.996
Wind Direction	0.060	1	0.005	0.942
Prey Accessibility	1.458	1	0.128	0.772
Wind Speed * Wind Direction	1.176	1	0.103	0.749
Prey Accessibility * Wind Speed	1.850	1	0.102	0.689
Prey Accessibility * Wind Direction	2.163	1	0.190	0.665
Error	11.386	44		
Total Foraging				
Wind Speed	13.482	1	0.765	0.387
Wind Direction	1.302	1	0.074	0.787
Prey Accessibility	203.609	1	11.549	0.001
Wind Speed * Wind Direction	11.943	1	0.677	0.415
Prey Accessibility * Wind Speed	3.071	1	0.174	0.678
Prey Accessibility * Wind Direction	0.654	1	0.037	0.848
Error	17.630	44		
Resting				
Wind Speed	87.477	1	0.914	0.344
Wind Direction	11.095	1	0.116	0.735
Prey Accessibility	136.406	1	1.425	0.239
Wind Speed * Wind Direction	73.336	1	0.766	0.386
Prey Accessibility * Wind Speed	68.278	1	0.713	0.403
Prey Accessibility * Wind Direction	16.9	1	0.177	0.676
Error	95.710	44		
Maintaining				
Wind Speed	0.000	1	0.000	0.998
Wind Direction	19.433	1	0.793	0.378
Prey Accessibility	28.072	1	1.145	0.290
Wind Speed * Wind Direction	3.449	1	0.141	0.709
Prey Accessibility * Wind Speed	10.653	1	0.435	0.513
Prey Accessibility * Wind Direction	2.421	1	0.099	0.755
Error	24.513	44		

Appendix 2-3 continued

Activity Category	Mean Squares	df	F Ratio	P value
Swimming				
Wind Speed	193.178	1	1.614	0.211
Wind Direction	7.492	1	0.063	0.804
Prey Accessibility	80.685	1	0.674	0.416
Wind Speed * Wind Direction	3.468	1	0.029	0.866
Prey Accessibility * Wind Speed	45.895	1	0.383	0.539
Prey Accessibility * Wind Direction	4.307	1	0.0036	0.850
Error	119.700	44		
Numbers of Auklets Flying				
Wind Speed	18474.660	1	18.085	<0.0001
Wind Direction	11385.491	1	11.145	0.002
Prey Accessibility	8343.120	1	8.167	0.006
Wind Speed * Wind Direction	519.645	1	0.509	0.479
Prey Accessibility * Wind Speed	15991.682	1	15.654	<0.0001
Prey Accessibility * Wind Direction	12284.180	1	12.025	0.001
Error	1021.547	44		
Number of Auklets				
Wind Speed	4726.443	1	2.216	0.144
Wind Direction	89.696	1	0.042	0.838
Prey Accessibility	7794.248	1	3.655	0.062
Wind Speed * Wind Direction	318.803	1	0.149	0.701
Prey Accessibility * Wind Speed	1279.434	1	0.600	0.443
Prey Accessibility * Wind Direction	454.685	1	0.213	0.647
Error	2132.526	44		
Group Size of Auklets				
Wind Speed	0.025	1	0.026	0.872
Wind Direction	0.606	1	0.633	0.430
Prey Accessibility	0.599	1	0.584	0.449
Wind Speed * Wind Direction	0.092	1	0.096	0.758
Prey Accessibility * Wind Speed	0.439	1	0.458	0.502
Prey Accessibility * Wind Direction	0.513	1	0.536	0.468
Error	0.957	44		
Number of Feeding Flocks				
Wind Speed	2.165	1	1.718	0.197
Wind Direction	1.256	1	0.997	0.324
Prey Accessibility	17.149	1	13.610	0.001
Wind Speed * Wind Direction	0.036	1	0.028	0.867
Prey Accessibility * Wind Speed	1.834	1	1.455	0.234
Prey Accessibility * Wind Direction	1.685	1	1.337	0.254
Error	1.260	44		

Appendix 2-4. Statistical results of multi-factor ANOVAs comparing the percentage of Rhinoceros Auklets in each activity category and the number of auklets, feeding flocks, auklets flying and auklet group sizes between daily categories within each breeding phase.

Activity Category	Mean Squares	df	F Ratio	P value
Incubation				
Flock Foraging				
Time of Day	0.289	3	0.212	0.887
Tidal Stage	1.702	3	0.786	0.516
Sea State	0.208	4	0.152	0.960
Error	1.363	19		
Solitary Foraging				
Time of Day	196.859	3	4.369	0.017
Tidal Stage	5.805	3	0.129	0.942
Sea State	5.089	4	0.113	0.976
Error	45.057	19		
Total Foraging				
Time of Day	189.504	3	4.259	0.018
Tidal Stage	10.909	3	0.245	0.864
Sea State	4.451	4	0.100	0.981
Error	44.493	19		
Resting				
Time of Day	211.169	3	1.437	0.263
Tidal Stage	201.645	3	1.372	0.282
Sea State	135.982	4	0.925	0.470
Error	146.952	19		
Maintaining				
Time of Day	43.804	3	1.211	0.333
Tidal Stage	4.832	3	0.134	0.939
Sea State	11.613	4	0.321	0.860
Error	36.165	19		
Swimming				
Time of Day	94.02	3	0.627	0.607
Tidal Stage	177.891	3	1.186	0.342
Sea State	71.323	4	0.475	0.753
Error	150.037	19		
Number of Auklets Flying				
Time of Day	3098.248	3	2.121	0.131
Tidal Stage	1498.568	3	1.026	0.403
Sea State	510.975	4	0.350	0.841
Error	1460.889	19		
Number of Auklets				
Time of Day	5435.496	3	1.675	0.206
Tidal Stage	111.737	3	0.343	0.795
Sea State	329.955	4	0.102	0.981
Error	3245.571	19		
Group Size of Auklets				
Time of Day	1.262	3	1.615	0.221
Tidal Stage	0.291	3	0.372	0.774
Sea State	0.892	4	1.142	0.368
Error	0.781	19		

Appendix 2-4 continued

Activity Category	Mean Squares	df	F Ratio	P value
Number of Feeding Flocks				
Time of Day	3.857	3	1.575	0.228
Tidal Stage	2.456	3	1.003	0.413
Sea State	0.838	4	0.342	0.846
Error	2.449	19		
Chick Rearing				
Flock Foraging				
Time of Day	11.108	3	0.616	0.608
Sea State	90.272	4	5.007	0.002
Tidal Stage	51.401	3	2.851	0.046
Time of Day * Tidal Stage	20.09	9	1.114	0.369
Error	18.029	53		
Solitary Foraging				
Time of Day	132.551	3	4.716	0.005
Sea State	8.979	4	0.319	0.864
Tidal Stage	8.560	3	0.305	0.822
Time of Day * Tidal Stage	11.298	9	0.402	0.929
Error	28.105	53		
Total Foraging				
Time of Day	122.921	3	2.846	0.046
Sea State	85.747	4	1.986	0.110
Tidal Stage	113.759	3	2.634	0.059
Time of Day * Tidal Stage	26.350	9	0.610	0.783
Error	43.185	53		
Resting				
Time of Day	116.481	3	0.973	0.413
Sea State	143.55	4	1.199	0.322
Tidal Stage	99.102	3	0.828	0.484
Time of Day * Tidal Stage	310.804	9	2.595	0.002
Error	119.770	53		
Maintaining				
Time of Day	149.096	3	2.039	0.120
Sea State	153.364	4	2.079	0.094
Tidal Stage	17.635	3	0.241	0.867
Time of Day * Tidal Stage	57.929	9	0.792	0.625
Error	73.131	53		
Swimming				
Time of Day	104.596	3	0.696	0.559
Sea State	251.310	4	1.671	0.170
Tidal Stage	357.247	3	2.376	0.080
Time of Day * Tidal Stage	358.542	9	2.384	0.024
Error	150.373	53		
Number of Auklets Flying				
Time of Day	6295.028	3	4.492	0.007
Sea State	1786.823	4	1.275	0.291
Tidal Stage	408.866	3	0.292	0.831
Time of Day * Tidal Stage	739.896	9	0.528	0.848
Error	1401.364	53		

Appendix 2-4 continued

Activity Category	Mean Squares	df	F Ratio	P value
Number of Auklets				
Time of Day	45967.097	3	23.632	<0.0001
Sea State	8230.986	4	4.232	0.005
Tidal Stage	2662.860	3	1.369	0.262
Time of Day * Tidal Stage	3948.144	9	2.030	0.054
Error	1945.128	53		
Group Size of Auklets				
Time of Day	21.967	3	8.553	<0.0001
Sea State	2.710	4	1.055	0.388
Tidal Stage	2.770	3	1.078	0.366
Time of Day * Tidal Stage	2.621	9	1.021	0.436
Error	2.568	53		
Number of Feeding Flocks				
Time of Day	1.941	3	1.653	0.434
Sea State	3.326	4	0.505	0.191
Tidal Stage	8.884	3	1.767	0.009
Time of Day * Tidal Stage	2.718	9	1.085	0.261
Error	2.095	53		
Post-Fledging				
Flock Foraging				
Time of Day	17.822	3	0.602	0.625
Sea State	29.254	3	0.988	0.427
Tidal Stage	26.229	3	0.886	0.472
Time of Day * Tidal Stage	28.532	9	0.963	0.506
Error	29.620	14		
Solitary Foraging				
Time of Day	45.895	3	4.723	0.018
Sea State	42.205	3	4.343	0.023
Tidal Stage	17.502	3	1.801	0.193
Time of Day * Tidal Stage	26.835	9	2.761	0.043
Error	9.718	14		
Total Foraging				
Time of Day	87.431	3	3.714	0.037
Sea State	19.310	3	0.820	0.504
Tidal Stage	13.802	3	0.586	0.634
Time of Day * Tidal Stage	40.380	9	1.716	0.176
Error	23.539	14		
Resting				
Time of Day	161.511	3	2.356	0.116
Sea State	19.708	3	0.287	0.834
Tidal Stage	205.871	3	3.003	0.066
Time of Day * Tidal Stage	68.112	9	0.994	0.487
Error	68.536	14		
Maintaining				
Time of Day	49.359	3	1.724	0.208
Sea State	32.510	3	1.135	0.369
Tidal Stage	209.218	3	7.307	0.003
Time of Day * Tidal Stage	100.869	9	3.523	0.017
Error	28.634	14		

Appendix 2-4 continued

Activity Category	Mean Squares	df	F Ratio	P value
Swimming				
Time of Day	137.217	3	0.901	0.465
Sea State	63.458	3	0.417	0.744
Tidal Stage	107.292	3	0.705	0.565
Time of Day * Tidal Stage	147.056	9	0.966	0.505
Error	152.293	14		
Number of Auklets Flying				
Time of Day	30436	3	0.024	0.995
Sea State	281.657	3	1.960	0.166
Tidal Stage	33.257	3	0.231	0.873
Time of Day * Tidal Stage	170.023	9	1.183	0.375
Error	143.734	14		
Number of Auklets				
Time of Day	2536.48	3	2.070	0.150
Sea State	677.737	3	0.553	0.654
Tidal Stage	475.452	3	0.388	0.703
Time of Day * Tidal Stage	2670.910	9	2.180	0.092
Error	1225.402	14		
Group Size of Auklets				
Time of Day	0.484	3	1.015	0.415
Sea State	0.405	3	0.849	0.490
Tidal Stage	0.573	3	1.201	0.346
Time of Day * Tidal Stage	0.681	9	1.428	0.265
Error	0.477	14		
Number of Feeding Flocks				
Time of Day	4.173	3	3.045	0.064
Sea State	0.967	3	0.706	0.564
Tidal Stage	0.803	3	0.586	0.634
Time of Day * Tidal Stage	2.162	9	1.578	0.214
Error	1.370	14		

Appendix 2-5. Statistical results of multi-factor ANOVAs comparing the dive and pause durations of Rhinoceros Auklets both between seasonal and daily categories.

Within days and seasons	Mean Squares	df	F Ratio	P value
Daily Comparisons				
Dive				
Time of Day	9.140	3	0.043	0.988
Sea State	272.662	4	1.293	0.278
Tidal Stage	278.096	3	1.319	0.272
Error	210.823	100		
Pause				
Time of Day	626.067	3	2.019	0.116
Sea State	1030.873	4	3.325	0.013
Tidal Stage	415.817	3	1.341	0.265
Error	310.060	100		
Seasonal Comparisons				
Dive				
Prey Density	19.404	1	0.091	0.764
Breeding Phase	263.767	2	1.231	0.296
Wind Direction	0.018	1	0.000	0.993
Breeding Stage *	25.952	2	0.121	0.886
Prey Accessibility	39.680	1	0.185	0.668
Error	214.321	105		
Pause				
Prey Density	148.303	1	0.474	0.493
Breeding Phase	2248.396	2	7.190	0.001
Wind Direction	1.762	1	0.006	0.940
Breeding Stage	10.388	2	0.033	0.967
Prey Accessibility	896.403	1	2.867	0.093
Error	312.711	105		

* Breeding Stage: adults holding fish, adults not holding fish and juvenile auklets

Appendix 3-1. Statistical results of single and multi-factor ANOVAs comparing the magnitude of association and spatial overlap of auklets and prey schools both between seasons and days.

Seasonal and Daily Variability	Mean Squares	df	F Ratio	P value
Magnitude of Association (r values)				
1995 - Seasonal				
Breeding Phase	0.001	1	0.019	0.897
Prey Density	0.254	1	5.069	0.074
Wind Direction	0.116	1	2.303	0.190
Wind Direction * Prey Density	0.019	1	0.381	0.564
Error	0.050	5		
1995 - Daily				
Tidal Stage	0.010	2	0.110	0.898
Error	0.089	7		
1996 - Seasonal				
Breeding Phase	0.032	2	0.689	0.518
Prey Density	0.036	1	0.764	0.397
Wind Direction	0.114	1	2.449	0.140
Prey Accessibility	0.065	1	1.395	0.257
Breeding Phase * Prey Density	0.006	2	0.131	0.878
Wind Direction * Prey Density	0.000	1	0.000	0.997
Error	0.047	14		
1996 - Daily				
Tidal Stage	0.028	2	0.703	0.509
Time of Day	0.202	1	5.140	0.037
Tidal Stage * Time of Day	0.056	2	1.426	0.268
Error	0.039	17		
Spatial Overlap (Ro values)				
1995				
Breeding Phase	0.045	1	6.234	0.050
Prey Density	0.064	1	8.912	0.031
Wind Direction	0.002	1	0.275	0.622
Wind Direction * Prey Density	0.008	1	1.212	0.338
Error	0.007	5		
1995 - Daily				
Tidal Stage	0.007	2	0.245	0.789
Error	0.029	7		
1996				
Breeding Phase	0.022	2	1.857	0.193
Prey Density	0.006	1	0.526	0.480
Wind Direction	0.000	1	0.039	0.846
Prey Accessibility	0.009	1	0.760	0.398
Breeding Phase * Prey Density	0.022	2	1.864	0.192
Wind Direction * Prey Density	0.001	1	0.105	0.751
Error	0.012	14		
1996 - Daily				
Tidal Stage	0.001	2	0.079	0.924
Time of Day	0.012	1	0.742	0.401
Tidal Stage * Time of Day	0.012	2	0.723	0.500
Error	0.017	17		

Appendix 3-2. Statistical results of chi-squared tests comparing the number of transects showing patch scales of auklets and prey at the 1 minute frame size with transects showing patch scales of auklets and prey at higher frame sizes both between years and within years.

Category	X^2 value	df	P value
Year			
Prey	4.591	1	0.032
Auklets	1.660	1	0.198
1995 - Breeding Phase			
Prey	2.857	1	0.091
Auklets	0.800	1	0.371
1996 - Breeding Phase			
Prey	2.698	2	0.259
Auklets	10.284	2	0.006
1996 - Prey Accessibility Periods			
Prey	8.074	1	0.004
Auklets	0.009	1	0.924

Appendix 3-3. Statistical results of two and multi-factor ANOVAs comparing the behaviour of seabirds in mixed-species feeding flocks both between seasonal and daily categories.

Seasonal Variability	Mean Squares	df	F Ratio	P value
1995 - Seasonal				
Foraging Intensity Index				
Breeding Phase	0.394	1	0.580	0.475
Wind Direction	0.079	1	0.116	0.745
Wind Direction * Breeding Phase	0.004	1	0.006	0.939
Error	0.678	6		
Total Number of Birds				
Breeding Phase	59.037	1	0.065	0.807
Wind Direction	475.231	1	0.524	0.496
Wind Direction * Breeding Phase	0.973	1	0.001	0.975
Error	906.916	6		
1995 - Daily				
Foraging Intensity Index				
Time of Day	0.272	2	0.415	0.678
Tidal Stage	0.021	1	0.032	0.864
Error	0.655	6		
Total Number of Birds				
Time of Day	503.668	2	0.888	0.460
Tidal Stage	2003.215	1	3.533	0.109
Error	566.940	6		
1996 - Seasonal				
Foraging Intensity Index				
Breeding Phase	0.451	2	1.321	0.296
Prey Density	0.012	1	0.035	0.854
Wind Direction	0.011	1	0.033	0.857
Prey Accessibility	0.001	1	0.004	0.950
Prey Density * Wind Direction	0.001	1	0.002	0.969
Error	0.341	15		
School Size Index				
Breeding Phase	0.441	2	0.187	0.831
Prey Density	0.268	1	0.113	0.741
Wind Direction	0.038	1	0.016	0.900
Prey Accessibility	2.577	1	1.092	0.313
Prey Density * Wind Direction	0.111	1	0.047	0.831
Error	2.360	15		
Persistence Index				
Breeding Phase	1.418	2	1.648	0.225
Prey Density	1.205	1	1.401	0.255
Wind Direction	2.056	1	2.390	0.143
Prey Accessibility	1.178	1	1.369	0.260
Prey Density * Wind Direction	0.381	1	0.442	0.516
Error	0.860	15		

Appendix 3-3 continued

Seasonal Variability	Mean Squares	df	F Ratio	P value
Total Number of Birds				
Breeding Phase	2477.577	2	4.755	0.025
Prey Density	25.299	1	0.049	0.829
Prey Accessibility	76.741	1	0.147	0.707
Wind Direction	0.230	1	0.000	0.983
Prey Density * Wind Direction	9.429	1	0.018	0.895
Error	521.003	15		
1996 - Daily				
Foraging Intensity Index				
Tidal Stage	0.021	3	0.064	0.978
Time of Day	0.469	1	1.451	0.245
Error	0.323	17		
School Size Index				
Tidal Stage	2.760	3	1.415	0.273
Time of Day	2.648	1	1.358	0.260
Error	1.950	17		
Persistence Index				
Tidal Stage	0.853	3	0.601	0.623
Time of Day	0.000	1	0.000	0.995
Error	1.420	17		
Total Number of Birds				
Tidal Stage	391.728	3	0.540	0.661
Time of Day	49.781	1	0.069	0.797
Error	725.653	17		

Appendix 3-4. Statistical results of paired sample t-tests comparing the behaviour of seabirds at mixed-species feeding flocks between flock-focused transects containing herring and those containing sand lance.

Category	df	t statistic	P value
School Size Index	13	0.189	0.854
Feeding Index	13	0.660	0.525
Persistence Index	13	0.884	0.402
Total Number of Birds	13	0.846	0.419

Appendix 4-1. Statistical results of independent sample t-tests comparing the mean mass of bill loads and burrow loads between years, the mean mass and length of all fish species combined collected at the colony between years, and the mean number of fish and species in both bill and burrow loads between years.

Category	df	t statistic	P value
Mean Bill Load Mass	20	-2.829	0.011
Mean Burrow Load Mass	52	0.420	0.676
Bill and Burrow Loads			
Mean Fish Mass *	285	-3.037	0.013
Mean Fish Length *	285	-4.229	<0.0001
Bill Load			
Number of fish	20	0.741	0.470
Number of species	20	0.337	0.739
Burrow Load			
Number of fish	52	1.224	0.226
Number of species	52	-0.521	0.605

* All fish species combined

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Title of Thesis/Dissertation:

Parental Investment in the Rhinoceros Auklet (*Cerorhinca monocerata*) at the colony and at sea off southwestern Vancouver Island

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Gail Kathleen Davoren
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