BREEDING BIOLOGY OF THE FORK-TAILED STORM-PETREL *OCEANODROMA FURCATA* ON KASATOCHI ISLAND, ALEUTIAN ISLANDS, ALASKA

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SUMMARY

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We present the first detailed account of breeding biology in Fork-tailed Storm-Petrels *Oceanodroma furcata* from the Aleutian Islands, Alaska, where nearly two thirds of the global breeding population occurs. We examined timing of breeding, breeding success, chick growth, parental provisioning and chick diet during two consecutive breeding seasons at a colony in the central Aleutians. Most adults laid eggs before late May, eggs hatched between mid-June and early August and chicks began fledging in mid-August. Timing of breeding varied between years, with an earlier mean hatch in 2005 than in 2006. Hatching success was consistently high in both years (89% in 2005, 91% in 2006), but fledging success varied substantially between years (58% in 2005, 89% in 2006), indicating that factors that influence chick survival may drive annual breeding success. Visitation rate, meal size and composition of chick diets also varied between years, suggesting that foraging conditions varied during our study. Food availability and weather conditions may both have contributed to the variation we observed in timing of breeding and fledging success.

Key words: Aleutian Islands, breeding biology, chick survival, *Oceanodroma furcata,* storm-petrel

INTRODUCTION

The Fork-tailed Storm-Petrel *Oceanodroma furcata* is an abundant and widespread pelagic seabird in the northern Pacific Ocean. The species nests on islands from California to Alaska and in northeastern Asia, with most of the birds concentrated on offshore islands in Alaska (Boersma & Silva 2001). The highest numbers of Fork-tailed Storm-Petrels occur in the Aleutian Islands, which support nearly two thirds of the entire global breeding population (Boersma & Silva 2001, Byrd *et al.* 2005, USFWS 2006).

Despite the importance of the Aleutian Islands for Fork-tailed Storm-Petrels, data on their breeding biology in this region are lacking. Studies have been conducted at colonies in the Gulf of Alaska (Quinlan 1979, Boersma *et al.* 1980, Simons 1981, Baird & Gould 1983), British Columbia (Vermeer *et al.* 1988), Washington (Boersma & Silva 2001) and California (Harris 1974), but knowledge of the species' breeding biology in the Aleutian Islands is limited to baseline productivity data collected at several long-term monitoring sites (e.g. Andersen 2007) and unpublished historical data (Byrd & Trapp 1977). Understanding the breeding biology of Fork-tailed Storm-Petrels in the core of its range is important not only to the conservation of the species, but also for its potential use as an indicator of changing marine conditions in the northern Pacific ecosystem (Boersma *et al.* 1980, Boersma & Parrish 1998, Piatt *et al.* 2006).

Our goal was to conduct the first detailed study of Fork-tailed Storm-Petrel breeding biology in the Aleutian Islands. We examined timing of breeding, breeding success, chick growth, parental provisioning and chick diet at a colony in the central Aleutian Islands during two consecutive breeding seasons.

METHODS

Study site

We conducted our study at Kasatochi Island (52°11′N, 175°30′W), located within the Alaska Maritime National Wildlife Refuge in the central Aleutian Islands, Alaska (Fig. 1). Kasatochi is a small volcanic island of about 300 ha, with a large crater lake in the center. The climate is typical of the Aleutian Islands region, characterized by rain, thick fog, strong winds and frequent storms. Terrain includes rock cliffs, boulder beaches, grassy slopes and vegetated talus fields, which provide habitat for hundreds of thousands of breeding seabirds. The breeding population of Fork-tailed Storm-Petrels on the island during our study was estimated to be at least 2000 birds (Drummond & Rehder 2005, Drummond 2006).

After the present study, Kasatochi erupted violently on 7 August 2008, burying the entire island in lava and ash; the storm-petrel colony and all other seabird colonies on the island were destroyed (Alaska Volcano Observatory 2008, R. Buchhiet & J. Williams pers. comm.).

Study species

Fork-tailed Storm-Petrels are nocturnal, burrow-nesting seabirds that breed on islands in colonies ranging from fewer than 100 to more than 1 000 000 birds (Sowls *et al.* 1978, Boersma & Silva 2001, Byrd *et al.* 2005, USFWS 2006). The breeding period lasts up to four months, prolonged by episodes of egg neglect (Boersma *et al.* 1980, Simons 1981) and slow chick growth (Boersma *et al.* 1980). Females lay a single egg and both sexes participate in incubation and chick-rearing. Adults brood chicks for about five days post-hatch (Boersma *et al.* 1980), after which they leave the nest and return only briefly every one to four nights to feed chicks (Simons 1981). Chicks fledge after about two months (Boersma *et al.* 1980).

Timing of breeding, reproductive success, chick growth and visitation rate

We followed Fork-tailed Storm-Petrel nests during two breeding seasons (25 May–23 August 2005 and 21 May–1 September 2006) to determine timing of breeding (hatch date), reproductive success (hatching success, fledging success, overall success), chick growth (growth rate, final fledging mass) and visitation rate. In each year, we used all accessible nests in which we could view complete nest contents by flashlight (n = 79 in 2005, n = 103 in 2006). All nests used in 2005 were monitored in 2006 to determine the proportion of nest reuse. Once an egg or incubating bird was observed at the beginning of the season, we did not check nests again until close to predicted hatch in mid-June, when we checked nests daily to determine hatch date. After chicks hatched, we visited nests every two days until the nest failed or the chick fledged.

Chicks were considered failed if they died or disappeared from the nest at less than 50 days of age and fledged if they disappeared from the nest at 50 days of age or older. In cases in which we left the island while the chick was still in the nest, we considered chicks at those nests successful if they were 40 days of age or older and apparently healthy at our departure (n = 11 in 2005, n = 40 in 2006). The foregoing assumption is based on patterns of chick mortality in Fork-tailed Storm-Petrels, in which mortality occurs almost entirely in chicks younger than 20 days (Boersma *et al.* 1980, B. Drummond pers. obs.). The few chicks that were less than 40 days of age at our departure (n = 3 in 2005, n = 4 in 2006) were omitted from analyses of fledging success and overall success. We estimated hatching success as the number of eggs hatched divided by the number of eggs laid, fledging success as the number of chicks fledged divided by the number of eggs hatched, and overall success as the number of chicks fledged divided by the number of eggs laid.

We examined chick growth by measuring chicks from a subset of accessible nests (n = 26 in 2005, n = 43 in 2006), beginning after the brooding period ended [5.1 ± 2.4 days post-hatch (Drummond 2007)]. On each nest check (except on stormy days when removing the chick from the nest could be harmful), we measured mass [±0.5 g using a 100-g Pesola spring scale (Pesola, Baar, Switzerland)], wing chord length (±1 mm using a 150-mm wing ruler) and diagonal tarsus length (±0.1 mm using a dial calliper). From chick measurements, we calculated mean mass gain (g/day) from hatching to peak weight, and wing and tarsus growth (mm/day) during the linear growth periods, which we determined by fitting regression lines to the data. Because fledging size can affect post-fledging survival in some seabirds (e.g. Olson 1997, Sagar & Horning 1998), we also calculated mass at fledging for chicks that fledged before we departed the island.

We used toothpick knock-downs to record parental visits at night (Quinlan 1979), and we present visitation rate as a proxy for feeding rate. Toothpicks were placed across nest entrances in the evening and were checked the following morning; those that had been knocked down indicated that the nest had been visited that night by a parent carrying food. Visitation rate was defined as the percentage of nights a nest was visited between the end of brooding and death or departure of the chick from the nest. We assume that visitation rate generally represents feeding rate, because once brooding ends, adults return to the nest primarily to feed the chick (Simons 1981, Boersma & Silva 2001). We consider this measure an underestimate of true visitation rate, however, because it does not record incidents of two parental visits in a single night.

Chick meal size and diet composition

To determine chick meal size and diet composition, we captured adult storm-petrels (n = 32 in 2005, n = 53 in 2006) in mist nets at night, when birds were returning to the colony with food for chicks. When caught, birds spontaneously regurgitated the food they were carrying onto plastic sheeting stretched under the net. We captured birds at three regularly-spaced intervals during the nestling period: early (mid-July, when at least 70% of chicks were 0–20 days old), mid (late July, when

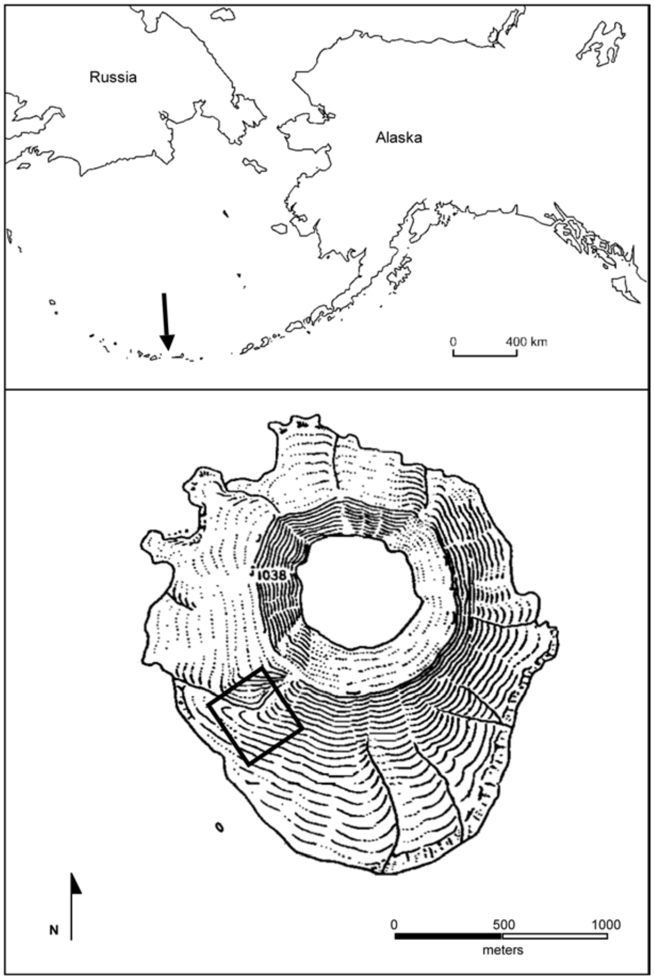

Fig. 1. Location of the Fork-tailed Storm-Petrel *Oceanodroma furcata* colony at Kasatochi Island, Aleutian Islands, Alaska.

at least 70% of chicks were 20–40 days old), and late (mid-August, when at least 70% of chicks were 40 or more days old). Sampling occurred between 23h00 and 03h00 on a single dry, overcast night during each period, except during the late nestling period in 2005 when sampling occurred over two nights because of rain.

To measure meal size, defined as the mass of an individual food load, we weighed regurgitation samples on site (±0.5 g with a 30-g Pesola scale). Samples were then preserved in 70% ethyl alcohol and 2% glycerine (2005) or Streck (Streck Laboratories, Omaha, NE, USA) tissue fixative (2006) and later identified to species or lowest taxonomic level possible (many to genus or species, and most to at least family) by K. Turco (Falco Consulting, Fairbanks, AK, USA). Small amounts of partially-digested fish and squid were unidentifiable and were categorized as such. From prey data, we determined diet composition by calculating the percentage occurrence and percentage biomass of prey items in chick diets during each of the three sampling periods (Vermeer & Devito 1988). Percentage occurrence was defined as the number of regurgitation samples containing a specific prey item divided by the number of samples. Percentage biomass was the mass of a prey item in a diet sample divided by the mass of the diet sample, calculated by multiplying the number of individuals of a prey item in a sample by a standard laboratory value for mass of that prey item.

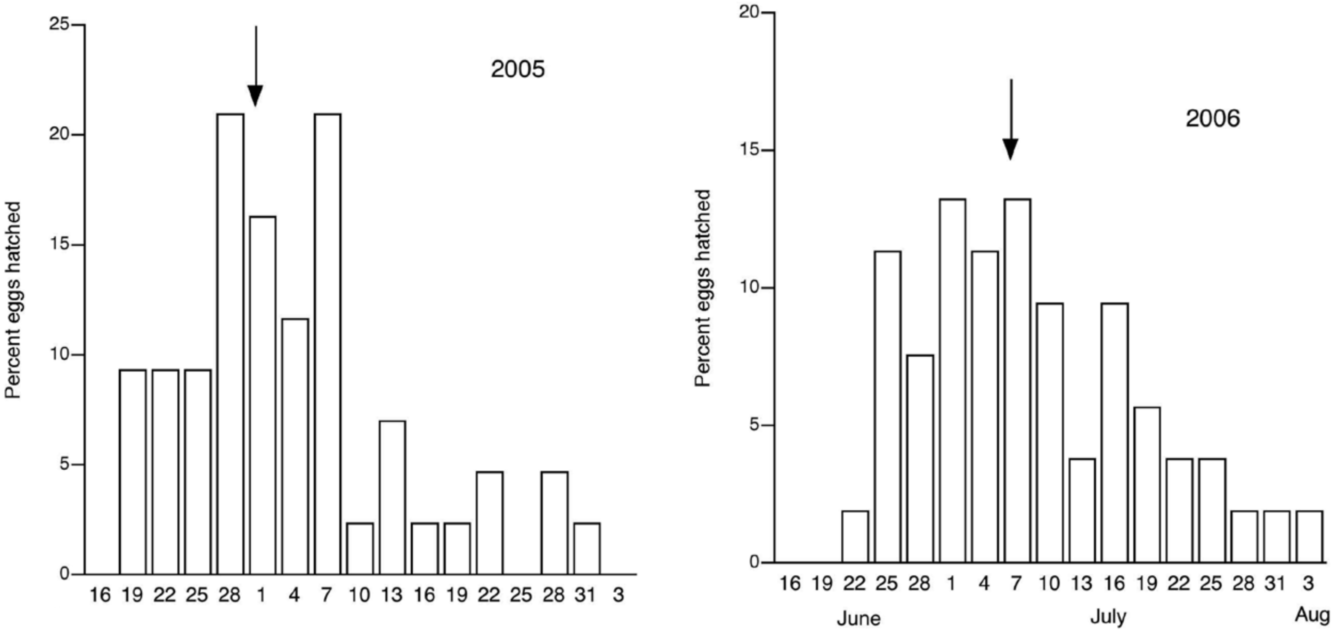

Fig. 2. Distribution of hatching dates of Fork-tailed Storm-Petrel *Oceanodroma furcata* eggs at Kasatochi Island, Alaska, in 2005 (n = 53) and 2006 (n = 53). Arrows indicate mean hatch date (1 July ± 10.1 days in 2005, 6 July ± 10.1 days in 2006).

TABLE 1
Reproductive performance of Fork-tailed Storm-Petrels *Oceanodroma furcata* at Kasatochi Island, Alaska, 2005 and 2006

Parameter	2005	2006	χ^2	df	*P* value
Eggs laid	79	103			
Eggs failed [n (% of all eggs)]	9 (11)	9 (9)			
Abandoned	7 (9)	5 (5)			
Broken or cracked	1 (1)	1 (1)			
Disappeared	1 (1)	3 (3)			
Eggs hatched [n (% of all eggs)]	70 (89)	94 (91)			
Chicks died	28 (35)	10 (9)			
Chicks survived	39 (49)	80 (78)			
Chicks 30–39 days at departure[a]	3 (4)	4 (4)			
Hatching success (%)	88.6	91.3	1.10	1	0.294
Fledging success (%)	58.2	88.9	24.66	1	<0.001
Overall success (%)	51.3	80.8	23.21	1	<0.001

[a] Chicks aged 30–39 days at our departure from the island were excluded from estimates of chick survival and overall success.

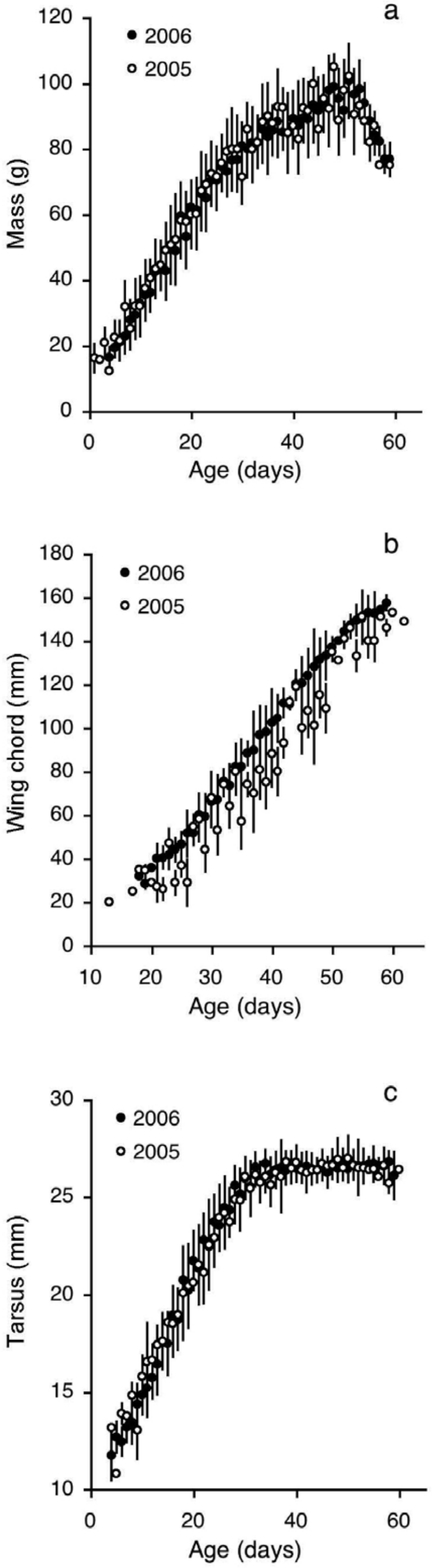

Fig. 3. Mean (± standard deviation) growth of (a) mass, (b) wing chord, and (c) tarsus in Fork-tailed Storm-Petrel *Oceanodroma furcata* chicks over the nestling period at Kasatochi Island, Alaska. Data include all known-age chicks that survived to fledge (n = 25 in 2005, n = 34 in 2006).

Data analysis

Of all nest sites monitored, 26 were occupied in 2005 only, 50 in 2006 only and 53 in both years. Sites used in both years were likely occupied by the same pair each year (Drummond 2007), because Fork-tailed Storm-Petrels have high nest-site fidelity (Boersma & Silva 2001). Therefore, parameters potentially related to individual birds, such as hatch date and feeding rate (e.g. Weimerskirch 1990), taken at the same nest in different years, are likely not independent. To account for this situation, we performed separate analyses for each year and restricted between-year comparisons to nests used in both years (n = 53). Meal size and diet composition were considered independent across years, because data were collected from mist-netted birds presumed not to be the same individuals in different years.

All statistical analyses were performed using JMP 5.0. We report means ± standard deviation and use α = 0.05 for statistical significance. For analyses of variance, we report only interaction terms that were significant at α = 0.05. Data for visitation rate and percentage biomass of prey were arcsine-transformed to better approximate a normal distribution. All variables otherwise met the assumptions of parametric tests, except for visitation rates in nests in which chicks died, for which we used a nonparametric test because of unequal variance (Ruxton 2006).

TABLE 2
Parameters of chick growth and parental provisioning[a] of Fork-tailed Storm-Petrels *Oceanodroma furcata* at Kasatochi Island, Alaska, 2005 and 2006

Parameter	2005	2006	*t*	df	*P* value
Linear growth rates					
Mass (g/d)	2.1±0.5 (n=25)	1.9±0.4 (n=38)	1.95	47	0.057
Wing chord (mm/d)	3.5±0.4 (n=22)	3.6±0.2 (n=37)	1.21	47	0.268
Tarsus (mm/d)	0.5±0.1 (n=25)	0.6±0.1 (n=38)	3.55	49	0.001
Fledging mass (g)	80.3±9.2 (n=3)	78.6±5.0 (n=12)	0.47	13	0.650
Visitation rate (%)	48.2±8.1 (n=43)	58.3±7.4 (n=73)	5.45	36	<0.001
Meal size (g)	6.5±1.5 (n=32)	8.2±1.5 (n=53)	2.21	82	0.030

[a] Mean ± standard deviation.

TABLE 3
Relationships between chick growth parameters and visitation rate at nests on Kasatochi Island, Alaska, 2005 and 2006

Parameter	2005			2006		
	r^2	n	*P*	r^2	n	*P*
Linear growth rate						
Mass (g/d)	0.001	15	0.942	0.136	33	0.035
Wing chord (mm/d)	0.070	15	0.341	0.089	32	0.097
Tarsus (mm/d)	0.007	15	0.773	0.009	33	0.598
Fledging mass (g)	0.070	3	0.209	0.032	12	0.580

RESULTS

Timing of breeding

In both years, most birds were incubating eggs upon our arrival at the island in late May. Hatching began in mid-June and continued to late July (2005) and early August (2006) (Fig. 2). Fledging began in mid-August and continued through our departure from the island in both years. Eggs hatched significantly earlier in 2005 (mean: 1 July ± 10.1 days) than in 2006 (mean: 6 July ± 10.1 days; paired $t_{20} = 2.14$; $P = 0.045$). Hatch date did not predict fledging success in either year (2005: $r^2 < 0.011$, n = 49, $P = 0.884$; 2006: $r^2 = 0.050$, n = 48, $P = 0.178$).

Reproductive success

Hatching success ranged between 89% and 91% and did not differ significantly between years (Table 1). The greatest source of egg failure was abandonment (Table 1). Fledging success, in contrast, varied between 58% and 89%, with significantly higher chick survival and, ultimately, overall reproductive success in 2006 than in 2005 (Table 1). Chick mortality occurred primarily when chicks were young, with approximately 81% of known-age chick deaths occurring before 10 days of age and 91% before 15 days of age in both years (n = 34). Only a single chick in each year died after the age of 20 days. Of nests used in 2005, 67% were reoccupied in 2006. As compared with nests that had been successful, nests that

TABLE 4
Percentage occurrence of prey items in diet samples collected from Fork-tailed Storm-Petrels *Oceanodroma furcata* at early, mid, and late nestling periods[a] at Kasatochi Island, Alaska, 2005 and 2006

Prey type	2005				2006			
	Early	Mid	Late	Total	Early	Mid	Late	Total
Crustaceans								
Amphipods	50.0	50.0	80.0	59.4	81.8	60.0	59.4	64.2
Parathemisto spp.	0.0	0.0	10.0	3.1	0.0	0.0	0.0	0.0
P. pacifica	0.0	0.0	10.0	3.1	36.4	0.0	0.0	7.5
Hyperia spp.	10.0	0.0	0.0	3.1	0.0	0.0	0.0	0.0
H. medusarum	0.0	0.0	0.0	0.0	0.0	0.0	3.1	1.9
Lysianassidae	50.0	50.0	80.0	59.4	63.6	60.0	50.0	54.7
Anoyx spp.	0.0	0.0	0.0	0.0	0.0	0.0	12.5	7.5
Unidentified amphipod	0.0	0.0	0.0	0.0	0.0	0.0	3.1	1.9
Copepods	10.0	0.0	0.0	3.1	45.5	10.0	0.0	11.3
Neocalanus cristatus	10.0	0.0	0.0	3.1	45.5	10.0	0.0	11.3
Euphausiids	10.0	0.0	0.0	3.1	18.2	10.0	3.1	7.5
Thysanoessa longipes	10.0	0.0	0.0	3.1	0.0	0.0	0.0	0.0
Unidentified euphausiid	0.0	0.0	0.0	0.0	18.2	10.0	3.1	7.5
Decapods	50.0	8.3	20.0	25.0	63.6	60.0	25.0	39.6
Atelecyclidae megalopa	30.0	8.3	10.0	15.6	63.6	40.0	21.9	34.0
Unidentified shrimp	20.0	0.0	10.0	9.4	9.1	30.0	3.1	9.4
Molluscs								
Squid	20.0	16.7	20.0	18.8	0.0	10.0	12.5	9.4
Fish								
Myctophids	80.0	91.7	90.0	87.5	63.3	90.0	78.1	77.4
Unidentified fish	0.0	0.0	10.0	3.1	9.1	10.0	25.0	18.9
Other (plastic)	20.0	16.7	0.0	12.5	0.0	0.0	0.0	0.0
Samples (n)	10	12	10	32	11	10	32	52

[a] "Early" samples collected when 70% chicks were 0–20 days (18 July 2005 and 16 July 2006); "mid" samples, when 70% chicks were 20–40 days (25 and 28 July 2005 and 31 July 2006); "late" samples, when 70% chicks were ≥40 days (14 and 16 August 2005 and 16 August 2006).

failed in the first year were significantly less likely to be reoccupied the following year ($\chi^2_1 = 11.78$, $P = 0.003$).

Chick growth and parental provisioning

Chicks attained a peak body mass (101.5 ± 7.5 g) at an average of 47.9 ± 5.2 days and then lost mass before fledging (Fig. 3). Wing chord and tarsus measurements reached asymptotes at 53.2 ± 7.2 days and 29.0 ± 2.3 days respectively (Fig. 3). Only tarsal growth rate varied significantly between years, with faster growth in 2006 than in 2005 (Table 2).

Visitation rates at individual nests varied from 32% to 75% (mean: 54.5% ± 9.1%; n = 116). Visitation rate and meal size were both significantly higher in 2006 than in 2005 (Table 2). However, there was no significant difference in visitation rate between nests where chicks died and where they survived (2005: $t_{21} = 0.50$, $P = 0.623$; 2006: $t_7 = 1.47$, $P = 0.184$). Chicks that were fed more frequently gained weight faster in 2006 but not in 2005 (Table 3). Visitation rate was not directly related to wing chord or tarsal growth, nor to final mass at fledging (Table 3).

Chick diet

Myctophid fish occurred in more than 75% of diet samples (Table 4) and made up more than 80% of the prey biomass (Table 5) in both years. Amphipods and decapods occurred in 25% to 64% of samples, but each contributed little to prey biomass (<1% to 1%). Small plastic particles were found in diet samples in 2005 but not in 2006 (Table 4).

The percentage occurrence of myctophid fish in chick diets did not vary between years ($\chi^2_1 = 1.41$, $P = 0.236$) or across the nestling period ($\chi^2_2 = 2.79$, $P = 0.248$). In contrast, the percentage biomass

TABLE 5

Percentage biomass of prey items in diet samples collected from Fork-tailed Storm-Petrels *Oceanodroma furcata* at early, mid and late nestling periods[a] at Kasatochi Island, Alaska, 2005 and 2006

Prey type	Mass standard (mg)[b]	2005				2006			
		Early	Mid	Late	Total	Early	Mid	Late	Total
Crustaceans									
Amphipods	—	0.2	0.1	0.4	0.3	0.3	0.1	0.2	0.2
Parathemisto spp.	3.0	0.0	0.0	<0.1	<0.1	0.0	0.0	0.0	0.0
P. pacifica	2.0	0.0	0.0	<0.1	<0.1	0.1	0.0	0.0	<0.1
Hyperia spp.	2.0	<0.1	0.0	0.0	<0.1	0.0	0.0	0.0	0.0
H. medusarum	3.9	0.0	0.0	0.0	0.0	0.0	0.0	<0.1	0.0
Lysianassidae	4.0	0.2	0.1	0.3	0.2	0.2	0.1	0.2	0.2
Anoyx spp.	8.0	0.0	0.0	0.0	0.0	0.0	0.0	<0.1	<0.1
Unidentified amphipod	2.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Copepods	—	0.1	0.0	0.0	<0.1	40.8	2.0	0.0	9.1
Neocalanus cristatus	13.0	0.1	0.0	0.0	<0.1	40.8	2.0	0.0	9.1
Euphausiids	—	7.8	0.0	0.0	2.4	2.4	0.4	1.0	1.1
Thysanoessa longipes	75.0	7.8	0.0	0.0	2.4	0.0	0.0	0.0	0.0
Unidentified euphausiid	22.7	0.0	0.0	0.0	0.0	2.4	0.4	1.0	1.1
Decapods	—	1.9	1.1	0.5	1.1	4.1	0.9	0.5	1.4
Atelecyclidae megalopa	15.0	1.4	1.1	0.3	0.9	4.0	0.8	0.2	1.1
Unidentified shrimp	50.0	0.5	0.0	0.2	0.2	0.1	0.2	0.4	0.3
Molluscs									
Squid	20.0	0.5	0.5	0.3	0.4	0.0	0.1	0.5	0.3
Fish									
Myctophids	2100.0	89.5	98.3	90.4	92.9	50.8	95.3	87.6	82.0
Unidentified fish	485.0	0.0	0.0	8.4	2.9	1.7	1.3	10.1	6.0
Samples (n)		10	12	10	32	11	10	32	53

[a] "Early" samples collected when 70% chicks were 0–20 days (18 July 2005 and 16 July 2006); "mid" samples, when 70% chicks were 20–40 days (25 and 28 July 2005 and 31 July 2006); "late" samples, when 70% chicks were ≥40 days (14 and 16 August 2005 and 16 August 2006).

[b] Standard laboratory mass value of each prey item used in percentage biomass calculations.

of myctophid fish varied across year ($F_{1,83} = 4.25$, $P = 0.042$) and nestling period ($F_{2,83} = 4.59$, $P = 0.013$), with a higher biomass in chick diets in 2005 than in 2006, and later in the nestling period. These differences appeared driven by an unusually low amount of myctophid fish in chick diets during the early nesting period in 2006, when biomass of myctophid fish was just 51% and appeared to be replaced mainly by copepods (Table 5).

DISCUSSION

Timing of breeding

Timing of breeding varied between years at Kasatochi, with later hatching in 2006 than in 2005. Annual variation in seabird phenology may be driven by food availability (e.g. Bertram *et al.* 2001) or weather (e.g. Payne & Prince 1979). We lack independent measures of storm-petrel prey supply during our study to determine how food availability relates to timing of breeding at Kasatochi, although variation in timing is thought to reflect fluctuation in food supply at other Fork-tailed Storm-Petrel colonies (Quinlan 1979, Boersma *et al.* 1980). However, differences in timing of breeding at Kasatochi coincide with differences in spring temperature, with colder spring temperatures in the central Aleutian Islands in 2006 than in 2005 (NOAA 2007). Snow cover can postpone breeding in seabirds by preventing access to nest sites (Payne & Prince 1979) and has been associated with delayed breeding of Fork-tailed Storm-Petrels on Buldir Island, Alaska (Byrd & Trapp 1977). If snow persisted longer during the colder spring of 2006, storm-petrel breeding could have been delayed that year.

Compared with other colonies throughout the species' range, phenology at Kasatochi appeared to fit a pattern of later nesting with increasing latitude. Mean hatch dates on Kasatochi (1 July in 2005, 6 July in 2006) were earlier than at colonies farther north in the Barren Islands [peaking 20–23 July (Boersma *et al.* 1980)] and Semidi Islands [mean: 15 July (Hatch & Hatch 1990)], but later than those to the south in British Columbia [peaking late May–early June (Vermeer *et al.* 1988)] and California [peaking late May (Harris 1974)].

Reproductive success

Hatching success was high in both years of our study, with only about 10% egg loss each year. Egg failure in Fork-tailed Storm-Petrels may be biased by investigator disturbance, because storm-petrels are especially susceptible to disturbance during incubation and prone to egg abandonment (e.g. Marks & Leasure 1992). We attempted to minimize disturbance by viewing nests by flashlight without physically disturbing the nest inhabitants. In addition, we did not check nests with incubating adults until just before hatch, and we monitored nests every two days only after chicks hatched, when egg abandonment was no longer a concern. Given that rates of egg failure at Kasatochi were low compared with those at colonies in the Gulf of Alaska [16%–30% (Quinlan 1979, Boersma *et al.* 1980)] and British Columbia [29% (Vermeer *et al.* 1988)], where more invasive sampling occurred, we believe investigator effects at Kasatochi to be minimal.

Fledging success varied dramatically between years and consequently drove differences in overall reproductive success. Therefore, factors affecting chick survival may be most influential in determining annual nesting success in Fork-tailed Storm-Petrels at Kasatochi. Chick mortality occurred consistently when chicks were less than 20 days old, suggesting that the early nestling period was most critical in determining chick survival. This pattern of heavy mortality in young chicks has been similarly documented at other Fork-tailed Storm-Petrel colonies (Byrd & Trapp 1977, Boersma *et al.* 1980, Simons 1981) and likely occurs because, as compared to larger chicks, smaller chicks have more difficulty thermoregulating and withstanding long fasts between meals (Boersma 1986). This hypothesis is consistent with evidence that visitation rates were higher earlier in the nestling period (Drummond 2007), when chicks would presumably require more frequent food deliveries.

Inclement weather can influence storm-petrel chick mortality by flooding nests or preventing parents from returning with food (Boersma *et al.* 1980, Boersma & Silva 2001). Weather during the breeding season at Kasatochi varied between years, with colder summer temperatures and more violent storms in 2005 than in 2006 (Drummond 2006, USFWS unpubl. data). Given that chick survival was lower in 2005 than 2006, it is possible that poorer weather conditions in 2005 were in part responsible for lower chick survival that year. If inclement weather affects breeding success of storm-petrels in the Aleutian Islands, potential large-scale changes in climate in the Bering Sea (NAST 2000) could have implications for future conservation.

Parasitism by fungus beetles (Leiodidae) and predation both contribute to chick mortality at other Fork-tailed Storm-Petrel colonies (Wheelwright & Boersma 1979, Quinlan 1983), but we found no evidence of either chick parasites or nest predators during our study. Like most of the Aleutian Islands, Kasatochi lacks naturally-occurring mammalian predators. Arctic Foxes *Vulpes lagopus* were introduced to Kasatochi in 1927 and were present for several decades, but all foxes were removed in 1985 (Bailey 1993). Resident Bald Eagles *Haliaeetus leucocephalus* and Glaucous-winged Gulls *Larus glaucescens* occasionally prey on adult birds (Drummond & Larned 2007), but have not been observed accessing storm-petrel nest sites on the island (B. Drummond pers. obs.). Given the vulnerability of storm-petrels to predation at the nest site (e.g. Warham 1990), the lack of such predators at Kasatochi and many other colonies in the Aleutian Islands is likely crucial to the success of Fork-tailed Storm-Petrel populations.

Finally, food availability may also affect storm-petrel chick survival, with higher survival in years of greater food supply (Boersma *et al.* 1980, Simons 1981). Feeding rates and meal sizes often reflect foraging conditions in seabirds and may be used as indirect measures of food availability during the breeding season (e.g. Granadeiro *et al.* 2000, Suryan *et al.* 2000). At Kasatochi, visitation rates and meal sizes were higher in 2006 than in 2005, suggesting that food availability may have been better in 2006 when chick survival was higher. However, without direct independent measures of food supply during our study, it is unclear exactly how foraging conditions contributed to chick survival at Kasatochi.

Direct comparisons of breeding success across other sites are difficult because of variation in monitoring techniques (Boersma *et al.* 1980, Simons 1981, Vermeer *et al.* 1988). We viewed nests by flashlight instead of the traditional method of reaching an arm into the burrow to feel nest contents (e.g. Vermeer *et al.* 1988). This approach limited our sample to those nests that could be observed without invasive sampling and may have biased our sample toward relatively exposed nest sites. If those nests were poorer quality sites or occupied by younger, less experienced breeders, then our measures of breeding success could have been lower than the actual success rates of the whole colony. However, because of the sensitivity of storm-petrels to investigator disturbance (e.g. Marks & Leasure 1992), we considered this limitation necessary.

Chick growth and parental provisioning

Average visitation rate and meal size were both higher in 2006 compared with 2005. These parameters are sensitive to variation in food resources in many seabird species, with greater food availability being associated with higher feeding rates (e.g. Suryan *et al.* 2000) and larger food loads (e.g. Granadeiro *et al.* 2000). There is evidence that Fork-tailed Storm-Petrel feeding rates, at least, vary in response to changes in food supply (Simons 1981, Boersma & Parrish 1998, Boersma & Silva 2001), suggesting that higher visitation rates and larger meal sizes observed at Kasatochi in 2006 could reflect higher food availability during the nestling period that year as compared with 2005.

Visitation rate affected chick mass gain only in 2006 and did not relate to structural chick growth or fledging mass. The lack of a strong relationship between parental provisioning and chick growth in our study is somewhat surprising, given that chick growth at other Fork-tailed Storm-Petrel colonies depends in part on feeding rate (Boersma 1986). It is likely that our estimates of parental provisioning were limited both by our use of visitation rate as a proxy for feeding rate and by our inability to quantify meal size at individual nests, which may be an important provisioning component for Fork-tailed Storm-Petrel chicks, with their gorge-and-fast feeding system (Boersma 1986).

Chick diet

Myctophid fish were the most important prey item of Fork-tailed Storm-Petrel chicks at Kasatochi in both years. This finding is generally consistent with recent diet sampling in the Aleutian Islands and southeastern Alaska (Dragoo *et al.* 2008). In addition, unidentified, partially-digested fish were found in most or all chick diets in the Gulf of Alaska and British Columbia (Quinlan 1979, Vermeer & Devito 1988). The importance of fish to developing chicks is supported by evidence that Fork-tailed Storm-Petrels may shift their diets to include greater amounts of fish after the chicks hatch (Boersma *et al.* 1980, Vermeer & Devito 1988, Boersma & Silva 2001).

Percentage biomass of myctophids in chick diets varied between years because of a substantial decrease in myctophids during the early nestling period in 2006. This reduction in myctophid biomass was replaced entirely by the copepod *Neocalanus cristatus.* Availability of *N. cristatus* varies seasonally in the North Pacific Ocean, peaking in near-surface waters in June and declining through the fall (Miller *et al.* 1984). This seasonal abundance is reflected in storm-petrel diets, with *N. cristatus* appearing in diets of Fork-tailed Storm-Petrels in British Columbia and Leach's Storm-Petrels *Oceanodroma leucorhoa* in Japan only through the month of June (Watanuki 1985, Vermeer & Devito 1988). The presence of *N. cristatus* in chick diets in the early nestling period in 2006 may be a result of delayed copepod timing that year, such that peak abundance occurred later than usual. Delayed copepod abundance in 2006 is supported by evidence that spring temperatures in the central Aleutians were colder in 2006 than in 2005 (NOAA 2007) and that timing of breeding of many seabird species at Kasatochi was delayed that year (Drummond 2006).

SUMMARY

We present the first detailed description of Fork-tailed Storm-Petrel breeding biology in the Aleutian Islands, a region supporting most of the species' breeding population. During our two-year study, we found variation in a number of reproductive parameters, including timing of breeding, fledging success, visitation rate, meal size and chick diet. Such annual variation has also been found at other Fork-tailed Storm-Petrel colonies (e.g. Boersma *et al.* 1980, Simons 1981, Boersma & Parrish 1998) and is generally thought to reflect changes in food supply, making the species a useful monitor of fluctuations in the marine environment (Boersma *et al.* 1980, Boersma & Parrish 1998, Piatt *et al.* 2006). Evidence suggests that weather and foraging conditions may both have contributed to the variation we observed. Numerous factors can influence breeding biology and success in seabirds, and long-term studies are essential to accurately identify and characterize causes of variation (e.g. Bradley *et al.* 1991). Our study provides an initial dataset for understanding Fork-tailed Storm-Petrel breeding biology in the core of the breeding range, which will be an important baseline for future research and may contribute to our use of the species as an indicator of marine conditions in the region.

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