HABITAT USE, DIET AND BREEDING BIOLOGY OF TUFTED PUFFINS IN PRINCE WILLIAM SOUND, ALASKA

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ABSTRACT—Habitat use, diet and breeding biology of tufted puffins (*Fratercula cirrhata*) were studied in Prince William Sound, Alaska, during summer 1995. On Seal Island, 112 puffin burrows (71% active) were located. Of 95 accessible burrows, 49% were typical earthen burrows, whereas the remainder were atypical for the species (e.g., under tree roots). Hatching success (≤79%), fledging success (≥82%), chick growth rates (17.7 g / day), asymptotic (600 g) and fledging (563 g) weights, meal sizes (14.2 g), meal delivery rates (5.32 meals / day), and daily rations (75.5 g / day) were all average or above-average for tufted puffins in Alaska. A total of 42 chick meals, comprising 125 individual prey were collected. Meals were composed of juvenile pollock (12.7% of total mass), herring (21.8%), prowfish (32.3%), salmonids (24.1%), and capelin, sandlance and squid (<5% each). Tufted puffin populations in Prince William Sound are relatively small, and may be limited by low densities of prey in the Sound, nest-site availability, and heavy rainfall.

Tufted puffins (*Fratercula cirrhata*) are widely distributed throughout the North Pacific, with breeding colonies in North America that range from California to the Arctic Ocean (Byrd and others 1993). Although 45% of this population of 2.7 million birds is concentrated in the Gulf of Alaska, relatively few puffins breed in Prince William Sound despite having numerous islands that are available for nesting. Colony censuses and boat-based surveys suggest that only about 5000 tufted puffins breed in Prince William Sound during summer (Sowls and others 1978; Klosiewski and Laing 1994).

Tufted puffins breed mostly on treeless islands and prefer to nest near the tops of steep maritime slopes (Vermeer 1979). Most tufted puffins make their nests by burrowing deep into soft peat or sod substrate, although they regularly make use of rock crevices on cliff faces or talus slopes. In contrast, closely-related rhinoceros auklets (*Cerorhinca monocerata*) nest extensively on islands with trees, often burrowing under the roots of trees adjacent to cliff-edges (Vermeer 1979). Such behavior has not been reported for tufted puffins.

Tufted puffins are flexible in their choice of prey and consume a wide variety of forage species throughout their range (Vermeer 1979; Wehle 1983; Hatch and Sanger 1992). In the northern Gulf of Alaska, tufted puffins eat small to mid-sized forage fish, including sandlance (*Ammodytes hexapterus*), capelin (*Mallotus villosus*), herring (*Clupea harengus*), juvenile walleye pollock (*Theragra chalcogramma*) and Pacific cod (*Gadus pacifica*). Availability of high quality prey within reasonable foraging distance of colonies is required to sustain chick production and healthy populations.

When the T / V *Exxon Valdez* spilled $>43\times10^6$ l of crude oil into Prince William Sound and the Gulf of Alaska in 1989, it appeared that few tufted puffins were killed outright by exposure to oil (Piatt et. al. 1990). However, effects of the spill on seabird populations by direct mortality or indirectly through effects on prey availability have been difficult to assess because of poor baseline data and natural background variability (Piatt and Anderson 1996). For example, a marked change in diet has been observed for puffins and other seabirds in the Gulf of Alaska during the past 2 decades. This change has been attributed tentatively to a large-scale shift in the Gulf of Alaska marine climate and associated changes in the availability of forage fish. These natural changes may have directly affected the population biology of piscivorous birds and mammals in the Gulf of Alaska (Piatt and Anderson 1996).

Our study was designed to gather basic information on the diet and biology of tufted puffins in Prince William Sound, and to assess indirectly the availability of local forage fish. It was part of a larger research project on seabirds and forage fish funded by the *Exxon Valdez* Oil Spill Trustee Council. Puffins are useful indicators of forage fish stocks because they eat what is locally available, and it is relatively easy to study their diets and breeding biology (Hatch and Sanger 1992). Other than population counts, almost no information on tufted puffins in Prince William Sound had been gathered prior to this study. We report here on the populations, diets, chick growth, breeding success, and nest-site selection by tufted puffins at Smith, Little Smith and Seal islands—the largest colonies for this species in Prince William Sound.

STUDY AREA AND METHODS

From 24 June to 17 July 1995, we observed seabirds at Smith (60°31.2′ N, 147°21.6′ W) and Little Smith (60°31.2′ N, 147°25.2′ W) islands in Prince William Sound, Alaska. Tufted puffins were observed almost daily from an inflatable boat to determine where they were nesting. We conducted 3 surveys of both islands, counting all birds within 200 m of shore and all birds visible on land. Maximum numbers of other breeding seabirds at the islands included: 33 pigeon guillemots (*Cepphus columba*); 200 marbled murrelets (*Brachyramphus marmoratus*); 250 parakeet auklets (*Cyclorrhynchus psittacula*); 60 horned puffins (*Fratercula corniculata*); and 83 glaucous-winged gulls (*Larus glaucescens*). We were unable to find puffins nesting in accessible habitat on either island, and therefore we moved our camp 7 km south to Seal Island (60°25.8′ N, 147°24.6′ W).

Seal Island is a small, low-elevation, tree-covered island with rocky beaches around much of its perimeter. We could access most puffin breeding areas by walking around the island. We worked on Seal Island from 17 July until 8 September 1995. We surveyed the island by boat to locate puffin breeding areas and census birds at sea, and we cut overland trails to breeding sites. We counted rafting and flying puffins opportunistically and recorded high counts for each day. Maximum numbers of other seabirds observed on Seal Island included: 40 pigeon guillemots; 10 marbled murrelets; 60 parakeet auklets; 6 horned puffins; 80 glaucous-winged gulls; and 600 black-legged kittiwakes (*Rissa tridactyla*).

Puffin nesting habitat on Seal island was divided into 8 study plots based on general physiographic features. All plots, with the exception of 1 islet off the northeast shore, were located on the south half of the island. Within each plot we attempted to locate all occupied puffin burrows. Occupation was inferred when a chick was found when the burrow was accessed; a chick meal was found during screening of the burrow (see below); an adult bird was observed delivering a meal to the burrow; obvious signs of breeding activity were observed (excrement, eggshells or strong odor); or a screen was removed by a bird from the entrance of the burrow.

Eleven tufted puffin chicks were measured throughout the chick-rearing period to obtain growth and development data. To gain access to these chicks, ≥1 hole was excavated in the soil, then plugged once the chick was returned to the burrow. Each burrow was visited once every 2 to 6 days and the following data collected: chick weight (±1 g); length of wing chord (±1 mm); length of exposed culmen (±0.1 mm); and length of fifth and outer primary (±1 mm). Maximum growth rates (g/day) were calculated for each of 10 chicks by measuring the slope of mass gained versus calendar date during the linear phase of growth (Gaston 1985).

To obtain nestling diet information, meal samples were collected using the burrow-screening technique (Hatch and Sanger 1992). Puffin burrow entrances were covered with a piece of fine-mesh hardware cloth to prevent adult birds from entering. Adults delivering meals to chicks often drop prey at the burrow entrance when the screen is encountered. We screened 67 different burrows regularly, leaving the screens in place for 2 to 3 hr. Individual burrows were screened 1 to 9 times at intervals of 2 to 8 days. For safety, static lines and climbing harnesses were used to access almost all burrows.

Chick meals were collected and later identified to species (when possible), weighed (±0.1 g) and measured (±0.1 mm). Subsamples were frozen for energetic analyses (DDR, in prep.), and some specimens were saved for later identification at the Univ. of Alaska, Fairbanks (K. Turco, Institute of Marine Sciences). After sufficient subsamples of the major prey species had been obtained, we washed, weighed and measured fish samples at the burrow and returned the meal to the chick. No meals were collected from chicks that were used to assess growth rates.

To obtain data on chick provisioning rates, 6 Tufted Puffin burrows were monitored during 4 all-day watches on 28 July (16.5 hr), 11 August (16.0 hr), 20 August (15.5 hr) and 27 August (14.5 hr). Observations were made with binoculars from a blind, at a distance of 15 to 20 m from burrows. Information recorded during these watches included the number of times an adult visited a particular burrow and whether the bird delivered a meal.

RESULTS

Numbers and Habitat Use

On 27 June we counted a maximum of 300 individual tufted puffins around Smith Island and 160 around Little Smith Island. Active colony sites on Smith Island were located on grassy and rocky slopes at the top of steep cliffs (100 m elevation) on both sides of the east cape, and near the top of a steep escarpment (100 to 150 m) along the north coast. These were the only areas where puffins were observed on land, and all sites were inaccessible to us. Puffins were concentrated on the east side of Little Smith, and some birds were observed landing near the top of steep cliffs (70 to 100 m).

On 19 July we counted a maximum of 125 tufted puffins around Seal Island. We located 112 puffin burrows along 1.2 km of shoreline on the eastern and southern coasts. Burrows tended to be clumped in groups. Individual burrows were 0.5 to 10 m apart. Of the 112 burrows located, at least 80 (71.4%) were active in 1995. Of 95 burrows that we examined, 47 (49.5%) were typical earthen tunnels, 45 (47.4%) were associated with tree roots, and 3 (3.1%) were in rock crevices. Most nest sites were located at the interface between forest and low-elevation cliff tops above rocky beaches, wherever grassy turf was found.

Chick Growth and Development

Fourteen burrows were monitored to assess breeding success and obtain growth data from nestlings. Eleven of these burrows contained hatchlings during the 1st nest check in late July, and 3 burrows contained eggs—2 of which never hatched and 1 from which the chick died upon hatching. Judging from chick development, we estimate mid-hatching occurred on about 20 July. Of the 11 chicks that were monitored, 9 (82%) had fledged by the time we left on 8 September. The remaining 2 chicks appeared ready to fledge (weights = 485 g and 685 g) and probably did so successfully (Wehle 1983). Thus, maximum breeding success was about 79% (79% hatch, 100% fledge). We estimate that mid-fledging occurred on about 1 September.

Although there was considerable variation among chicks (Fig. 1), the maximum daily growth rate during the linear phase averaged 17.7 g/day (SD = 2.8, N=10). For those chicks that could be measured throughout growth and to fledging (N = 7), asymptotic mass was 600 g (SD = = 49), fledging mass was 563 g (SD = 53), wing length at fledging was 143.3 mm (SD = 8.6), and culmen length at fledging was 40.1 mm (SD = 1.6).

Chick Meal Collections

We collected 42 chick meals during the study. Of these, 35 were collected in 364 screening attempts (1072 nest-hr) for an overall screening success rate of 9.6%. We opportunistically picked up an additional 7 meals where they had been dropped on the ground. Prey items were only collected from 31% of all puffin burrows that were screened (n=67). Most meals (43%) were collected upon the 1st screening of a burrow, and success declined markedly on subsequent attempts—suggesting that puffins learned to avoid dropping meals at screened burrow entrances. This effect has not been examined at other puffin colonies, where investigators have not collected meals from individually marked burrows (Hatch and Sanger 1992; JFP, unpubl. data).

We collected 125 prey items. The average weight of meal loads (N = 35) was 14.2 g (SD = 15.9), and on average, 3.2 prey items were delivered per load (range: 1 to 11). Juvenile walleye pollock and herring accounted for most (81.6%) of the fish delivered (Fig. 2), and occurred most frequently in individual meal loads (31% and 38%, respectively). However, in terms of biomass, juvenile prowfish (*Zaprora silenus*) and salmon (*Onchorynchus* spp.) were the dominant species (Fig. 2) because of their much larger masses (Table 1). Prowfish and salmon also occurred frequently in meal loads (17% and 10%, respectively). By number or mass, sandlance (N = 3), capelin (N = 1) and squid (Gonatidae, N = 1) were minor components of the diet, although sandlance occurred in 7% of meal loads.

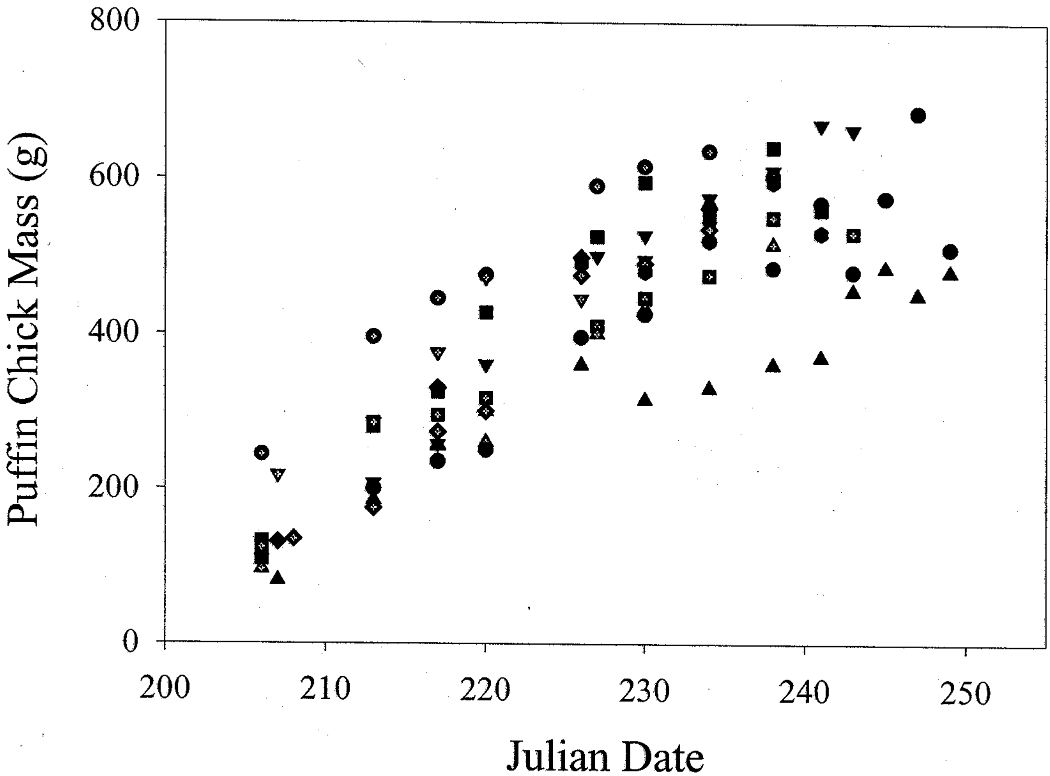

FIGURE 1. Growth of tufted puffin chick mass during late summer 1995, at Seal Island, Prince William Sound (note: 1 August is Julian Day 213). Different symbols indicate measurements from individual chicks (N = 11).

Feeding Rates

Tufted puffins were active at their nest sites throughout the day (Fig. 3). Peak feeding activity occurred during the morning hours (before 0900 hr), and feedings generally tapered off through the day (Fig. 3). Adults were most active during the afternoon and late evening hours, however, as measured by the frequency of non-feeding entrances into the burrow (Fig. 3). Social behaviors (for example, resting at the colony, prospecting, bill gaping, billing and vocalizing; see Harris 1984) were observed more commonly in the afternoon and evening than in the morning.

In total, adults were observed entering the 6 study burrows 468 times during the 4 days of observation (see Methods), and on 103 of those visits they delivered food. Daily feeding rates varied from a high of 7.0 meals/chick/day observed on 11 August, to a low of 3.0 meals/chick/day on 27 August. The latter rate is biased because puffins reduce the frequency of chick-feedings just prior to fledging of chicks (Harris 1984). The average feeding rate during the first three watches was 5.32 (SD = 1.49) meals/chick/day, and reflects more accurately the average rate of feeding for most of the chick-rearing period. Thus, the average amount of food provided to tufted puffin chicks during the period of maximum food demand (approximately 25 July to 25 August) was 75.5 g/day (delivery rate times average meal size).

DISCUSSION

No other data on the biology of tufted puffins in Prince William Sound are available for interpretation. Compared to puffins elsewhere in Alaska and the Pacific Northwest, however, it appears that tufted puffins fared quite well at Seal Island in 1995 (Table 2). In terms of food delivery, chick growth and production, Seal Island puffins did as well or better than puffins at other major colonies in successful years (see references in Table 2).

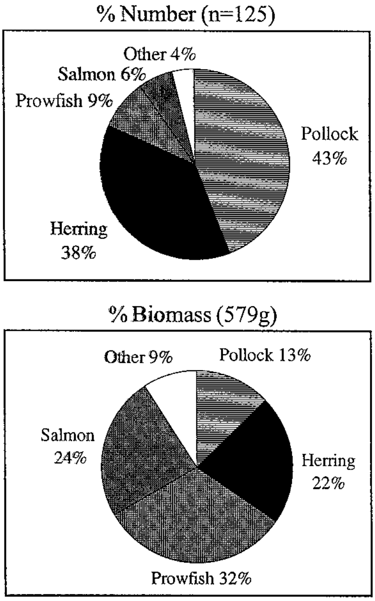

FIGURE 2. Composition of tufted puffin chick diets at Seal Island, Prince William Sound, during summer, 1995.

TABLE 1. Mean length and weight of forage fish collected from Tufted Puffin chicks at Seal Island, July–August, 1995.

Species	*N*	Length (SD)	Weight (SD)
Pollock	43	62.6 (7.9)	1.37 (0.61)
Herring	22	76.4 (22.0)	3.81 (6.6)
Prowfish	10	111.7 (24.8)	18.0 (11.4)
Salmon spp.	7	141.6 (7.6)	20.2 (5.8)
Sandlance	3	89.3 (6.7)	2.04 (0.56)
Capelin	1	147	21.7
Squid	1	220	25.3

In contrast to other studies (Table 2), the diet of tufted puffins at Seal Island was mostly prowfish and salmon, although pollock and herring were numerically dominant. In a wide-ranging study of tufted puffin diets in the Gulf of Alaska (Hatch and Sanger 1992), prowfish ranked 5^{th} in importance (by weight), whereas salmon were generally very rare (ranking 30^{th}). A small sample (N = 2) of puffin chick meals from Naked Island, Prince William Sound in 1986 (Hatch and Sanger 1992) showed that diets there were comprised of salmon (76%) and pollock (24%).

Hydroacoustic and trawl surveys of forage fish populations in the immediate vicinity of Seal Island in 1995 (Haldorson and others 1996) revealed that pollock (mostly 0+ age-class) were by far the most abundant (99% of trawl catches) forage fish in shallow and deep waters. Excluding pollock, capelin (44%), juvenile salmon (21%), prowfish (5%), herring (3%) and sandlance (1%) were the commonest forage fish in the area. However, forage fish densities were generally low in Prince William Sound (for example, 0.01 to 0.1 g/m^3; Haldorson and others 1996) compared to areas with large seabird populations (0.1 to 10 g/m^3 in lower Cook Inlet or Chukchi Sea; Piatt and others 1990; JFP, unpubl. data). Forage fish densities appeared adequate to support the small tufted puffin colonies that we observed, but may ultimately limit the expansion of populations in Prince William Sound. On the other hand, tufted puffins are opportunistic feeders and subsist successfully elsewhere in Alaska on a wide variety of prey types. Furthermore, Prince William Sound supports much larger populations of other piscivorous seabirds (for example, murrelets and kittiwakes; Klosiewski and Laing 1994). In any case, 1 yr of data is insufficient to test the hypothesis that food is limiting puffin populations.

If food is not limiting, the question arises: Why are there not more tufted puffins breeding in Prince William Sound? Puffins are notoriously difficult to census at colonies, and boat-based surveys have their own biases, but it appears that populations have remained relative-

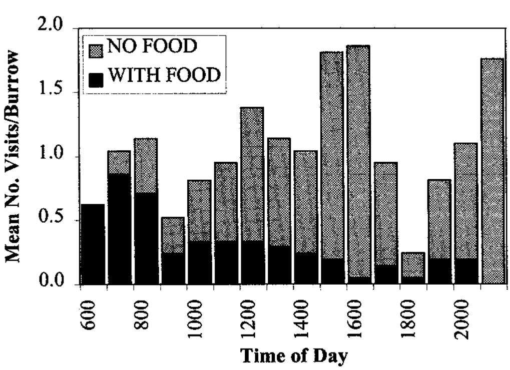

FIGURE 3. Diurnal pattern of activity of adult tufted puffins at their burrows on Seal Island, Prince William Sound. Bars indicate the number of times an adult puffin entered its nesting burrow with or without food, for each hour of the day. Values are averages from 4 different days of observation, and 6 different nest-sites (see Methods).

TABLE 2. Breeding and feeding parameters for tufted puffins at selected colonies.

Location	Year	Fledging success (chicks/egg hatched)	Maximum chick growth rate (g/day)	Asymptotic chick weight (g)	Meal size (g)	Food delivery rate (meals/day)	Daily food ration (g/day)	Major prey in diet	Source
Prince William Sound	1995	≥82	17.7	600	14.2	5.3	75.5	Prowfish, salmon	This study
Barren Islands	1976	69	16.5	600	14.9	—	—	Capelin	Amaral 1977; Manuwal and Boersma 1977
	1977	79	16.5	595	20.4	3.8	80	Capelin, sandlance	Amaral 1977; Manuwal and Boersma 1977
	1995	—	11.5	—	10.3	5.5	57	Capelin, pollock	Art Kettle, unpubl. data
Sitkalidak Strait	1977	88	19.0	590	19.3	—	—	Capelin, sandlance	Baird and Moe 1978
Ugaiushak Island	1976	86	19.0	600	9.7	—	—	Sandlance	Wehle 1983
	1977	95	21.4	555	14.4	—	—	Sandlance, capelin	Wehle 1983
Buldir Island	1975	0	6.8	360	11.9	—	—	Sandlance, squid	Wehle 1983
Triangle Island (BC)	1977	2	11.8	~260	13.9	1–2	28	Sandlance, saury	Vermeer and Cullen 1979
	1978	74	18.2	579	22.0	3–4	75–80	Sandlance	Vermeer and Cullen 1979
Goat Island (OR)	1982	≤35	9.0	530	15.2	4.7	71.3	Anchovy, herring	Boone 1985

ly stable during the past 25 yr. Boat surveys in 1973 suggested that Prince William Sound supported a tufted puffin population in summer of 4,439 ±4,543 individuals (Klosiewski and Laing 1994). Similar surveys in 1991 suggested a population of 5,043 ±2,011 individuals (Agler and others 1994). In 1976 (Sowls and others 1978), 554 and 166 tufted puffins were counted at Smith and Little Smith islands, respectively, while we counted a maximum of 300 and 160 tufted puffins, respectively, in 1995.

We can suggest 2 other reasons why tufted puffin populations may be limited in Prince William Sound. First, tufted puffins are primarily a burrow-nesting species, and the use of any breeding habitats other than steep, grassy maritime slopes is rare (Gill and Sanger 1979; Vermeer 1979). Tufted puffins prefer to burrow in areas with sufficient soil depth, up to 1.5 m (Wehle 1980). On Seal Island, only half of nest-sites were typical earthen tunnels, whereas most of the remainder incorporated hollows under tree roots into their construction. While this is not unusual for rhinoceros auklets (Vermeer 1979), it has never been reported for tufted puffins. The nesting situation is similar on Naked Island in Prince William Sound (JFP, pers. obs.). Although Prince William Sound has many islands available for nesting, most are either completely forested, or, in northern glaciated areas, completely barren and free of soil. Thus, it seems likely that nest sites for tufted puffins are limited in Prince William Sound.

Secondly, as in Southeast Alaska and coastal British Columbia, it rains frequently in Prince William Sound during summer. On Seal Island, we recorded rain on 93% of days ($N = 14$) in July (total 8.0 cm) and on 42% of days in August (10.9 cm). Long-term (1950s to 1990s; U.S. National Weather Service 1997) average rainfall in Prince William Sound is much greater (about 25 cm in August at 3 sites) than in the Gulf of Alaska (10 cm at 4 sites) or Aleutian islands (11 cm at 3 sites), where the bulk of Alaskan tufted puffin colonies are located. In an analysis of seabird breeding colonies with respect to climate, Kaiser and Forbes (1992) concluded that burrow-nesting seabirds select colony-sites with minimal rainfall. They noted that drier nesting sites offer several advantages, including reduced burrow erosion, low risk of flooding, and easier maintenance of burrow microclimate. Heavy rainfall during chick rearing can seriously reduce chick survival, because wet chicks may die of hypothermia (Piatt and others 1990; Kaiser and Forbes 1992).

In summary, tufted puffin colonies in Prince William Sound are relatively small compared to those found just outside the Sound (for example, the Chiswell Islands), and elsewhere in the Gulf of Alaska. Forage fish densities in Prince William Sound during 1995 were apparently sufficient to support the existing tufted puffin colonies, but population growth may ultimately be limited by low prey densities. Populations may be limited also by a lack of suitable nesting habitat, and by the heavy rainfall in Prince William Sound.

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LITERATURE CITED

*AGLER BA, SEISER PE, KENDALL SJ, IRONS DB. 1994. Marine bird and sea otter population abundance in Prince William Sound, Alaska: trends following the T/V Exon Valdez oil spill, 1989–1993. *Exxon Valdez* oil spill restoration final reports, Restoration Project 93045. Anchorage AK: U.S. Fish and Wildlife Service.

AMARAL MJ. 1977. A comparative breeding biology of the tufted puffin and horned puffin in the Barren Islands, Alaska [dissertation]. Seattle: University of Washington. 98 p.

BAIRD PA, MOE RA. 1978. The breeding biology and feeding ecology of marine birds in the Sitkalidak Strait area, Kodiak Island, 1977. In: Lensick C, Wohl K, principal investigators. Population dynamics and trophic relationships of marine birds in the Gulf of Alaska and southern Bering Sea. Boulder, CO: National Oceanographic and Atmospheric Administration and USDI Bureau of Land Management. Environmental assessment of the Alaskan continental shelf. Annual reports of principal investigators for the year ending March 1978. Volume 3. Receptors—birds. p 313–524.

BOONE DL. 1985. Breeding biology and early life history of the tufted puffin (*Fratercula cirrhata*) [dissertation]. Corvallis, OR: Oregon State University. 46 p.

* unpublished

BYRD GV, MURPHY EC, KAISER GW, KONDRATYEV AY, SHIBAEV YV. 1993. Status and ecology of offshore fish-eating alcids (murres and puffins) in the North Pacific. In: Vermeer K, Briggs KT, Morgan KH Siegel-Causey D., editors. The status, ecology, and conservation of marine birds of the North Pacific. Ottawa: Canadian Wildlife Service. Special Publication. p 176–186.

GASTON AJ. 1985. Development of the young in the Atlantic Alcidae. In: Nettleship DN, Birkhead TR, eds. The Atlantic Alcidae. Orlando FL: Academic Press. p 319–354.

GILL R, SANGER GA. 1979. Tufted puffins nesting in an estuarine habitat. Auk 96:792–794.

*HALDORSON L, SHIRLEY TC, COYLE KC. 1996. Biomass and distribution of forage species in Prince William Sound. Anchorage, AK: *Exxon Valdez* Oil Spill Trustee Council. Annual Report. 78 p.

HARRIS MP. 1984. The puffin. Calton, UK: T&AD Poyser. 224 p.

HATCH SA, SANGER GA. 1992. Puffins as samplers of juvenile pollock and other forage fish in the Gulf of Alaska. Marine Ecology Progress Series 80:1–14.

KAISER GW, FORBES LS. 1992. Climatic and oceanographic influences on island use in four burrow-nesting alcids. Ornis Scandinavica 23:1–6.

*KLOSIEWSKI SP, LAING KK. 1994. Marine bird populations of Prince William Sound, Alaska, before and after the *Exxon Valdez* oil spill. Final report, natural resource damage assessment bird study number 2. Anchorage, AK: USDI Fish and Wildlife Service.

MANUWAL DA, BOERSMA PD. 1977. Dynamics of marine bird populations on the Barren Islands, Alaska. In: Bartonek JC, Lensink CJ, Gould PJ, Gill RE, Sanger GA, principal investigators. Population dynamics and trophic relationships of marine birds in the Gulf of Alaska and southern Bering Sea. Boulder, CO: National Oceanographic and Atmospheric Administration and USDI Bureau of Land Management. Environmental assessment of the Alaskan continental shelf. Annual reports of principal investigators for the year ending March 1977. Volume 4. Receptors—birds. p 294–420.

PIATT JF, ROBERTS BD, LIDSTER WW, WELLS JL, HATCH SA. 1990. Effects of human disturbance on breeding Least and Crested Auklets at St. Lawrence Island, Alaska. Auk 107:342–350.

PIATT JF, LENSINK CJ, BUTLER W, KENDZIOREK M, NYSEWANDER D. 1990. Immediate impact of the *Exxon Valdez* oil spill on marine birds. Auk 107: 387–397.

PIATT JF, WELLS JL, MACCHARLES A, FADELY B. 1990. The distribution of seabirds and their prey in relation to ocean currents in the southeastern Chukchi Sea. Canadian Wildlife Service Occasional Papers 68:21–31.

PIATT JF, ANDERSON PJ. 1996. Response of common murres to the *Exxon Valdez* oil spill and long-term changes in the Gulf of Alaska marine ecosystem. In: Rice SD, Spies RB, Wolfe DA, Wright BA, editors. *Exxon Valdez* oil spill symposium proceedings. Bethesda, MD: American Fisheries Society. Symposium 18. p 720–737.

SOWLS AL, HATCH SA, LENSINK CJ. 1978. Catalog of Alaskan seabird colonies. USDI Fish and Wildlife Service Biological Services Program. FWS/OBS-78/78.

U.S. NATIONAL WEATHER SERVICE. 1997. <http://www.alaska.net/~nwsar/> Revised August 1997, accessed 10 September 1997.

VERMEER K. 1979. Nesting requirements, food and breeding distribution of rhinoceros auklets, *Cerorhinca monocerata*, and tufted puffins, *Lunda cirrhata*. Ardea 67:101–110.

VERMEER K, CULLEN L. 1979. Growth of rhinoceros auklets and tufted puffins, Triangle Island, British Columbia. Ardea 67:22–27.

WEHLE DHR. 1980. The breeding biology of the puffins: TUFTED PUFFIN (*Lunda cirrhata*), horned puffin (*Fratercula corniculata*), common puffin (*Fratercula arctica*), and rhinoceros auklet (*Cerorhinca monocerata*) [dissertation]. Fairbanks, AK: University of Alaska, Fairbanks. 313 p.

WEHLE DHR. 1983. The food, feeding and development of young tufted and horned puffins in Alaska. Condor 85:427–442.

Submitted 15 February 1997, accepted 17 September 1997. Corresponding editor: S. R. Johnson.