

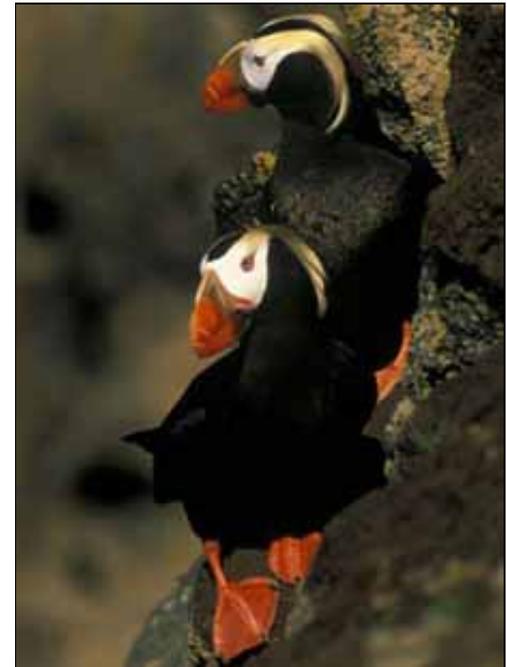
FRENCH:
Macareux huppé
YUP'IK:
Pugharutwuk
ALEUT:
Och-chuh
RUSSIAN:
Toporok
JAPANESE:
Etopirika

Tufted Puffin

Fratercula cirrhata

Tufted Puffins are cool. Unlike their familiar brethren—Horned (*Fratercula corniculata*) and Atlantic (*F. arctica*) puffins, whose appearances convey comic charm and innocence—Tufted Puffins exude stern confidence. With all-black body plumage, striking white robber's mask, chunky orange bill, and streaming golden head-plumes, this is one member of the auk family whose appearance—like that of a biker in leather regalia—says, "Don't mess with me!" Their status as seabird tough-guys is not unwarranted. Few other seabirds breed over such a vast geographic range and extreme of climatic regimes, from cactus-covered rocks in southern California to frozen cliffs of the coastal Alaskan Arctic. And few other seabirds range so widely at sea, from icy waters of the Chukchi Sea to the warm, subtropical expanse of the Central North Pacific Ocean, and east to west from the California Current to the Kuroshio Current of Japan.

While known for carrying bill-fulls of small fish to its young and breeding on continental-shelf habitats that teem with abundant forage fish such as sand-lance (*Ammodytes hexapterus*) and juvenile pollock (*Theragra chalcogramma*), this species has many life-history attributes that remind one of the more pelagic shearwaters (*Puffinus* spp.). Adult Tufted Puffins are the most pelagic of the Alcidae (Bent 1919, Kuroda 1955,



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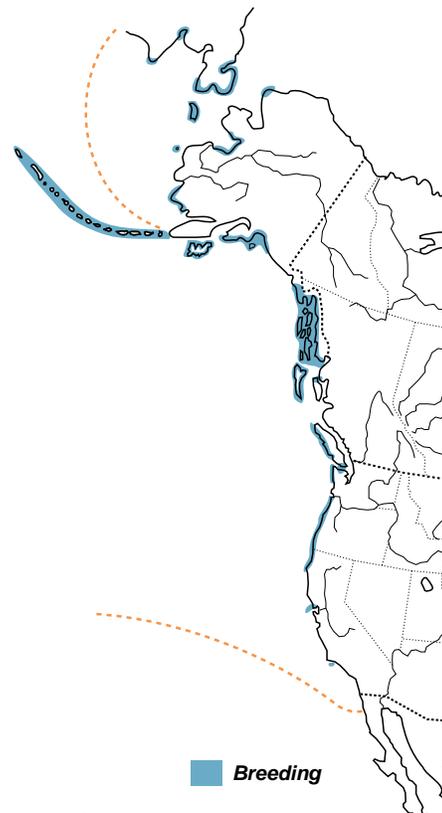


Figure 1. Distribution of the Tufted Puffin in North America and easternmost Russia. The Tufted Puffin winters in the Pacific Ocean north and south to the dashed lines and is rarely found in breeding areas during winter. This species also breeds in other parts of Asia. See text for details.

The Birds of North America

Life Histories for the 21st Century

Shuntov 1972), ranging widely from colonies in summer to find fish for their young, but feeding themselves largely on invertebrates, especially squid and euphausiids. During the nonbreeding season, adults migrate far south to oceanic waters of the Central North Pacific, where their diet consists largely of squid, euphausiids, and pelagic fish. Juveniles migrate south to the Central North Pacific after fledging (Shuntov 1972) and may not return to coastal breeding areas for several years. Thus, the Tufted Puffin, even more so than the Horned Puffin (Piatt and Kitaysky 2002), is a pelagic species that spends most of its life at great distances from land and has a diet more similar to shearwaters and petrels (*Pterodroma* spp.) than to most other alcids (Sanger 1987, Vermeer et al. 1987).

Wehle (1976, 1980, 1982a, 1982b, 1983), Amaral (1977), and Vermeer (1979; Vermeer and Cullen 1979; Vermeer et al. 1979, 1987) conducted the earliest directed studies on Tufted Puffins and collected wholly new information on breeding biology, behavior, chick growth, diets, and habitat use in the Aleutians, Gulf of Alaska, and British Columbia. Much incidental information is also available from early general field investigations of seabird colonies (compiled in Baird and Jones 1983, Byrd et al. 1993). Several more recent studies have added substantially to our knowledge of Tufted Puffin breeding biology (Boone 1986; Hatch and Hatch 1990a, 1990b; Kitaysky 1996, 1999; Kitaysky and Golubova 2000; Bertram et al. 2001; Gjerdrum 2001) and feeding ecology (Sanger 1983, 1987; Baird 1990, 1991; Hatch and Sanger 1992; Springer et al. 1996); in particular, monitoring studies conducted by the Alaska Maritime National Wildlife Refuge (NWR) on several large colonies provide continuous long-term data on breeding biology and diets (Byrd et al. 1989, 1991; Dragoo and Woodward 1996; Roseau et al. 2000; Williams and Daniels 2001). The pelagic distribution and ecology of the Tufted Puffin has also been reasonably well documented throughout its range (Kuroda 1955, 1960; Shuntov 1972, 1986; Hunt et al. 1981, Gould et al. 1982; Wahl et al. 1989, 1993; Piatt et al. 1990a, 1992; Gould and Piatt 1993; Piatt 1993, 2002; Tyler et al. 1993). For the future, studies of adult survival and recruitment would complement long-term monitoring of populations at key colonies. More attention should be directed toward conservation of dwindling and threatened populations in Japan, California, Washington, and Oregon.

DISTINGUISHING CHARACTERISTICS

Large alcid (about 40 cm length, 775 g) with large, laterally compressed, triangular bill. Breeding (Alternate)-plumage adults brown-black with large, white face-mask and long, golden head-plumes that drape down the neck. Large, mostly orange bill has variable

number of grooves on upper mandible and bright-orange rictal rosette at base of gape. Legs and feet bright yellowish-orange to reddish. Male slightly larger than female, but sexes otherwise alike in appearance. Nonbreeding (Basic)-plumage adult similar to breeding adult, but white portion of face becomes gray-brown, plumes disappear, and it sheds bill plates and loses rictal rosette; bill becomes smaller, loses ridges, but remains orange. Juvenile similar to Basic-plumaged adult, but bill shorter, narrower, and brownish gray in color.

Neck short and retracted into shoulders in flight, giving stocky appearance. At sea, flight rapid and direct. Swims and dives well, takes off from water after gathering momentum. Has difficulty maneuvering while landing, uses runways for takeoffs and landings. Walks upright with ease over rocks, clinging to surface with claws. Reclines with tarsus pressed flat, but walks on its toes.

Large size, dark back and belly, white face, and large, orange bill make this one of the most distinguishable of all alcids. Immature and Basic-plumage Tufted Puffins have darker faces and smaller bills, thus sometimes confused with Rhinoceros Auklet (*Cerorhinca monocerata*), which is slightly smaller, slimmer billed, and paler on belly (some juvenile Tufted Puffins may be pale on belly, however); Tufted Puffins in these plumages usually show broad grayish streak behind eye. Tufted Puffin distinguished from similar-sized murrets (*Uria* spp.) and Horned Puffin by dark breast in all plumages and from Horned Puffin also by head-plumes and lack of yellow in bill during breeding.

DISTRIBUTION

Widespread in North Pacific Ocean, from mid-Transition Zone (about 35°N) to Beaufort Sea (Udvardy 1963). Extensive breeding range; nests on coastline and offshore islands in California, Oregon, Washington, British Columbia, Gulf of Alaska, Aleutians, Japan, Sea of Okhotsk, Kurils, and Bering and Chukchi Seas. Winters over a broad area of North Central Pacific, generally over deep oceanic waters.

THE AMERICAS

Breeding range. Extends from California (Channel Is.) to Chukchi Sea. About 80% of colonies and world population breed in North America (Fig. 1). In California, small numbers recently re-established breeding at Prince I. near San Miguel I. (34°03'N), westernmost of n. Channel Is., s. California (McChesney et al. 1995); largest colonies in state at Farallon Is. off San Francisco, central California, and Castle Rock off Crescent City, n. California (Carter et al. 1992). Thousands off coast of Oregon (Three Arches Rock) and Washington (Carroll, Jagged, Alexander Is.). Tens of

thousands at colonies in British Columbia (Triangle and Kerouard Is.) and se. Alaska (St. Lazaria, Forrester). Largest colonies concentrated in e. Aleutians (Egg, Kaligagan, Aiktak, Vsevidov, Chagulak Is.), and along Alaska Peninsula (Amagat, Castle Rock, Suklik, Barren, Triplet Is.). Population dispersed among most Aleutian islands (notably Buldir, Chagulak, Koniujii Is.) and few islands in Bering and Chukchi Seas (e.g., Pribilofs, St. Matthew, St. Lawrence, Diomedes Is.), and at a few coastal and island sites along Alaska mainland. Most northerly well-established colony is at Cape Lisburne (69°53'N) in Chukchi Sea.

Summer, nonbreeding range. Nonbreeders observed regularly during spring and summer in oceanic waters of Central North Pacific. Kuroda (1955) counted 24 flightless immatures Jun–Jul in western portion of Central North Pacific. Shuntov (1972) noted Tufted Puffins remaining far at sea in summer were mostly immatures. Individuals recorded regularly throughout entire Central North Pacific during summer (Kuroda 1960, Wahl et al. 1989, Gould and Piatt 1993, Springer et al. 1999). Subadult and few adult birds caught during summer in high-seas drift-nets as far south as 38°N, suggesting year-round residence in Central North Pacific (Int. N. Pac. Fish. Comm. 1992, P. J. Gould unpubl.). Total bycatch in drift-net fisheries in Central Pacific, prosecuted mostly in summer, may have once exceeded 120,000 individuals/yr (DeGange et al. 1993), so summer populations there must be substantial. Pelagic surveys of region in summer also suggest similar populations (based on observed densities of 0.07–0.41 birds/km² in Subarctic and Transitional waters; Springer et al. 1999).

Winter range. Winters offshore, throughout North Pacific south to 35°N (Shuntov 1972). Excluded from n. Bering, Chukchi, and Okhotsk Seas by ice in winter. Densities at sea in se. Bering Sea and Gulf of Alaska diminish greatly in fall and winter to <2% of summer densities, suggesting most Tufted Puffins move farther south (Gould et al. 1982). Rare on coastal Christmas Bird Counts in Alaska or British Columbia. Few remain as year-round residents among islands from Kodiak to Attu (Gabrielson and Lincoln 1959). Almost absent in coastal and shelf waters of British Columbia (Wahl et al. 1993), Washington, Oregon, and California (Tyler et al. 1993) during winter months.

Other records. Accidental in Maine (mouth of Kennebec River, Sagadahoc Co.) based on specimen obtained and illustrated by J. J. Audubon, who said it was “shot by a fisherman gunner, while standing on some floating ice, in the winter of 1831–32” (Palmer 1949 quoting Audubon 1835: 354; illustration of specimen is plate 249 in Audubon's *Birds of America*); specimen at Vassar College examined by Palmer (1949). Although origin of this bird has been questioned and no other vagrant records exist across North America, there is a record of Tufted Puffin from Sweden (see

below) and other Pacific alcids, such as Ancient (*Synthliboramphus antiquus*) and Long-billed (*Brachyramphus perdix*) murrelets and Crested (*Aethia cristatella*) and Parakeet (*A. psittacula*) auklets, exhibit long-range vagrancy of a similar magnitude.

OUTSIDE THE AMERICAS

Breeding range. About 22% of colonies and 18% of world population found in Asia, almost entirely Russia. Range similar to that of Horned Puffin, but rarer in Arctic Basin and only accidental on Wrangel I. Nests northwest on Kolyuchin I. along n. Chukchi Peninsula, one and s. Chukchi Peninsula (Konyukhov et al. 1999), Big Diomedes I., Ratmanova I., Anadyr Bay, and Olyoumka I. In Kamchatka region, population has increased, and new colonies have appeared in recent years. Largest colonies in Commander Is. and northern part of Sea of Okhotsk, Talan I. (largest colony outside Americas estimated at 140,000 birds), Shantar Is., Iona I., n. Primorie, Sakhalin I., and n. Kuril Is. (Kondratyev et al. 2000). In Japan, populations near extinction. Currently fewer than 30 individuals breeding on 6 colonies around coast of Hokkaido (Brazil 1991, Osa and Watanuki 2002).

Winter range. Excluded from Sea of Okhotsk and n. Bering Sea in winter by ice. Recorded in vicinity of Commander Is. (caught in Dec–Jan), off coast of Kamchatka, Sakhalin I., and the Kurils (Flint and Golovkin 1990). Scarce winter visitor to pelagic waters off Hokkaido and n. Honshu, as far south as Niigata-ken on Sea of Japan coast and Miyagi-ken on Pacific coast (Brazil 1991).

From Okhotsk and Bering Seas, majority of Tufted Puffins wander into Pacific Ocean, where they disperse toward the immense equatorial region (Shuntov 1972), ranging south to north from about middle of Transition Zone (approx. 35°N) to Subarctic waters off Alaska continental shelf and Aleutians, and west to east from Japan to California. Placed in “Northern Transition” guild of North Pacific seabirds, which regularly range from Subarctic to mid-Transitional waters (Gould and Piatt 1993). Central North Pacific likely an important nursery and overwintering area for juvenile and nonbreeding Tufted Puffins (Kuroda 1955, Gould et al. 1982). Bycatch records in high-seas drift-nets place Tufted Puffins well into Transitional waters (below approx. 40°N) during fall and winter (Int. N. Pac. Fish. Comm. 1992, P. J. Gould unpubl.).

Other records. Accidental in winter to Hawaiian Is. based on carcass collected at Laysan I. (25°50'N, 171°50'W; Clapp 1986). Accidental in Jun to s. Sweden (mouth of Lagan River; Haraldsson 1995).

HISTORICAL CHANGES

Most changes at periphery of range. In California (McChesney et al. 1995), reached southern limit of range at Channel Is., where probably hundreds nested

in good numbers during late 1800s at Prince, Santa Cruz, Anacapa, and Santa Barbara Is., and possibly several other locations. Apparently extirpated early in 1900s, and only recently a few have begun breeding again at Prince I. Small populations (hundreds) recently extirpated from San Juan Is. in Strait of Juan de Fuca, WA (U. Wilson unpubl.). In Japan, populations once numbering in hundreds around Hokkaido have been reduced to remnant at 6 colonies and extirpated at another 8 sites (Brazil 1991, Osa and Watanuki 2002). As for other seabirds, predation by introduced foxes may have eliminated or reduced populations on many Aleutian islands (Murie 1959, Bailey 1993, Bailey and Kaiser 1993).

FOSSIL HISTORY

Same as for Horned Puffin (Piatt and Kitaysky 2002). In Pacific, only known puffin fossils are those of *Cerorhinca*, which Chandler (1991) synonymized into *Fratercula*. The holotype and only known specimen of *C. dubia* is an associated leg from late Miocene, Clarendonian (North American Land Mammal Age [NALMA], 9–10 Ma), of Lompoc, CA. The Dubious Puffin is slightly (2%) smaller than extant “Rhinoceros Puffin” *C. monocerata* (cf. Chandler 1991). *C. minor* and *C. reai*, also from Pacific, are 25–30% smaller than “Rhinoceros Puffin” (Chandler 1991). *C. minor* is from late Miocene or early Pliocene, late Hemphillian (NALMA, 5 Ma) deposits on Cedros I., Baja California, Mexico. *C. reai* is from late Pliocene, late Blancan (NALMA, 2 Ma) from San Diego Co., CA. In Atlantic, earliest puffins known (Olson 1985) from late Miocene to early Pliocene (approx. 5 Ma), including *Fratercula* and possibly *Lunda* (now synonymized with *Fratercula*).

SYSTEMATICS

GEOGRAPHIC VARIATION; SUBSPECIES

Monotypic. No geographic variation described, but see Measurements, below, regarding subtle differences in body mass and wing length.

RELATED SPECIES

Classification of Alcidae has changed repeatedly during past 2 centuries (Gaston and Jones 1998). Tufted Puffin currently classified in tribe Fraterculini, which includes all puffins (genus *Fratercula*) and Rhinoceros Auklet (genus *Cerorhinca*); Tufted Puffin formerly placed in monotypic genus *Lunda* (Am. Ornithol. Union 1998). Phylogeny of Alcidae has been estimated based on analysis of morphological and ecological characters (Strauch 1985) and genetics, including comparison of allozymes and sequences of mitochondrial DNA (Moum et al. 1994, Friesen et al. 1996), which together suggest following classification: Family consists of 6

major lineages, each ranked as a separate tribe; Rhinoceros Auklet clearly allied with puffins and basal to puffin clade (this species also known as Horn-billed Puffin); Atlantic and Horned puffins are sister species. Divergence of major alcids' lineages and divergence of puffins from true auklets (tribe Aethini) occurred in late Miocene (10–12 Ma). Radiation of puffins in Pacific came much later during second major Pliocene glaciation (2.3–2.5 Ma), when puffins diverged into a subarctic/boreal form (Rhinoceros Auklet), with brown plumage and nocturnal behavior, and an arctic/subarctic form, with specialized claw for digging burrows (leading to other puffins). This split was followed about 0.3 million yr later by divergence of an all-black lineage (leading to Tufted Puffin) and a lineage with eye scales (leading to Horned and Atlantic puffins).

MIGRATION

NATURE OF MIGRATION IN THE SPECIES

As in other alcids, migration not complete. In Bering Sea and Sea of Okhotsk, birds are pushed south by advancing ice in winter. Some remain near breeding colonies in Aleutians and Gulf of Alaska, but most undergo general postbreeding dispersal to overwintering grounds in North Central Pacific (see Distribution, above) where juveniles possibly remain for 1–2 yr before returning to breeding areas (Gould and Piatt 1993). Adults return to colonies en masse in spring (Wehle 1980).

TIMING AND ROUTES OF MIGRATION

Pelagic areas of Bering Sea, Gulf of Alaska, and Sea of Okhotsk mostly vacated by late Oct and devoid of puffins throughout winter (Shuntov 1972, Hunt et al. 1981, Gould et al. 1982, Harrison 1982). Similarly, vacate coastal and shelf waters from British Columbia to California (Tyler et al. 1993, Wahl et al. 1993). No specific migratory routes; postbreeding dispersal and movement over a large area of North Pacific (Shuntov 1972). Return to colonies at same time from year to year; time of return earlier in south than in north. At Farallons, first individuals seen 24 Mar \pm 7 d SD ($n = 13$; Ainley and Boekelheide 1990); early Apr at Goat I. (Hodder 2002). By late Apr, has moved into shelf waters of Gulf of Alaska (Harrison 1982) and begun to attend colonies between 4 and 9 May in 5 yr at Semidi Is. (about 10 d earlier than Horned Puffin; Hatch and Hatch 1990a). Arrival earlier at lower latitudes (Wehle 1980): early May at Shumagin Is. (55°N) and Semidi Is. (56°N), late May–early Jun at St. Lawrence I. (63°N), early Jun at Little Diomed I. (65°N), and mid-Jun at Cape Thompson (68°N). Correspondingly, departure dates earlier in southern colonies than northern ones.

MIGRATORY BEHAVIOR

Nothing known about migration behavior at sea. First arrival at colonies generally consists of a few individuals appearing offshore, followed within days by population arriving en masse (Wehle 1980). Attendance highly variable, with birds settling and departing from nesting areas over quasicyclic periods of 4–5 d (Wehle 1976, ASK, JFP). Laying, hatching, and fledging fairly synchronous, so departure from colonies occurs over a 2- to 3-wk period as chicks fledge. Puffins probably leave colonies for wintering areas immediately after fledging.

CONTROL AND PHYSIOLOGY

No information.

HABITAT

BREEDING RANGE

Breeds colonially on steep, rocky islands and mainland cliffs. Nests typically excavated in deep, vegetated turf on steep slopes or plateaus, well above shoreline. Where mammalian predators (e.g., foxes) are present, or normal habitat absent, breeding usually restricted to inaccessible cliff crevices or inside sea caves. Breeds on small (<1 ha) islets and rocks, but largest colonies on substantial offshore islands (>1–10 km²) scattered widely around coast from California to arctic Alaska. Climate throughout breeding range generally cool (<15°C), wet (persistent rain and fog), and overcast during summer. Local climate, especially heavy rainfall, may limit use of some islands (Kaiser and Forbes 1992).

Forages in low densities (generally <2–4 birds/km²) in bay, shelf, and shelf-edge habitats throughout Alaska (Hunt et al. 1981; Gould et al. 1982; Harrison 1982; Piatt et al. 1990a, 1992; Piatt 1993, 2002); generally within 100 km of colonies (see Food habits, below). Densities lower in areas with smaller populations: <1 bird/km² along outer coasts of Washington and Oregon, <0.1 birds/km² off California (Ainley and Boekelheide 1990, Tyler et al. 1993). Tends to forage more offshore in shelf and shelf-edge waters than coastally. Offshore distribution in British Columbia further indicated from carbon stable isotope analyses of muscle tissue, suggesting that Tufted Puffins fed offshore with Cassin's Auklets (*Ptychoramphus aleuticus*) and much farther than Rhinoceros Auklets, Marbled (*Brachyramphus marmoratus*), and Ancient murrelets, and Pigeon Guillemots (*Cephus columba*; Hobson et al. 1994).

WINTER RANGE

From California to Alaska, few found in coastal or shelf areas during winter. Although some may overwinter among Aleutian Is. (Gabrielson and Lincoln

1959), majority appear to inhabit deep, oceanic waters of Central North Pacific (see Distribution, above). This vast area consists of Subarctic, Transitional, and Subtropical Domains characterized by fairly uniform water properties from west to east (Japan to California), but with large property gradients from north to south (Alaska to Hawaiian Is.; Gould and Piatt 1993). Oceanic habitat influenced by physical processes such as currents and water mass boundaries, vertical stratification, and surface mixing from storms. Abundant forage species in Central Pacific include squid (Teuthidae), lanternfish (Myctophidae), northern smoothtongue (*Leuroglossus stilbius*), Pacific saury (*Cololabis saira*), and euphausiids (Springer et al. 1999).

SPRING AND FALL MIGRATION

No information.

FOOD HABITS

FEEDING

Main foods taken. Morphology of tongue and bill intermediate between fish- and plankton-eating alcid (Bédard 1969). Correspondingly, about 50–70% of adult diet is invertebrates and remainder fish, but adults feed mostly fish to young (Wehle 1982a, 1983). Breeding season: mostly small schooling fishes such as anchovy (*Engraulis mordax*), capelin (*Mallotus villosus*), lanternfish (especially Myctophidae), juvenile pollock (*Theragra chalcogramma*), rockfish (*Sebastes* spp.), greenling (Hexagrammidae), and sandlance; adults take more squid, polychaetes, and euphausiids. Nonbreeding season: predominantly squid and euphausiids.

Microhabitat for foraging. In Chukchi Sea (Piatt et al. 1990a), n. Bering Sea (Haney 1991, Piatt et al. 1992, Elphick and Hunt 1993), s. Bering Sea (Hunt et al. 1981), and Gulf of Alaska (Piatt 1993, 2002), forages widely offshore in continental shelf and slope waters. In California and British Columbia, forages over continental shelf slope (Ainley and Boekelheide 1990, Wahl et al. 1993).

Association with fine-scale oceanographic features not well described, perhaps owing to generally low densities in most areas. In Bering and Chukchi Seas, clear association with well-stratified Alaska coastal waters (Piatt et al. 1990a, Haney 1991, Elphick and Hunt 1993). Large feeding flocks commonly observed near island passes in Aleutians where rip currents concentrate prey (JFP).

Food capture and consumption. Prey captured underwater using wing-propelled "flight" at possible speeds of 1–2 m/s (Piatt and Nettleship 1985). Dive depths unknown, but a function of body size in Alcidae (Burger 1991); maximum depths estimated from regression as 102 m for 743-g female, 110 m for 80-g

male. Usual dives shallower; most probably <60 m. Captive Tufted Puffins foraged near bottom more frequently than other puffins and murre, but still spent most time searching in midwater (Duffy et al. 1987). Captures and eats prey underwater, except food carried to chicks. Adapted for capturing and carrying many fish in bill at one time (Bédard 1969) and routinely carries 5–20 fish in deliveries to chicks (a “bill-load”), with observed maximum of 29 larval fish (Wehle 1983). Feeds during day and at dusk.

Often forages in small groups of 10–20 individuals in association with other fish-feeding seabirds such as shearwaters, Black-legged Kittiwakes (*Rissa tridactyla*), Glaucous-winged Gulls (*Larus glaucescens*), murre (*Uria* spp.), Horned Puffins, and Rhinoceros Auklets (Hoffman et al. 1981). Independent of mixed-species flocks, foraging group size typically small, averaging only 1.2 birds/flock ($n = 122$; Ostrand et al. 1998). In rare circumstances, feeding aggregations of hundreds or thousands may form near large colonies where strong currents create tide rips and concentrate prey (e.g., Baby Pass, Akutan I., e. Aleutians; JFP). Usual pelagic densities are <1–2 birds/km².

DIET

Excellent information for nestlings, more limited for adults.

Nestlings. Mostly fish at colonies situated on coastal/shelf habitats (e.g., British Columbia, Alaska Peninsula; see Appendix 1), but more invertebrates where colonies are close to oceanic habitats (e.g., Farallons, Bogoslof, Buldir Is.). In contrast to Horned Puffins, which feed chicks mostly sand lance in all areas (Piatt and Kitaysky 2002), Tufted Puffins select a smorgasbord of prey for their young, apparently taking whatever pelagic fish are most abundant or available to them in the vicinity of each breeding colony. Thus, at Farallon Is., CA, individuals harvest mostly rockfish and anchovy, species most widely consumed by other seabirds in the area (Ainley and Boekelheide 1990). Similarly, takes mostly rockfish and sand lance at Triangle I. (off n. Vancouver I., British Columbia); sand lance, juvenile pollock, and capelin along Alaska Peninsula (prey eaten most frequently by 5 common seabirds in n. Gulf of Alaska; Piatt and Anderson 1996); pollock and pelagic species such as lanternfish or greenling at oceanic islands in the Aleutians. At islands with close access to pelagic habitat (e.g., Farallons, Semidis, Bogoslof, Buldir Is.), invertebrates such as squid (especially Gonatidae), euphausiids (especially *Thysanoessa* spp.), and octopus (Octopoda) form significant part of chick diets.

Compared to Horned Puffins, and many other seabirds, Tufted Puffins select a wide variety of prey to feed their chicks. For example, of 45,743 prey collected from both species in 1988–1994 (JFP, S. Hatch, J. Williams, and G. V. Byrd unpubl.), Tufted Puffin

chick diets included 47 different species, whereas Horned Puffins included only 20 species (Piatt and Kitaysky 2002). Hatch and Sanger (1992) reported similar results. Less abundant taxa may be common at some sites in some years and may form a persistent part of diets among years: Pacific saury at the Farallons and Triangle I. (Vermeer et al. 1979, Ainley and Boekelheide 1990); herring (*Clupea harengus*) at Talan, Triangle, and Goat Is. (Boone 1986, Kitaysky 1996, Gjerdrum 2001); Pacific cod (*Gadus macrocephalus*), prongfish (*Zaprora silenus*), and sandfish (*Trichodon trichodon*) along Alaska Peninsula; and Atka mackerel (*Pleurogrammus monopterygius*) and sablefish (*Anoplopoma fimbria*) in the Aleutians (JFP, J. Williams, and G. V. Byrd unpubl.) and Triangle I. (C. Gjerdrum unpubl.). Interestingly, diets almost always include small numbers of bottom fish, particularly sculpins and flatfish, perhaps confirming speculation that Tufted Puffins spend some time searching the bottom (Duffy et al. 1987).

Fish delivered to chicks normally range in size from about 20 to 200 mm, and average about 60–80 mm (Wehle 1983, Hatch and Sanger 1992). These sizes typically represent age class 0 of large demersal species such as cod, pollock, and rockfish and ages 1–4 of common forage species such as sand lance, capelin, and anchovy (Ainley and Boekelheide 1990, Hatch and Sanger 1992, Robards et al. 1999a). Bill-loads may include only 1 or 2 larger fish or dozens of small, juvenile fish. Number of fish delivered/load can, therefore, vary widely (range 1–29), but averages 5.0 ($n = 10$ colony yr; Manuwal and Boersma 1977, Baird and Jones 1983, Wehle 1983, Boone 1986, Piatt et al. 1997, Gjerdrum 2001). On average, adults deliver 13.5 g/load \pm 3.9 SD ($n = 19$ colony yr). However, meal sizes probably underestimated in most studies because adults will partially eat meals bound for chicks if prevented from delivering food by investigators (Piatt et al. 1997).

Adults. Fewer data. Sometimes assumed adult diets similar to those of chicks (Hatch and Sanger 1992), or importance of soft-bodied invertebrates in adult diets discounted because they tend to be digested more quickly (Gaston and Jones 1998). In fact, data suggest adults consume mostly invertebrates year-round (Appendix 2). In most of the following cases, and unless stated otherwise, we report diets as percentages of total number of prey in stomachs rather than percent mass because some data are available in numbers only, and this allows for comparison across studies. This tends to overinflate the relative importance of small invertebrates such as euphausiids or polychaetes, but generally not squid, which are often of a size similar to (or larger than) fish (Baird 1991, Springer et al. 1996). From all sources, we report samples sizes only from stomachs that contained food.

We could find no data on adult diets from California, Oregon, Washington, or British Columbia. In Alaska, Moe and Day (1977) examined 8 adults from Shumagin Is. (Alaska Peninsula) and found diets composed largely of euphausiids (66%), squid (4%), and sandlance (18%). Wehle (1982a) reported adult ($n = 20$) diets made up of fish (31%) and invertebrates (69%)—mostly squid (32%)—at Ugaiushak I. (Alaska Peninsula) and diets ($n = 86$) composed mostly of squid (76%) and fish (20%) at Buldir I. (w. Aleutians; data from 13 subadults combined with 73 adults; no difference in composition). At Sitkadiak Strait, Baird (1991) showed that breeding ($n = 98$) and nonbreeding ($n = 163$) Tufted Puffins ate mostly fish (>60%, almost all capelin) and euphausiids (>30% for nonbreeders) in 1977 and mostly euphausiids (>70%) in 1978, while feeding their chicks mostly capelin and sandlance (>80%) in both years. Springer et al. (1996) reported that adults in w. Aleutians at Buldir ($n = 19$) ate 100% squid and at Agattu ($n = 22$) ate mostly squid (33%), polychaetes (52%), and sandlance (14%). Net-drowned birds ($n = 98$) collected in pelagic waters off Kamchatka (Ogi 1980) contained mostly squid, euphausiids, pteropods (Gastropoda), and juvenile fish. Diets of birds ($n = 58$) collected in the Sub-Arctic Current composed mostly of fish, including Atka mackerel and northern smoothtongue, a bathypelagic species. Ogi's findings, however, confirm importance of euphausiids to adult Tufted Puffins, revealing that they made up 37% of food volume off Kamchatka, 50% in Sea of Okhotsk, and 31% in Sub-Arctic Current.

Larger samples (Tanaka 1989; Appendix 2) collected from drift-net fisheries during 1980s corroborate Ogi's (1980) original findings. Birds (adults and subadults combined) collected over a large area of sw. Bering Sea ($n = 212$) and waters east of the Kurils ($n = 95$) and south of the w. Aleutians ($n = 289$) all contained mostly invertebrates (59–78% by mass); mostly squid (41–61% by mass) and euphausiids (<18% by mass). Our own unpublished studies of adult diets in the Aleutians and Gulf of Alaska also confirm importance of invertebrates to birds at their breeding colonies (Appendix 2). Squid were of great importance (83%) to birds ($n = 231$) collected near Buldir and other oceanic islands in the w. Aleutians, as were polychaetes (9%). In e. Aleutians and w. Alaska Peninsula, squid less important in adult diets (17%), but euphausiids (57%) abundant in diets, while fish of all types relatively scarce (<22%) and dominated by juvenile pollock. Along e. Alaska Peninsula, squid remain a common prey (15%), but fish most important (28% gadids, 27% sandlance), and mollusks (22%) round out list of important prey types. Finally, in a collection of 364 Tufted Puffins mostly (93%) from Gulf of Alaska and then mostly (73%) from around Kodiak I. during breeding season, Sanger (1983, 1987) found that these birds ate mostly euphausiids (45%),

squid (22%), and fish (26%); mostly capelin (17%) and sandlance (5%). Capelin largely disappeared from diets of adult puffins in n. Gulf of Alaska between the time of Sanger's study (1978) and ours (1988–1998), apparently because of a large-scale shift in composition of fish communities that resulted from a climatic regime shift in late 1970s (Piatt and Anderson 1996, Anderson and Piatt 1999). Capelin were replaced largely by less nutritious juvenile pollock, apparently resulting in decreased productivity and population size of some seabirds (Piatt and Anderson 1996).

In summary, data suggest a strong dependence on invertebrates by adult Tufted Puffins and a marked difference between what adults eat and what they feed their chicks (mostly fish). Squid, in particular, make up a very large proportion of adult diets in oceanic habitats or at colonies with close access to shelf-edge or slope habitats. More surprisingly, euphausiids a major component of diets at center of Tufted Puffin abundance in e. Aleutians and w. Alaska Peninsula, as well as around Kodiak and the Kuril Is. While it is true that the importance of euphausiids is overemphasized in analyses using percent numbers, it is also true that euphausiids and other Crustacea are rapidly digested and have no hard parts to remain for identification—in contrast to fish otoliths and squid beaks—and so their importance in diets is likely to be underestimated in traditional diet studies (Hobson et al. 1994). This is at least part of the reason why mean trophic level [TL] for Tufted Puffin calculated from traditional stomach analyses (TL = 4.1) shows greatest discrepancy with mean trophic level calculated from stable isotope analyses (TL = 3.3) for 19 species of seabirds in Gulf of Alaska, which put Tufted Puffins (from Shumagin Is.) at almost the same trophic level as Crested Auklets (TL = 3.1), obligate euphausiid feeders (Hobson et al. 1994).

Subadults, adults in winter. No information. Diets of subadults in summer basically similar to that of adults. Although significant differences observed between adults and subadults in terms of the proportion of different taxa taken (Tanaka 1989, Baird 1991), these differences not consistent among areas or years and therefore do not suggest a systematic bias of age classes for or against particular prey; e.g., differences in proportions of fish, squid, and crustaceans eaten by yearlings ($n = 271$; 36, 55, and 9%, respectively), subadults ($n = 133$; 34, 54, and 12%, respectively) and adults ($n = 193$; 29, 43 and 28%, respectively) are not dramatic and may be explained as much by area sampled as by age class (Tanaka 1989).

FOOD SELECTION AND STORAGE

Does not store food. Some evidence for selection of preferred prey, especially those with high nutritive and caloric value for chicks. At Barren Is. in 1996–1999, adults fed chicks 15–52% capelin (Roseneau et

al. 2000; Appendix 1), whereas capelin made up <4% of total midwater trawl catches ($n = 108$) around that area during same years (Abookire and Piatt 2002).

NUTRITION AND ENERGETICS

No direct measures of energetic or nutritive requirements of adults. Energy demands of chicks increase with age. Average daily energy requirement for captive chicks fed ad libitum was 539.0 kJ/d (fledging at 45 d; Kitaysky 1999). For wild chicks with minimal feeding rates and long development time (64 d), average daily intake 279.3 kJ/d. Other measures of daily needs for wild chicks are 545.5 kJ/d (Talan I.) and 489.1 kJ/d (Semidi I.).

Nutritive value of food largely a function of fat and protein densities (Montevicchi and Piatt 1984, Van Pelt et al. 1997, Robards et al. 1999a). Energy density (kJ/g wet mass) of common prey eaten by Tufted Puffins in Alaska during summer varies widely among species (e.g., between about 2 and 8 kJ/g) and seasonally (e.g., between 3 and 10 kJ/g). See Piatt and Kitaysky 2002 for more details.

METABOLISM AND TEMPERATURE REGULATION

No measurements of field metabolic rate. Resting metabolic rate (RMR) of chicks (Kitaysky 1999) can be estimated from regression equation: $\log \text{RMR (kJ/d)} = 0.867 + 0.70 \log \text{MASS(g)}$. Puffin chicks adjust metabolic rate to food supply and can reduce metabolic rate by at least 47% during food shortage. Captive subadult consumed 40% of body mass on average, but daily food intake varied between 20 and 50% in cycles of 3–6 d, suggesting hunger and feeding behavior regulated by endocrine system (JFP). Body temperature of captive chicks fed ad libitum $39.1^\circ\text{C} \pm 0.39 \text{ SD}$ ($n = 7$); in food-restricted chicks, $38.4^\circ\text{C} \pm 0.37 \text{ SD}$ ($n = 7$; ASK). Higher food intake and increased body temperature associated with higher concentrations of total and free fractions of metabolism-regulating hormone triiodothyronine (T3) in blood of chicks (ASK).

DRINKING, PELLET-CASTING, AND DEFECATION

No information on drinking; metabolic water obtained from food. Does not regurgitate pellets. Adult defecates outside nest-chamber in burrow or in side chamber where ≥ 2 exist in burrow (JFP and ASK). Chicks defecate at nest site when small, at burrow entrance when older.

SOUNDS

VOCALIZATIONS

Development. When hungry, or when adult returns with food, chicks make continuous *peep, peep, peep*. Well-fed chicks with crops filled with food make

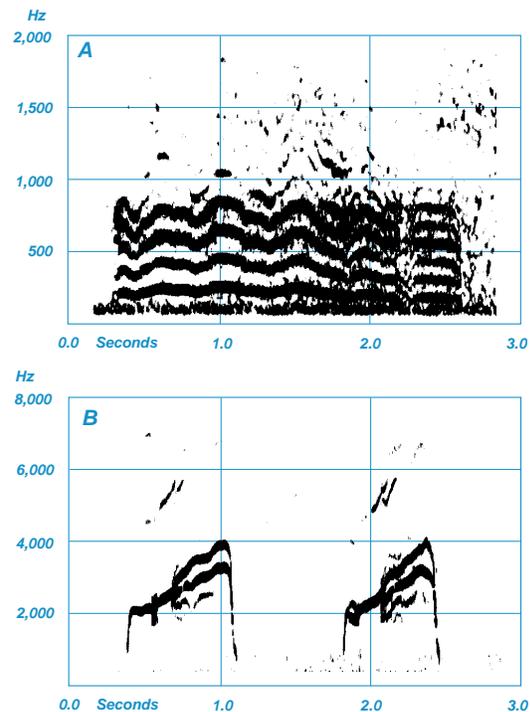


Figure 2. A. “Purring” call of an adult Tufted Puffin; recorded Aiktak I., AK, July 1995, by K. Turco (Alaska Spirit Speaks: Sound and Science, Fairbanks, AK). B. “Uiiiep uiiiep” call of a well-fed chick; recorded by T. van Pelt (US Geol. Surv.). Prepared by staff of the Borror Lab of Bioacoustics, the Ohio State Univ., using a Kay Elemetrics DSP 5500 Sona-Graph (with an effective frequency resolution of 37.5 Hz for the adult “purr” and 150 Hz for the chick “Uiiiep” call and a 200-point FFT transform size for both).

different sound: *uiiiep, uiiiep, uiiiep*. Adult-type vocalizations develop in first winter (JFP, ASK, observing captive birds).

Vocal array. Little studied. Vocal at colonies, also in social gatherings at sea. Repertoire consists of call notes given by both sexes (Fig. 2). Calls similar to other puffins, a low growling *errr*, either single or uttered several times, especially when disturbed. Wehle (1980) described 4 different types of calls with different functions:

SHORT ERRR. Primary function threat or warning.

PURRING. Similar to Short *Err* growl but longer in duration and softer, “having the low purring quality of a cat” (Wehle 1980: 41), might repeat call every 20–35 s. Function unknown, heard from birds resting at colony.

BISYLLABIC CALL. Growl characterized by a short, sharp *er* syllable followed by a higher pitch and longer syllable. Second syllable trails off gradually in pitch and intensity. Heard at colony and on water.

MULTINOTE CALL. Growl consists of a minimum of 3 syllables, with third and final syllable repeated many times. "The third and following syllables were cyclic repetitions of the second syllable, and varied rhythmically in frequency and intensity giving the call a sirenlike sound" (Wehle 1980: 41). Usually made by birds in burrows.

Phenology. No quantitative information. No information outside breeding season, although captive subadults vocalize year-round (JFP). Calls heard throughout period of colony attendance, with greatest activity during egg-laying and incubation.

Daily pattern. Most vocalization takes place during daytime activity period, both at colony and on water.

Places of vocalizing. Vocal at colony, while standing on talus or grassy slopes outside nest site, in social resting areas, and inside nesting burrows. Some vocalization on water where gathered in social aggregations, especially during interactions with other birds.

NONVOCAL SOUNDS

No information.

BEHAVIOR

LOCOMOTION

On land. Walks upright with ease over rocks, clinging to surface with claws. Capable of hopping. Reclines with tarsus pressed flat, but walks on its toes.

Flight. Direct and powerful, and probably more maneuverable than other puffins (midair collisions rare). Wing area 480–490 cm² (Shiomi and Ogi 1991), giving wing-loading of 1.64 g/cm² in 801-g bird, exactly as predicted in volant alcid of that body size (Livezey 1988). Vermeer (1979) reported wing-loading of 1.46 g/cm². Uses feet as rudders. Often crashes into tall grass, rocks, and talus slopes during landing. When departing from colonies covered with thick vegetation, uses angled slopes and elevated rocks or walks to cliff edge before initiating flight. Also uses "departure" passes (1–3 m wide) or plots (2–3 × 3–4 m in diameter)—bare routes and platforms situated on periphery of nesting colonies that lack vegetation due to constant arrivals and departures of puffins (Mikhtaryantz 1977). Takes off from water after gathering momentum, sometimes using feet as paddles until airborne. During commutes between foraging grounds and nesting colonies, often travels in groups of 2–20 and frequently joins groups of flying Horned Puffins and murres. Before landing at colony, makes a few circles around landing area and then flies directly to nest-burrow entrance.

Swimming and diving. Swims on surface by paddling with feet. Powerful underwater swimmer and diver. Similar to other alcids, propels itself

underwater by using flightlike beating of half-opened wings (see Food habits: feeding, above).

SELF-MAINTENANCE

Preening, stretching, bathing. Three types of body-maintenance behaviors described (Wehle 1980):

HEAD-DIPPING. During swimming, Head-Dips by submerging head above eyes into water. May be repeated frequently with head-shaking to eliminate water.

WING-FLAPPING. Erects itself on water, fluffs feathers and vigorously flaps wings 2–4 times. Also occurs when a bird lays to one side so that one wing is underwater while other is vertical to water. After bathing on one side, turns on other and repeats Wing-Flapping (ASK).

PREENING. Preen on land and on water. Side of bill repeatedly rubbed on uropygial gland and secretion smeared over body-feathers while Preening and arranging feathers, which aids in waterproofing and feather maintenance.

Sleeping, roosting. During daylight, breeding individuals sleep and roost in nest, in roosting areas at breeding colony, and on water close to colony. At night, spends time in nest or on water in vicinity of breeding colony.

Daily time budget. Not well quantified, but see Colony attendance behavior, below.

COLONY-ATTENDANCE BEHAVIOR

Daily pattern of attendance at the colony. Early in reproductive season (prelaying and incubation), 2 peaks of daily colony attendance. At midlatitudes, morning peak 08:00–14:00, evening peak 18:00–21:00. Considerable variation in diurnal-attendance patterns from day to day. During pre-egg-laying stage, birds completely cease attending colony in stormy and snowy weather (ASK). Later in season, and throughout their range, attend throughout day, often with peak in evening (Wehle 1976, Amaral 1977, Boone 1986, Ainley and Boekelheide 1990). However, while peaks in attendance typically occur in evening, peaks in visitation to feed chicks highest in morning hours (Vermeer et al. 1979, Wehle 1983, Piatt et al. 1997, Gjerdrum 2001). During peaks of colony attendance, large numbers of birds may gather on water and socialize before visiting breeding sites on land.

Attendance in relation to time of year. Present at colonies only during breeding season; May–Sep in Alaska (see Migration, above). Mikhtaryantz (1978) described cyclic (3–6 d a full cycle) colony attendance on Commander Is. during entire reproductive season (May–Aug). During interval from first visits to permanent occupancy of colony at Ugaiushak I., birds present at or near colony for 4- to 5-d periods followed by equal number of days at sea (Wehle 1980). Amaral

(1977) reported a 3- to 5-d cycle at the Barrens. At Sitkadilak Strait, cycle involved 1 d at colony followed by 2 d absent (Baird and Jones 1983). All "cycles" reported should more properly be called "quasicycles," meaning that regular fluctuations occur—possibly because of changes in food supply and/or metabolic control of foraging behavior (see Food habits: metabolism and temperature regulation, above)—but that both period and amplitude are irregular, and fluctuations tend to drift in and out of phase (Brown and Rothery 1993). No information on proportion of local breeding population present during activity peaks or whether individuals present in one peak are same birds observed in following peak.

AGONISTIC BEHAVIOR

Physical interactions. Territorial species that protects nesting burrow and close surroundings from conspecifics and other birds. Fights among individuals common upon arrival at breeding colonies. Sometimes both members of a pair attack an intruder. Aggression occurs by locking bills, scratching with nails, and beating wings. Aggressive encounters might continue for 2–3 min and end when one participant runs away while other chases it for 2–3 m and occasionally up to 30 m (Mikhtaryantz 1977).

During late incubation, some pipping eggs may be pushed out of nesting burrow; perhaps by young or inexperienced parents. During chick-rearing, non-breeding pairs looking for nest burrow were seen to kill chicks of other parents while latter were away at sea (ASK).

Communicative interactions. In aggressive display, Tufted Puffin silent, threatens intruder by holding bill open for several seconds, shaking head, and approaching. Aggression occurs if threat display ignored. Several forms of aggressive posture (Wehle 1980, Kharitonov 1990):

FORWARD-THREAT POSTURE. Displayed at 2 levels of intensity. Low intensity: Closed bill kept vertically down, tail lifted almost vertically, body and head horizontally directed toward a subject of aggression; sometimes displayed when moving, then wings held spread. High intensity: Display in still posture for 3–4 s; bill half-opened and held at 45° angle and directed toward a subject, tufts erected.

BILL-GAPING. Used as a threat exhibited in response to an intruder on nest territory, before and after fight. Bird stands upright with erected neck and bill held toward a recipient. Tufts erected; neck- and head-feathers ruffled. Lower and upper mandibles held wide apart, exposing bright lining of mouth; tongue may or may not protrude. Usually does not exceed 5 s in duration.

BILLING. Neck bent down, bill moved upward and from side to side in fast motions. Generally, one bird bills with another (see Sexual behavior, below).

LANDING DISPLAY. Displays immediately after landing. Body held low to ground with wings outstretched above back. Head may also be outstretched in line with body or bent downward to varying degrees. Position held for several seconds. At conclusion of display, puffin takes several exaggerated steps in this posture before slowly closing wings and resuming normal posture.

SPACING

Territoriality. Territorial behavior not well known. Pairs defend nest entrances. Male defends female at colony and on water (often porpoising long distances on water during aggressive chases at sea). Burrow densities at colonies can be high; e.g., (in burrows/m²): Barren Is., 0.33–0.69 (Amaral 1977); Suklik I., 0.16–0.76 (ASK, JFP); Egg I., 0.46–0.82 (Byrd et al. 1991); Aiktak I., 0.22–1.20 (Byrd et al. 1991); Talan I., 0.33–0.91 (Kharitonov 1990). On Talan I., distance between nearest-neighbor entrances estimated at 83 cm, shortest 15 cm ($n = 342$; Kharitonov 1990). Individual nesting territories 1–1.5 m² in diameter on Commander Is.; adults feeding young protect smaller territories than at earlier reproductive stages (Mikhtaryantz 1977, 1986). Closest neighbors share area about 3–4 m² in diameter, where territories of individual pairs overlap (Mikhtaryantz 1986).

SEXUAL BEHAVIOR

Mating system and sex ratio. Probably socially monogamous, as in Atlantic Puffin (Harris 1984); no quantitative information on extra-pair fertilizations. A random collection of birds reported in this paper suggests 1:1 sex ratio (Appendix 3).

Courtship and mate choice. Courtship begins shortly after arrival at breeding colonies (Wehle 1980). Mating occurs mostly on water and less so at colony (Mikhtaryantz 1977). Prior to copulation, male follows female at a distance of several meters. During chase, he stretches and lifts neck, directing bill straight up, opens and closes bill in a slow manner, and "jerks" head in a fast motion. Sometimes male bends neck and puts head back. Behavior continues for about 1 min. By opening and closing his bill, a male is thought to expose to a female the bright mouth-lining and expanded pink rosettes in corners of mouth (Amaral 1977, Wehle 1980). Eventually a female assumes a hunched, low-to-the-water posture with head and neck held close to body (Amaral 1977). On approaching a female, male increases frequency of "jerking" and exaggerates it. Male demonstrations followed by billing, when male and female face each other and repeatedly rub their bills together (Amaral 1977). During billing, male might grab female by the neck and/or back, a light grabbing by foot web also observed (Kharitonov 1990). Then a male approaches a female with lifted and slightly opened or flapping

wings, followed by copulation 30–60 s in duration (Mikhtaryantz 1977). During copulation, male raises off water, flaps its wings, and may or may not continue jerking its head, while female sinks so that only her head remains above water. After mating, female dives and surfaces within a few meters of male and finally flies 2–5 m away. At end, both mates flap their wings.

Female that avoids copulation bill-gapes (see below) toward a male, dives (if it occurs on water), and then flies away. Forced copulations known; observed more frequently at colony (Mikhtaryantz 1977). During such an encounter, male grabs female by neck or back and growls. Forced copulations may occur until midchick-rearing (Mikhtaryantz 1977).

Bowed-head display common prior to entering nesting burrow (Wehle 1980). During display, body held low and horizontal to ground with head downward so that tip of bill nearly touches ground. Swings head slowly from side to side. In some cases, side-to-side movement accompanied by rhythmic convulsions of body. Display has effect of drawing a nestmate to burrow.

Pair-bond activity also includes displaying with nest materials and billing (Wehle 1980).

Pair bond. Same burrows occupied year after year; but information on nest-site tenacity and pair bond scarce. On Ugaiushak I., minimum of 29% of banded Tufted Puffins returned to monitored nest sites (Wehle 1980). Site fidelity likely much higher, but disturbance caused high rate of site abandonment. On Talan I., 3 of 4 pairs in which both members were color-banded occupied same burrows and retained same partner during 2 consecutive seasons (V. Zubakin unpubl.).

Extra-pair copulations. No information.

SOCIAL AND INTERSPECIFIC BEHAVIOR

Degree of sociality. Less social and more dispersed at sea than other species of puffins. Nests solitarily, as well as in large mono- and multispecies colonies. Social and territorial displays (Wehle 1980) include Landing Displays (above) and Fly-Bys; latter common throughout breeding season. Puffins make repeated circular flights above breeding colony before landing at colony or on water in rafts near shore; may involve a few individuals or almost entire breeding population. Function unclear but also observed in other puffins and auklets.

Play. No information.

Nonpredatory interspecific interactions. Forms multispecies feeding flocks with other alcids and gulls (Hoffman et al. 1981). Highly aggressive toward other species. On Commander and Talan Is., adult Crested and Parakeet auklets and Ancient Murrelets found killed in nesting burrows of Tufted Puffins (Marakov 1966 in Mikhtaryantz 1977; ASK). Thought to compete with Horned Puffins for nesting habitat (Sealy 1973). On Talan I., twice took over rock-crevice

of Horned Puffins, destroyed their nests, and successfully raised their young (ASK). Wehle (1980) observed 2 instances of cohabitation with Parakeet Auklets and reported that Ancient Murrelets and Fork-tailed Storm-Petrels (*Oceanodroma furcata*) commonly nest in small side tunnels within puffin burrows. At Talan I., Tufted Puffins twice found incubating Crested Auklet eggs (chicks disappeared shortly after hatching). Wehle (1980) suggested that cohabitation with other species is more successful if other species is nocturnal in its colony attendance.

During chick-rearing, adults known to be kleptoparasitized by Red-legged (*Rissa brevirostris*) and Black-legged kittiwakes, which attack puffins in air and snatch fish directly from their bills (Mikhtaryantz 1977). Amaral (1977) observed only 10 attempts (all unsuccessful) of kleptoparasitism by Glaucous-winged Gulls in 1,500 deliveries of food by puffins. Wehle (1980) also reported only a few kleptoparasitism events by Glaucous-winged Gulls and Parasitic Jaegers (*Stercorarius parasiticus*) on Buldir and Ugaiushak Is. In contrast, kleptoparasitism by Glaucous-winged Gulls of adult Tufted Puffins returning with food ranged from 2 to 19% at Triangle I. in 2 yr of study (St. Clair et al. 2001). During bad food years, kleptoparasitism may exacerbate problems feeding chicks, but in general did not measurably affect reproductive success (St. Clair et al. 2001).

PREDATION

Avian predators, particularly eagles (Bald Eagles [*Haliaeetus leucocephalus*] in Northeast Pacific and Steller's Sea-Eagles [*H. pelagicus*] in Northwest Pacific), Peregrine Falcons (*Falco peregrinus*), Snowy Owls (*Nyctea scandiaca*), and Eagle Owls (*Bubo bubo*), prey on adults during reproductive season. Diet of Bald Eagles at Hall I. (Shumagin Is., AK) consisted of up to 30% Tufted Puffins (Moe 1977), and Peregrine Falcons take puffins there also (JFP). Large gulls and ravens occasionally prey on chicks. Snowy Owls took puffins on Buldir and Agattu Is. (Wehle 1980). Common Ravens (*Corvus corax*) and Glaucous-winged Gulls occasionally prey on eggs (Wehle 1980).

Mammalian predators—especially arctic (*Alopex lagopus*) and red (*Vulpes vulpes*) fox—kill and store adults, eggs, and chicks. Foxes can devastate Tufted Puffin colonies because eggs, chicks, and adults are easy to access, especially compared to crevice- or cliff-nesting seabirds (Petersen 1982). Foxes introduced in the Kurils, Commander, and Aleutian Is. had a devastating effect on Tufted Puffin populations there (Mikhtaryantz 1986, Bailey 1993, Bailey and Kaiser 1993). River otters (*Lutra canadensis*) practically eliminated chicks at a colony on Egg I. (near Sand Point, AK) in 1992 (JFP). In vicinity of Alaska Peninsula, colonies periodically visited by brown bears (*Ursus arctos*), which decimate breeding habitat by

excavating burrows and methodically overturning sod in search of chicks. In 1992 and 1993, for example, almost 100% of nestlings on Ugaiushak I. and nearby Central I. were eaten by brown bears (JFP, ASK). For the most part, Tufted Puffins are helpless against mammalian predators, which is why they breed almost exclusively on offshore islands free of those predators. See Conservation and management, below, for impacts of introduced predators.

BREEDING

PHENOLOGY

Four events distinguished upon arrival at breeding colonies: arrival in vicinity of colony, first visits to colony, establishment of continuous occupancy, and initiation of egg-laying (Wehle 1980). Total length of pre-egg stage averages about 3.5 wk. Arrives earlier at lower latitudes than at high latitudes. Farallons, CA (Ainley and Boekelheide 1990): mean arrival date 24 Mar (range 12 Mar–6 Apr), later in warm-water years. Other arrival dates: Goat I., OR (Boone 1986), 17–24 Apr in 2 yr; Barrens (Amaral 1977), on or before 14 May, with first colony visits 20 May; Ugaiushak (Wehle 1980), 24 May; Semidi I. (Hatch and Hatch 1990a), 4–9 May, with interval between arrival and laying averaging about 2 wk (shortest of any species breeding on island); Buldir I. (Wehle 1980), 17 May, first colony visits 23 May; Talan I. (ASK), 13 May, first colony visits 20 May and first signs of nest-building 26 May; Uelen (Chukchi Peninsula), 3 Jun (Portenko 1973); St. Lawrence I., 21–29 Jun; Cape Thompson, 8 and 16 Jun; Little Diomedea I., 26 May and 2 Jun (Sealy 1973). Time of arrival relatively constant among years, usually within same 1- to 2-wk period of each year.

Pair formation and nest occupation. Mates arrive at breeding grounds in pairs or form pairs shortly after arrival. Occupy nesting habitat about 1 wk after arrival, typical of all puffin species (Sealy 1973, Wehle 1976, Amaral 1977).

Laying of eggs. Figure 3. Lay eggs earlier at lower latitudes than high latitudes. Timing probably related to delay in food production and/or accessibility of nesting habitat as one goes north (Wehle 1980). Farallon Is. (Ainley and Boekelheide 1990): late Apr–early May. Goat I. (Boone 1986): concentrated during mid-May, sometimes to early Jun. Destruction I., WA (Burrell 1980): May–early Jun. At majority of sites in Gulf of Alaska, start laying in late May (Baird and Jones 1983); e.g., Sitkadilak Strait, Kodiak (Baird and Jones 1983), first eggs 27 May, median lay date on 5 Jun; Barrens (Amaral 1977), lays between last days of May and 24 Jun; Semidis (Hatch and Hatch 1990a), 20 May–20 Jun; Koniuji Is. (Moe and Day 1977), lays between 25 May and 13 Jun; Ugaiushak (Wehle 1980), lays 1–11 Jun. Timing somewhat later in Aleutian Is.;

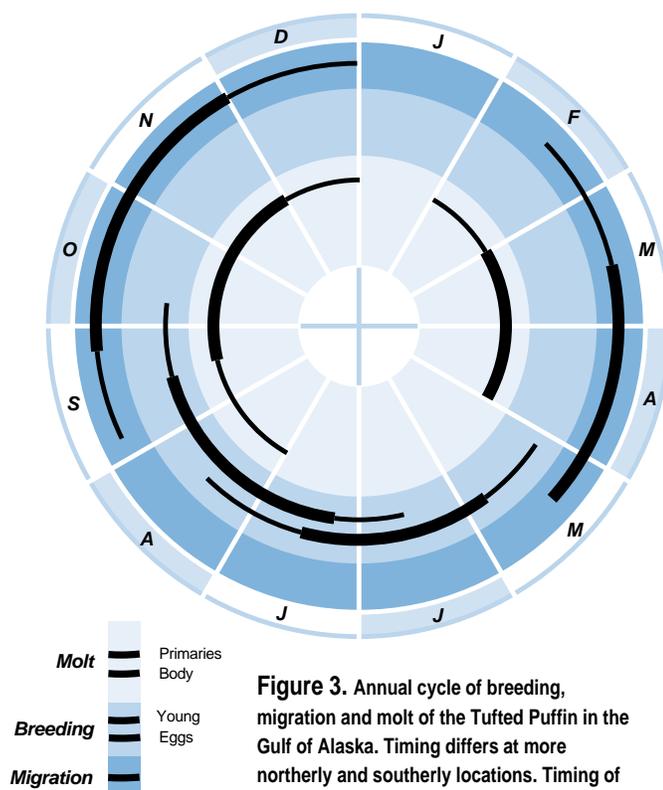


Figure 3. Annual cycle of breeding, migration and molt of the Tufted Puffin in the Gulf of Alaska. Timing differs at more northerly and southerly locations. Timing of migration and molt remains speculative. Thick lines indicate peak activity; thin lines, off-peak.

e.g., Buldir I. (Wehle 1980), lays 5–19 Jun; Commander Is. (Mikhtaryantz 1986), first eggs 9–13 Jun, median egg-laying 20–30 Jun; Talan I. (1987–1989), starts egg-laying during first week of Jun; last eggs early Jul; Iona I. (Kharitonov 1990), approximately 10–11 Jun (based on hatching dates).

Hatching of eggs. For assessing phenology, probably best data from most locations is on hatching. Farallons (Ainley and Boekelheide 1990): 7 Jun–6 Jul. Destruction I. (Burrell 1980): mean hatch 1 Jul (range 21 Jun–24 Jul). Triangle I., British Columbia: mean hatch 14–25 Jul in 1975–1977 (Vermeer et al. 1979), 9–23 Jul in 1980–1982 (A. Vallée unpubl.), 30 Jun–9 Jul in 1994–1997 (D. Bertram and C. Cassidy St. Clair unpubl.) and 22–27 Jun in 1999–2000 (Gjerdrum 2001). Gulf of Alaska (Baird and Jones 1983): historic peak hatch mid- to late Jul. Barrens: 7–31 Jul (Amaral 1977) and more recent (1995–1999) median dates of 18–31 Jul (Roseneau et al. 2000). Ugaiushak (Wehle 1980): 7–20 Jul hatching. Big Koniuji and Hall I. (Shumagin Is.; Moe and Day 1977): hatch 28 Jul–14 Aug. Somewhat later in Aleutian Is. Aiktak I.: 27 Jul–7 Aug (Howard and Woodward 1999). At Buldir I. in 1970s, chicks hatched 18 Jul–2 Aug (Wehle 1980) and more recent time series (1988–1999) shows mean hatch date 7–25 Jul (Williams and Daniels 2001). Agattu I. (Byrd et al. 1991): 12–24 Jul median dates. Commander Is.

(Mikhtaryantz 1986): start 20–30 Jul, majority hatch 1–10 Aug, last in second half of Aug. Talan I. (Golubova 1992, ASK): first chicks hatched 6 Jul, last chicks 15 Aug.

Fledging and departure from colony. Farallons (Ainley and Boekelheide 1990) fledging late Jul through Aug. Last chicks to leave Goat I. (Boone 1986) seen 13 Sep 1981 and 24 Aug 1982. Destruction I. (Burrell 1980) mean fledge 13 Aug. Triangle I.: mean fledging 22 Aug (range 11 Aug–10 Sep) in 1977–1978 (K. Vermeer unpubl.), 7 Sep (range 14 Aug–21 Sep) in 1980–1981 (A. Vallée unpubl.), 15 Aug (range 10–24 Aug) in 1994–1997 (D. Bertram and C. Cassidy St. Clair unpubl.), and 9 Aug (range 31 Jul–23 Aug) in 1998–2000 (Gjerdrum 2001, D. Bertram unpubl.). Barrens (Baird and Jones 1983) fledging 20 Aug–22 Sep. Sitkadiak Strait (Baird and Jones 1983): most fledged by 7 Sep (range 21 Aug–23 Sep). First fledging dates at Buldir I. during 1988–1999 ranged between 10 and 30 Aug. Talan I. (1987–1989): first fledglings 27 Aug, peak mid-Sep; fledgling also observed early Oct. Sakhalin I. (Gizenko 1955): first chicks late Aug, last chicks late Sep. Commander Is. (Koslova 1957): a fledgling collected on Bering I. 15 Oct.

Chick completely independent of parents after fledging.

NEST SITE

Selection. No information.

Site characteristics. Most common nesting habitat is earthen burrows (Wehle 1980). Burrow densities appear highest along cliff edges, steep sea slopes covered with dense vegetation and deep layer of soil (Amaral 1977, Vermeer 1979). Lower densities in rock-crevice habitats, among beach boulders, and in cracks and crevices of sea cliffs. Occasionally nests on open ground under bushes (Bent 1919) and bunches of grass (Mikhtaryantz 1977), in sandy burrows on estuarine islets (and Sanger 1979). Densities may exceed 1 burrow/m² (see Behavior: spacing, above). Occupancy of burrows can vary markedly among colonies and years; average occupancy rates at 9 sites in Aleutians ranged between 41 and 86%, but most typically 50–75% (Byrd et al. 1991). Vegetation in nesting areas often lush; consists of forbs, grasses, and sedges in Alaska, including *Angelica lucida*, *Heraclium lanatum*, *Festuca* spp., *Carex* spp., and *Elymus arenarius mollis*. See also Habitat, above.

NEST

Construction process. Using feet and occasionally bill, excavates crevices or burrows or clears area of soil, debris, feces, or mud. Collects nesting materials (dry grass, small twigs, feathers) in vicinity of nests or at sea (along with algae and other floating materials, including scraps of plastic line and gill-nets). Brings nest materials to nest held crosswise in bill. Amount

of nest material varies from well-built nests with defined cup to few straws on floor of rock crevice. Mikhtaryantz (1986) observed partitioning of nest-building tasks between mating partners: one involved more in cleaning/digging nesting burrow and the other in delivering nesting materials.

Structure and composition. Nests examined at Ariy Kamen (Commander Is.; Mikhtaryantz 1986) contained dry stems and leaves (54.8% of nests examined), dry and green grasses (16.1%), green grasses only (12.9%), dry grasses and bird feathers (13%), or dry grasses and algae (3.2%). Nests that are relatively exposed or situated in rock crevices contained larger amounts of nesting materials compared to nests situated in earthen burrows.

Dimensions. Diameter of burrow entrance: mean height 18.0 cm, mean width 19.3 cm, mean length 86.4 cm (Amaral 1977). According to Gizenko (1955), mean height 13.5–14.5 cm, width 16–17 cm. Alaska Maritime NWR and Canadian Wildlife Service use 14.5-cm diameter as cutoff to distinguish Tufted Puffin burrows from those of smaller species (e.g., murrelets, storm-petrels; Byrd et al. 1991, Williams and Daniels 2000). Depending on type of substrate, some burrows can be as deep as 160 cm; majority dug straight into slope for about 30 cm and then turned with an angle for another 60–90 cm (Amaral 1977). On Ugaiushak, burrows extend up to 5 m from entrance in sea cliff (Wehle 1980). Side branches occur in >50% of burrows (Baird and Jones 1983).

Microclimate. At Ugaiushak (Wehle 1980): Temperature of burrow substrate at arrival, 2.1°C (min. 0°C, max. 4°C; $n = 65$), at egg-laying, 9.0°C (min. 9°C, max. = 10.5°C; $n = 23$); at hatching, 14.5°C (min. 13°C, max. 15.5°C; $n = 4$). [N.B.: These data were erroneously reported for Horned Puffins in Piatt and Kitaysky 2002.]

Maintenance or reuse of nests. Same nests usually occupied year after year; likely by same birds (ASK), known for certain in 2 cases (Wehle 1980).

EGG

Shape. Elliptical or subelliptical. Shell thick, roughly granulated (Sealy 1973).

Size. Average length (71–74 mm), breadth (48–49 mm), and volume (81–85 ml) of eggs vary little among geographic regions. Goat I.: mean length (ML, in mm) 73.0 ± 2.82 SD ($n = 25$) \times mean breadth (MB, in mm) 49.3 ± 1.80 SD ($n = 25$; Boone 1986). Destruction I.: ML 72.8 ($n = 6$) \times MB 48.1 ($n = 6$; Frazer 1975). Triangle I.: ML 71.8 ± 2.29 SD ($n = 73$) \times MB 48.2 ± 1.22 SD ($n = 73$; G. Blackburn unpubl.). Barren Is.: ML 72.6 ($n = 127$) \times MB 49.0 ($n = 127$; P. D. Boersma unpubl. data). Hall I.: ML 73.4 ($n = 56$) \times MB 48.9 ($n = 56$; Moe and Day 1977). Buldir I.: ML 72.5 ± 3.05 SD ($n = 37$) \times MB 49.3 ± 1.48 SD ($n = 37$; Wehle 1980). Second eggs smaller in volume than first (3.1% difference at Ugaiushak [Wehle 1980], 7.0% at Goat I., OR [Boone 1986]).

Shell thickness of eggs collected at Goat I. prior to 1947: $0.427 \text{ mm} \pm 0.042 \text{ SD}$ ($n = 23$); 1949–1953: $0.419 \text{ mm} \pm 0.013 \text{ SD}$ ($n = 5$); in 1979: $0.367 \text{ mm} \pm 0.016 \text{ SD}$ ($n = 3$); and in 1982: $0.409 \text{ mm} \pm 0.021$ ($n = 5$; Henny et al. 1982, Boone 1986).

Mass. Average mass of eggs about 85–95 g from various collections. Goat I.: $90.3 \text{ g} \pm 7.79 \text{ SD}$ ($n = 25$; Boone 1986). Triangle I.: $85.1 \text{ g} \pm 6.67 \text{ SD}$ ($n = 73$; G. Blackburn unpubl.). Ugaiushak I.: $93.9 \text{ g} \pm 5.67 \text{ SD}$ ($n = 39$; Wehle 1980). Buldir I.: $94.4 \text{ g} \pm 7.48 \text{ SD}$ ($n = 37$; Wehle 1980). Mass of known fresh eggs at Talan I.: $87.9 \text{ g} \pm 0.48 \text{ SE}$ ($n = 80$; ASK); at Ugaiushak: $95.0 \text{ g} \pm 6.04 \text{ SD}$ ($n = 9$; Wehle 1980). Mass loss during incubation: $14.3 \text{ g} \pm 0.89 \text{ SE}$ or about 16% ($n = 17$; Talan I.; ASK), 17% (Manuwal and Boersma 1977), and 13% ($n = 9$; Ugaiushak I.; Wehle 1980). Mass of egg in proportion to female body mass 10.9–12.9% (Wehle 1980).

Color. Dull white, dirty white, or creamy white. One egg from 54 examined at Commander Is. was bluish white in color (Mikhtaryantz 1986). May show faint markings, spots, or scrawls of pale lavender-gray or pale olive on buff (Sealy 1973, Gaston and Jones 1998). Some have few dark-brown and lilac spots and scrawls (Portenko 1973, Mikhtaryantz 1986). Eggs become soiled during incubation.

Clutch size. One (see also Demography and populations, below).

Egg-laying. Little known. Replacement egg may be laid if first is lost; 10–21 d needed to synthesize a new egg (in 7 nests; Wehle 1980).

INCUBATION

Onset of broodiness and incubation in relation to laying. Incubation starts immediately after egg-laying.

Incubation patches. Two lateral similar-size brood patches present in both sexes (Wehle 1980): $62.4 \text{ mm} \pm 8.06 \text{ SD} \times 24.5 \text{ mm} \pm 3.13 \text{ SD}$ ($n = 26$). Defeathering begins several days before egg-laying. Signs of refeathering at end of incubation (in 50% of individuals), but only a few birds attained complete refeathering during midchick-rearing (Wehle 1980).

Incubation period. Mean $43.9 \text{ d} \pm 1.5 \text{ SD}$ at one observable nest over 9 yr at Farallon Is. (Ainley and Boekelheide 1990). At Goat I., mean for all precisely known incubation periods $42.8 \text{ d} \pm 1.7 \text{ SD}$ (Boone 1986). Mean 46.2 d (range 42–53, $n = 35$ eggs) at Ugaiushak (Wehle 1980). Mean 45.2 d (range 43–53, $n = 4$ nests) at Barren Is. (Amaral 1977). At Commander Is., 41–49 d ($n = 19$). Mean 45 d (range 41–54) from Gulf of Alaska (Baird and Jones 1983). Mean $43.5 \text{ d} \pm 0.72 \text{ SE}$ (range 42–46, $n = 6$) at Talan I. (ASK). Incubation temperature 38.2° C ($n = 1$; Sealy 1973).

Parental behavior. Little known. Both sexes incubate. Egg can be left unattended several hours to a day, incubated up to ≥ 1 d by same birds without incubation exchange (Wehle 1980, Mikhtaryantz 1986). Continuous 19-h observation of a nest (Amaral 1977)

showed that with 4 incubation shifts, one parent incubated for 11.5 h, the other for 3.5 h, and the egg was left unattended for a total of 8.5 h (2, 3, 1.5, and 1 h in duration).

Hardiness of eggs against temperature stress; effect of egg neglect. No quantitative information. Eggs can be left unattended for several hours a day, or even entire day, with little apparent effect (Wehle 1980).

HATCHING

Preliminary events and vocalizations. Chick starts producing sounds after pipping, if exposed to low ambient temperature chick produces long *uiiiep* distress call.

Shell-breaking and emergence. In 2 different seasons (Wehle 1980): days from first cracks to hatching: mean 3.3 (range 2–6, $n = 7$) and 4.3 d (range 1–12, $n = 16$); from first cracks to pipped, 3.0 d (range 2–4, $n = 3$) and 3.1 d (range 1–8, $n = 11$); from pipped to hatching, 1.4 d (range 1–2, $n = 5$) and 2.3 d (range 1–5, $n = 19$).

Parental assistance and disposal of eggshells. Eggshells present in nest for 1–3 d and then pushed out of nest chamber (Mikhtaryantz 1977, Wehle 1980).

YOUNG BIRDS

Condition at hatching. Semiprecocial chick, covered with long downy feathers, eyes open, white egg tooth usually present on upper bill until 15–20 d posthatch (Amaral 1977) but may fall off at 1–4 d posthatch. After day 6, hatchling can thermoregulate (Wehle 1980). Hatchling measurements at Goat I.: mass $63.5 \text{ g} \pm 7.9 \text{ SD}$ ($n = 22$), culmen $22.6 \text{ mm} \pm 1.3 \text{ SD}$ ($n = 7$), tarsus $26.3 \text{ mm} \pm 1.4 \text{ SD}$ ($n = 7$), manus $23.7 \text{ mm} \pm 2.4 \text{ SD}$. Triangle I.: mass $58.6 \text{ g} \pm 2.3 \text{ SE}$ ($n = 5$), culmen $22.6 \text{ mm} \pm 0.62 \text{ SE}$ ($n = 4$); tarsus $22.0 \text{ mm} \pm 0.1 \text{ SE}$ (C. Gjerdrum unpubl.). Hatching mass varied among colonies in Gulf of Alaska during 1976–1978 (Baird and Jones 1983): mean mass 61.4–70.3 g during 7 colony yr; e.g., Shumagin Is. $69.4 \text{ g} \pm 1.88 \text{ SE}$ ($n = 30$); Ugaiushak $69.4 \text{ g} \pm 3.0 \text{ SE}$ ($n = 18$), Sitkadilak Strait $70.3 \text{ g} \pm 4.2 \text{ SE}$ in 1977 ($n = 15$), $68.1 \text{ g} \pm 3.06 \text{ SE}$ in 1978 ($n = 16$). At Barrens: mass 68 g, manus 25.3 mm, tarsus 26.6 mm, culmen 22.0 mm (Manuwal and Boersma 1977). Talan I. (ASK): mass $57.4 \text{ g} \pm 1.1 \text{ SE}$ ($n = 22$), culmen $22.0 \text{ mm} \pm 0.14 \text{ SE}$ ($n = 20$), tarsus $20.9 \text{ mm} \pm 0.24 \text{ SE}$ ($n = 20$).

Growth and development. Chick growth and development highly variable, reflecting intermittent provisioning by parents (Kitaysky 1996, 1999). Also, growth rate usually reported for age range with linear phase of growth, but ages used vary among studies (e.g., 10–30 d [Gjerdrum 2001], 5–25 d [Kitaysky 1996]); this contributes a little to variability among studies. Reported growth rates range widely among studies, from -0.6 to 19.0 g/d . For example: Goat I., $6.6 \text{ g/d} \pm 1.7 \text{ SD}$ ($n = 8$) to $9.0 \text{ g/d} \pm 2.1 \text{ SD}$ ($n = 8$; Boone 1986);

Destruction I., 13.3 g/d ($n = 11$; Burrell 1980); Triangle I., -0.6 g/d (C. Cassidy St. Clair unpubl.) to 11.8 g/d (Vermeer and Cullen 1979) to 16.7 g/d ± 4.1 SD ($n = 45$; Gjerdrum 2001); Barren I., 3.3 g/d ± 1.6 SD ($n = 32$; Roseneau et al. 2000) to 16.2 g/d ± 3.2 SD ($n = 35$; Manuwal and Boersma 1977); Aiktak I., 7.3 g/d ± 3.2 SD ($n = 17$; G. V. Byrd unpubl.) to 14.8 g/d ± 4.1 SD ($n = 34$; Thomson and Smith 2000); Buldir I., 6.2 g/d ± 1.0 SD ($n = 6$) to 11.1 g/d ± 12.9 SD ($n = 12$; Byrd et al. 1991). Overall mean growth rate among 48 colony yr of study 10.9 g/d ± 4.7 SD (studies in addition to above: Amaral 1977; Wehle 1980, 1983; Baird and Jones 1983; Byrd and Douglas 1990; Kitaysky 1996; Piatt et al. 1997; Sztukowski and Oleszczuk 2001).

Chick developmental rate depends on daily food intake (Kitaysky 1999). Maximal body-mass growth rates of ad-libitum-fed (110 g/d) captive chicks were 12.5 g/d ± 0.56 SE and higher than in chicks fed 70 g/d (8.2 g/d ± 0.37 SE) and 57.0 g/d (7.6 g/d ± 0.80 SE). Similarly, rates of skeletal development were highest among chicks fed ad libitum (culmen 0.37 mm/d ± 0.013 SE, tarsus 0.45 mm/d ± 0.024 SE) and slowest among chicks fed 57.0 g of food daily (culmen 0.28 mm/d ± 0.029 SE, tarsus 0.26 mm/d ± 0.01 SE). Development of remiges followed same pattern: highest in ad-libitum-fed birds (primaries 2.02 mm/d ± 0.116 SE, secondaries 1.42 mm/d ± 0.116 SE) and lowest among chicks fed 57 g of food daily (primaries 1.51 mm/d ± 0.128 SE, secondaries 1.04 mm/d ± 0.072 SE). High variation in chick developmental rates related to ability of chicks to adjust metabolic rate to food provisioning (Kitaysky 1996). Hungry chicks were observed to decrease metabolic rate by 47.4%, providing substantial energy economy during food shortages.

PARENTAL CARE

Brooding. After hatch, chick brooded constantly during first 1–4 d (Amaral 1977), 1–3 d (Wehle 1980). Both parents participate. Brooding during day terminated after chicks can thermoregulate (Wehle 1980), but one parent usually spends night in nesting burrow until chick is about 6 wk old (ASK).

Feeding. Both sexes feed young during daylight hours. At Barren Is., first deliveries started 05:00 and peaked at 06:00–10:00 in morning, another peak at midday, and third preceding sunset (Amaral 1977). In late chick-rearing, fed throughout day, with several peaks of activity. At Ugaiushak, peak in early morning, and smaller peak in early evening (Wehle 1983). At Triangle and Seal Is., feeding peaked in early morning and tapered off for rest of day (Vermeer et al. 1979, Piatt et al. 1997). In 1999–2000 at Triangle, smaller peak in feeding in evening (Gjerdrum 2001). Adults delivering food spend little time in burrow and leave within 1 min after arrival. Chick-provisioning rates

vary considerably from day to day and may reflect daily fluctuations in availability of food resources (Kitaysky 1996).

Overall, self-respecting puffin parents try to deliver 2 meals/d each, and overall mean rate of meal delivery is 4.02 meals/d ± 1.43 SD ($n = 16$ colony yr). At Barren Is., adults delivered 1.6 meals/d to 1- to 7-d-old chicks and 3.8 meals/d (range 2–6) to 24- to 36-d-old chicks in 1976 (Amaral 1977), and 3.3 meals/d (range 2–6) in 1977 (Manuwal and Boersma 1977). At Triangle I., 3.5 meals/d in 1978 (Vermeer and Cullen 1979) and 4.2 meals/d ± 1.2 SD ($n = 66$ nests) to 5.0 meals/d ± 2.2 SD ($n = 46$) in 1999 and 2000, respectively (Gjerdrum 2001). Feeding rates at Suklik, Midun, and Aiktak Is. were monitored over 3 yr (JFP) and ranged between 1.9 meals/d ± 1.4 SD ($n = 15$ nests) and 5.7 meals/d ± 2.1 SD ($n = 21$ nests); lowest delivery rates observed during an unusually warm (El Niño) summer (Bailey et al. 1995). At Suklik I. (Kitaysky 1996), provisioning rate highly variable: 17.7 g/d ± 2.32 SE (4–5 Aug; $n = 10$ nests), 88.2 g/d ± 14.8 SE (16–17 Aug; $n = 10$), 44.7 g/d ± 6.75 SE (22–23 Aug; $n = 9$), 45.9 g/d ± 11.82 SE (29–30 Aug; $n = 10$). Daily provisioning rates independent of age of chick and its short- or long-term energy requirements (Kitaysky 1996).

Nest sanitation. Incubating individual leaves nest chamber for defecation. Chick defecates close to nest entrance or in tunnels to side of main nest chamber.

COOPERATIVE BREEDING

Not known in this species.

BROOD PARASITISM

Not known in this species.

FLEDGLING STAGE

Departure from nest. Departs nest at dusk and during night by flying or walking from nests directly to open water. Adults do not accompany chicks at sea or provide postfledging parental care.

Period from hatching to departure. Range of nestling periods reported in Wehle 1980 as 38–59 d for several studies with small sample sizes. At Goat I., 57.6 and 50.5 d, respectively, in 1981 and 1982. At Destruction I. (Burrell 1980): 50.4 d (range 43–59, $n = 11$). At Triangle I. (C. Gjerdrum, C. Cassidy St. Clair, and D. Bertram unpubl.): 43.0 d ± 2.4 SD ($n = 32$) in 1978, 48.6 d ± 5.2 SD ($n = 37$) in 1995, 44.6 d ± 2.9 SD ($n = 89$) in 1999, and 45.2 d ± 2.7 SD ($n = 86$) in 2000. At Ugaiushak (Wehle 1980): 44.8 d (range 40–48, $n = 9$) in 1976 and 41.8 d (range 41–42, $n = 4$) in 1977. Overall studies ($n = 14$), average nestling period 48.2 d ± 4.1 SD. Daily rates of food intake affect duration of fledgling period (Kitaysky 1996): chicks fed ad-libitum in captivity reached fledging conditions within 45.3 d ± 2.6 SE, wild chicks that received 70 g of food daily developed to fledging conditions within 55.5 d

± 2.0 SE, and chicks fed by parents at 53 g/d reached fledging conditions within 63.6 d ± 4.5 SE.

Growth. Substantially smaller than adult at fledging in most measurements (e.g., mass 63% of adult), but tarsus fully developed. Plumage fully developed, but remiges only 67% (10th primary) and 77% (second secondary) size of adult's, wing-chord 78%. From Talan I. (ASK), measurements of chick at hatching: mass 57.4 g ± 1.10 SE ($n = 22$), culmen 22.0 mm ± 0.14 SE ($n = 20$), tarsus 20.9 mm ± 0.24 SE ($n = 20$), and wing-chord 20.7 mm ± 0.15 SE ($n = 20$). Chick measurements at fledging: mass 472.9 mm ± 3.29 SE ($n = 131$), culmen 39.8 mm ± 0.12 SE ($n = 134$), tarsus 34.3 mm ± 0.12 SE ($n = 134$), wing-chord 157.7 mm ± 0.43 SE ($n = 131$), P1 remiges 83.7 mm ± 0.72 SE ($n = 25$), S2 remiges 52.3 mm ± 0.48 SE ($n = 25$), back-feathers 39.2 mm ± 0.58 SE ($n = 25$), belly-feathers 30.6 mm ± 0.40 SE ($n = 25$), and tail-feathers 48.4 mm ± 0.61 SE ($n = 25$). For comparison, adult measurements at same site: mass 747.5 g ± 5.60 SE ($n = 92$), culmen 58.2 mm ± 0.29 SE ($n = 92$), tarsus 35.5 mm ± 0.21 SE ($n = 92$), wing-chord 201.5 mm ± 0.87 SE ($n = 94$), P1 remiges 123.6 mm ± 2.45 SE ($n = 11$), S2 remiges 68.9 mm ± 1.37 SE ($n = 11$), back-feathers 46.9 mm ± 1.50 SE ($n = 11$), belly-feathers 36.4 mm ± 0.46 SE ($n = 8$), and tail-feathers 63.0 mm ± 0.51 SE ($n = 88$).

While fledgling period and fledging body mass can vary markedly among colonies, and within and between years, development of wings and feathers fairly constant (Kitaysky 1996). Mass at fledging reported from Triangle I. (C. Gjerdrum, C. Cassidy St. Clair, and D. Bertram unpubl.), 270.0 ($n = 1$) in 1996 to 540.0 ($n = 36$) in 1978; Barren Is. (Amaral 1977), 550 g ($n = 10$); Ugaiushak I. (Wehle 1983), 556 and 567 g, respectively, in 1976 and 1977; and Seal I. (Piatt et al. 1997), 563 g ($n = 7$). Fledging mass from Talan I. 472.9 g ± 3.29 SE, 453.6 g ± 3.17 SE, 474.3 g ± 3.87 SE in 1987–1989, respectively (Kitaysky 1996). Average of 25 colony yr: 477 g ± 99.2 SD (range 270–609). Most young exhibit some loss of mass just prior to fledging. Asymptotic mass of chicks prior to fledging in 22 colony yr: 503 g ± 102.5 SD (range 270–600).

Association with parents or other young. No information.

Ability to get around, feed, and care for self. Little information. Can fly poorly, dives and swims well. May walk to sea during fledging (ASK).

IMMATURE STAGE

Little known; immatures apparently move to Central North Pacific for 1–2 yr before return to breeding areas (see Migration, above). Seven captive chicks (ASK, E. Kitaiskaia, and JFP unpubl.), fed 110 g/d since 10 d posthatch until fledging and ad libitum thereafter, grew at rate of 10.8 g/d to peak mass of 515 g, “fledged” at about 45 d (based on behavior), then entered a phase of linear growth (2.7 g/d)

between 45 and 125 d (reaching 732 g), followed by a mass recession between 125 and 165 d, when mass declined to 680 g. Another group of 7 captive chicks, fed 50 g/d since 10 d posthatch until fledging and ad libitum thereafter, grew at rate of 5.3 g/d to peak mass of 381 g, “fledged” at about 56 d (based on behavior), then entered a phase of linear growth (3.3 g/d) between 45 and 145 d when mass reached 675 g. Birds from 2 treatments were morphologically (body mass and skeletal elements) similar by age 165 d posthatch.

DEMOGRAPHY AND POPULATIONS

MEASURES OF BREEDING ACTIVITY

Age at first breeding. No data. May be similar to Atlantic Puffin; i.e., sometimes in third or fourth year, but most not until fifth year (Harris 1984).

Clutch. One egg. Replacement may be laid 10–21 d after loss of first egg (Wehle 1980).

Annual and lifetime reproductive success. No information on lifetime reproductive success. Annual reproductive success (number of chicks fledged/egg laid) varies among years and locations (see Table 1). Over all colony yr of study, average hatching success 64% ± 22 SD ($n = 58$), fledging success 64% ± 28 SD ($n = 57$), and breeding success 0.43 chicks/pair ± 0.22 SD ($n = 70$). These figures do not account for varying proportion of birds that attempt to breed (laying success); difficult to measure in puffins and estimated at 45–75% in a few studies. Most data obtained at 5 sites in North Pacific (Triangle, Barren, Aiktak, Buldir, Talan Is.). Geographic and temporal variability probably related to fluctuations in food supplies and correlated with oceanographic conditions (Kitaysky and Golubova 2000).

Reproductive success affected at each stage of breeding. Eggs may fail to hatch from infertility, predation, flooding, or rolling out of nest site (Wehle 1980, Baird 1990) or due to abandonment when food scarce (Vermeer and Cullen 1979) or human disturbance (Pierce and Simons 1986). Chicks may die from predation or starvation at nest site (Vermeer et al. 1979, Wehle 1980). Chicks vulnerable to predation near fledging stage as they become more active and leave security of nesting crevice or burrow (Amaral 1977). Chicks vulnerable to mortality by exposure to cold, wet weather (Amaral 1977, Baird 1990), particularly before endothermy is achieved.

LIFE SPAN AND SURVIVORSHIP

No information.

DISEASE AND BODY PARASITES

A number of helminthic parasites, but fauna must be considered particularly depauperate compared to

Table 1. Measures of Tufted Puffin breeding parameters. Data shown as mean (range, where available).

Colony location/ span of years	Effort <i>n</i> = years nests	Hatching success (%)	Fledging success (%)	Breeding success (%) ¹	Sources ²
Triangle I., British Columbia 1975–2001	14 1,267	55	41	30 (0–77)	A
Barren I., AK 1976–1999	11 861	49 ^a	75	41 (22–60)	B
Gulf of Alaska ³ 1976–1978	8 447	67	82	55 (24–80)	C
Aiktak I., AK 1996–2001	6 432	56	82	46 (22–73)	D
Buldir I., AK 1975–2001	14 588 ^b	67	63	41 (17–62)	E
Talan I., Russia 1987–2001	12 588 ^b	77 ^c	66 ^c	47 (14–96)	F
All colonies 1975–2001	70 4,294	64 ^d	64 ^d	43 (0–96)	G

¹Breeding success = chicks fledged/nest with eggs.

²Sources: A = Vermeer and Cullen 1979, Gjerdrum 2001, A. Vallée unpubl., D. Bertram unpubl., G. Blackburn unpubl.; B = Baird and Jones 1983; Byrd et al. 1993; Roseneau et al. 1997, 2000; C = Moe and Day 1979, Wehle 1980, Baird and Jones 1983, Byrd et al. 1993; D = Howard and Woodward 1999, Sztukowski and Oleszczuk 2001, Thomson and Smith 2000, G. V. Byrd unpubl.; E = Byrd et al. 1993, Williams and Daniels 2001; F = Golubova 1992, Kitaysky and Golubova 2000, E. Golubova unpubl.; G = All sources above, plus Boone 1986, Piatt et al. 1997.

³Gulf of Alaska colonies include Sitkadilak Straits, Cliff I., Semidi I., Ugaiushak I., Hall I.

⁴Including also colonies at Goat I., OR; Kohl I., AK; and Seal I., AK.

^aMissing parameter values from 7 yr, 1993–1999.

^bCoincidental that *n* = 588 for both Buldir and Talan islands.

^cMissing parameter values from 3 yr, 1987, 1988, 1994.

^dMissing parameter values from 12 yr.

other alcid studied in detail (Hoberg, 1984, 1992a, 1992b, 1996). Based on current evidence, internal parasites in Tufted Puffins not known to cause morbidity or mortality. Parasitological studies have been conducted across geographic range of this alcid (Belogurov et al. 1968; Hoberg 1984, 1992a, 1996). Intestinal helminths uncommon, and a definable tapeworm fauna is absent, although a number of species of *Alcantaenia* and *Tetrabothrius* known as incidental parasites. Although 8 species of trematodes reported, flatworms other than *Pseudogymnophallus alcae* in the gall bladder and perhaps *Renicola* spp. in kidneys appear to be uncommon. Nematodes represented by species of *Skrjabinocerca* in esophagus, *Contracaecum* in proventriculus, and *Stegophorus* in gizzard, whereas acanthocephalans are incidental parasites. Helminth parasites constitute useful biogeographic, ecological, and trophic indicators for alcid and other seabirds (Hoberg 1996).

Ectoparasites also known to infest Tufted Puffins, but no definitive studies (Hoberg and Wehle 1982). Phthiraptera (lice), including *Saemundssonina* sp.,

reported at Buldir I., AK. Ticks including *Ixodes signatus* and the ubiquitous *Ixodes uriae* known from Tufted Puffins; probably occur with other seabirds throughout their breeding ranges. Tick infestations in some Tufted Puffin colonies (e.g., Bogoslof I.) extensive, infecting both adults and chicks; tens to hundreds can be observed roaming about in heavily infested burrow habitats (JFP, ASK).

CAUSES OF MORTALITY

Causes of adult mortality include predation (see Behavior: predation, above); starvation; and human factors such as oil pollution, net mortality, and harvest (see Conservation and management, below).

RANGE

Natal philopatry. No information.

Fidelity to breeding site and winter home range. Fidelity to breeding site well established in Atlantic Puffins (Harris 1984) and at least some adult Tufted Puffins known to return to same burrow in year subsequent to breeding (Wehle 1980).

Dispersal from colony. No information.

POPULATION STATUS

Numbers. Total population estimates of unknown accuracy owing to difficulty of censusing birds in burrow-nesting habitat. Most estimates based on observations of birds attending colonies, but ratio of birds attending at any given time to local population unknown. Some estimates from count of birds on water.

Most significant colonies in North America and Asia have been located (1,031 known colonies; Appendix 4; SOWLS et al. 1978 [and updated U.S. Fish and Wildlife Service [USFWS] Computerized Beringian Seabird Colony Catalog 1999], Watanuki et al. 1988, Speich and Wahl 1989, Campbell et al. 1990, Brazil 1991, Carter et al. 1992, Byrd et al. 1993, McChesney et al. 1995, Konyukhov et al. 1999, Kondratyev et al. 2000, Hodder 2002, Osa and Watanuki 2002). Total world colony population estimate is 2,970,000 birds, of which 82% (2,440,000) breed in North America. Small proportion of North American population in California (0.01%), Oregon (0.2%), Washington (0.9%), and British Columbia (3.1%). Remainder (96%) in Alaska, with by far largest concentrations along Alaska Peninsula (36%) and in e. Aleutians (45%). Population scattered throughout remaining Aleutian islands (7.3%) and in Bering (4.6%) and Chukchi (<0.01%) Seas.

The 802 known colonies in North America are widely distributed, but only about 50 colonies contain >10,000 birds, and these may account for >75% of North American population. Median size of colonies is only 140 birds, however, and it is possible that populations at some large colonies have been grossly overestimated. Nonetheless, important colonies indicated from large population estimates: Egg I. (163,000), Kaligagan I. (111,000), Aiktak I. (102,000), Amagat I. (100,000), Castle Rock (80,000), Shaiak I. (80,000), E. Amatuli I. (74,000), the Triplets (67,500), Vsevidof I. (65,400), Ogchul I. (58,000), North I. (53,400), Chagulak I. (11,600), W. Amatuli I. (50,000), Triangle I. (50,000), and Auklet I. (41,700).

Trends. We gathered raw census data from a variety of sources (Table 2) to estimate and compare trends among areas. We calculated trends as percent per annum change for the census window (range 5–28 yr) in each location (Table 2) and we also discuss trends from most recent 15 yr (1987–2001). Owing to variability among census counts or low numbers of counts (or both), calculated trends were marginal or insignificant in half of studies to date. Nonetheless, results suggest populations increasing in Gulf of Alaska and westward and declining throughout se. Alaska, British Columbia, Washington, Oregon, and California (Table 2). Many factors influence populations in these regions (below), so it is surprising (and improbable) that all northern populations are increasing (sign test, $p <$

0.01) and all southern populations decreasing (sign test, $p < 0.01$) by chance. This inverse pattern resembles that observed for several species of salmon and Steller sea lions (*Eumetopias jubatus*), whose populations in se. Alaska and southward (British Columbia, Washington, Oregon, California) tend to decline when populations in Gulf of Alaska and Bering Sea are increasing, and vice-versa; perhaps in response to decadal changes in eastward-flowing Westwind Drift Current that strikes British Columbia and diverges north to form Alaska Gyre and south to form California Current (Francis et al. 1998, Hare et al. 1999).

Tufted Puffins once bred commonly in s. California, on most of Channel Is. and at other sites (McChesney et al. 1995). All these colonies were extirpated in early 1990s; species recently re-established at Prince I. In central California, common and widespread; several thousand estimated at Farallons in late 1800s. Numbers declined drastically in 1900s owing to oil pollution, introduction of European rabbits (*Oryctolagus cuniculus*) and changes in food supplies (Ainley and Boekelheide 1990); many small colonies extirpated. Since 1972, when populations first enumerated (27 pairs), numbers increased on Farallons by about 7% per annum (pa) until 1986, when surveys were interrupted until beginning again in 1993 (Warzybok et al. 2001). Numbers variable since then, with population stable or declining slightly (–3.4%) during past 15 yr (Table 2). At Castle Rock, n. California, whole island population counted 6 times since 1970 and declining steadily (and significantly) from a high count of 56 birds then (Jaques and Strong 2001). Recent 15-yr trend is –10.1% pa decline.

Few systematic data from Oregon. In 1979, estimated 6,560 birds in Oregon, with 4,200 (64%) at Three Arches Rocks (Hodder 2002). In 1988, a total of 5,031 individuals counted; 3,040 at Three Arches Rocks. Trend for Three Arches Rocks 1979–1988 was –3.6% pa. In 2001, a casual survey of Tufted Puffins at Three Arches Rocks indicated that numbers had declined dramatically, perhaps >95% since 1988 (D. Pitkin pers. comm.). Elephant Rock colony (<100 birds) also in decline.

In Washington, 2 sources of continuous long-term data suggest marked declines during past 20 yr (Table 2). On pelagic-bird transects off Westport, initiated in 1972 and conducted every year since (Wahl and Tweit 2000), Tufted Puffin numbers were variable but stable throughout 1970s and 1980s, but started a steady decline in 1989 to order-of-magnitude lower counts in recent years. Trend for past 15 yr is –16.3% pa. At Tatoosh I., counts of Tufted Puffins from a selected area of the colony were variable but stable through 1980s and early 1990s, then dropped about 20-fold to near 0 in mid-1990s (R. T. Paine unpubl.). Recent 15-yr trend is –21.4% pa. Whole-island counts declined similarly from highs of 200–300 birds in 1979 to recent

Table 2. Population trends of Tufted Puffins in North America.

State/province/ area/location	Type of count	No. counts	Years	Population change		Source ¹
				%/annum	Probability	
Alaska						
W. Aleutians						
Tower Islet (Agattu I.)	Plot burrow	2	1982–1990	+5.6	ns	A
Nizki I.	Shoreline bird	4	1976–1998	+8.7	<0.05	A
Buldir I.	Plot burrow	5	1991–2001	+6.8	= 0.09	A
Central Aleutians						
Adak I.	Plot burrow	7	1988–1995	+17.9	<0.001	A
E. Aleutians						
Bogoslof I.	Plot burrow	6	1973–2000	+3.2	<0.001	A
Aiktak I.	Plot burrow	9	1989–2000	+2.5	<0.05	B
N. Gulf of Alaska						
Barren Is.	Plot burrow	5	1993–1997	+3.2	ns	B
Prince William Sound	Pelagic survey	7	1989–2000	+3.9	ns	C
Se. Alaska						
St. Lazaria I.	Plot burrow	5	1994–1998	–5.9	ns	D
British Columbia						
S. Queen Charlotte I.						
Kerouard Is.	Whole colony	2	1977–1986	–10.6	ns	E
N. Vancouver I.						
Triangle I.	Plot burrow	4	1984–1999	–1.0	ns	F
Washington						
Strait of Juan de Fuca						
Protection I.	Whole colony	8	1973–2001	–13.9	<0.05	G
Northern outer coast						
Tatoosh I.	Plot bird	17	1983–2001	–16.9	<0.001	H
Southern outer coast						
Westport	Pelagic survey	19	1983–2001	–13.6	<0.001	I
Oregon						
Outer coast						
Three Arches Rock	Whole colony	2	1979–1988	–3.6 (–20.6) ²	ns	J
California						
Northern coast						
Castle Rock	Whole colony	6	1972–1999	–6.3	<0.05	K
Central coast						
Farallon Is.	Whole colony	9	1993–2001	–3.4	ns	L

¹Sources: A = J. Williams and G. V. Byrd unpubl.; B = Dragoo et al. 2001; C = Lance et al. 1999; D = L. Slater and G. V. Byrd unpubl.; E = Campbell et al. 1990; F = Can. Wildl. Serv. unpubl.; D. Bertram pers. comm.; G = Speich and Wahl 1989, U. Wilson unpubl.; H = R. T. Paine unpubl.; I = Wahl and Tweit 2000; J = Hodder 2002; K = Jaques and Strong 2001; L = Warzybok et al. 2001.

²Rate of decline based on estimate of at least 95% decline in numbers between census in 1988 and casual survey in 2001 (D. Pitkin pers. comm.).

(1998–2001) highs of 14–30 birds (R. T. Paine unpubl.). Status of populations at other colonies along outer coast unknown. Populations severely reduced within sheltered inside waters of Strait of Juan de Fuca. Tufted Puffins at Protection I. historically numbered 400 individuals, down to perhaps 100 in late 1970s, 74 birds in 1986, and 18 birds in 2001 (Speich and Wahl 1989, U. Wilson unpubl.). Trend for Protection I. since 1973 is –

13.9% pa, and about –9.4% pa during past 15 yr. Smith I. population declined from historic high of 500 birds to 0 in 1986, but 6 were sighted in 2001, so colony still active. Populations in San Juan Is. that have been extirpated (counts of 0 in 1986 and 2001; U. Wilson unpubl.): Bare I. (historic count of 100 birds), Colville I. (30), and 9 other colonies that used to have <10 birds each.

At Triangle I., British Columbia, species counted on 4 different census plots on 4 occasions since 1984 (high mean of 69 birds/plot; Can. Wildl. Serv. unpubl.). Repeated measure MANOVA suggests no significant change in population for this period (D. Bertram pers. comm.). Regression of data from last 15-yr period suggests slight (but nonsignificant) negative trend of -1.8% pa. At St. Lazaria I. in se. Alaska, burrow counts highly variable, but also suggest a nonsignificant decline in populations in this region (Dragoo et al. 2001).

In Prince William Sound, AK, populations of Tufted Puffins apparently declined by 75% from about 10,000 birds in 1972 to about 2,300 birds in 1989 (no intervening surveys; Lance et al. 1999). More than 15 other seabird species supposedly declined by similar magnitudes in Prince William Sound between 1972 and 1989, but such changes were not corroborated by sea-bird colony counts in same area. In any case, change in Tufted Puffin population was not statistically significant owing to high variability among transect counts. Since 1989, however, populations have been surveyed 7 times and show a stable or slight increasing trend (nonsignificant) of $+3.9\%$ pa. Also in Gulf of Alaska, a short time series (1993–1997) of burrow censuses at Barren Is. suggest a similar weak increasing trend (nonsignificant) of $+3.2\%$ pa (Dragoo et al. 2001).

At Aiktak, Adak, and Buldir Is. in Aleutians, no counts before 1986, and regression of data from past 15 yr shows increasing trends of $+2.5\%$, $+17.9\%$, and $+6.8\%$ pa at each colony, respectively. Buldir data show mean density of puffins on 9 index plots (dimensions 150–314 m²; J. Williams unpubl.); Adak is total number (max. 130) of burrows at Gannet and Inner Rock (Sharf et al. 1996, J. Williams unpubl.), Aiktak data show mean density on 6 index plots (150–314 m²; G. V. Byrd unpubl.). At Bogoslof I. (G. V. Byrd unpubl.), numbers have been increasing steadily at $+3.2\%$ pa since first count of burrows in 1973 (119) to 2000 (299), and trend during last 15 yr is $+4.1\%$ pa. At Nizki I. (J. Williams unpubl.), 481 individuals counted on water in 1976 have steadily increased at $+8.7\%$ pa to 3,185 counted in 2000; trend is $+4.7\%$ pa during past 15 yr. Furthermore, number of burrows has increased from about 600 in 1976 to $>12,000$ in 1998. Increases at Nizki I. followed removal of foxes there in 1976; would not have occurred otherwise. Finally, on Tower Islet, south of Agattu I., number of burrows increased from about 1,400 in 1982 to 2,200 in 1990 (J. Williams unpubl.); puffins occupied breeding habitat that was not used when foxes were present prior to 1982.

Population trends in Bering and Chukchi Seas, Russia, poorly known. In Kamchatka region, populations have increased and new colonies have appeared in recent years (Kondratyev et al. 2000). In Commander Is., species increased four- to five-fold between 1970s and 1990s at several colonies.

Dramatic declines in Japan owing to introduced predators, adult mortality in gill-nets, oil pollution, and human disturbance at colonies. Until even 25 yr ago, Tufted Puffin was a common, albeit local visitor to se. Hokkaido, but now rare (Brazil 1991). Declines from tens or hundreds of birds to near 0 has been documented at several colonies during past 30–50 yr (Watanuki et al. 1988, Osa and Watanuki 2002). Only 30 birds remaining in Japan, and extirpation appears likely soon (Brazil 1991).

POPULATION REGULATION

Little known. As do other seabirds, puffins require predator-free nesting islands or mainland habitat and abundant supplies of food during breeding and nonbreeding seasons. Given wide distribution, abundance of offshore islands, and generally small colony sizes, populations probably not limited by breeding sites. Prey availability likely most important source of population regulation, and nonlinear functional relationships between Atlantic Puffin population parameters and prey abundance are well described (Anker-Nilssen et al. 1997).

CONSERVATION AND MANAGEMENT

EFFECTS OF HUMAN ACTIVITY

Hunting and harvest. Adults and eggs harvested for subsistence in most coastal areas of Alaska, particularly in Bering Strait region. While tens of thousands of seabirds and eggs harvested annually, focus is on accessible, aggregated species such as murrelets or auklets, and recent harvests of Tufted Puffin are minimal and localized (Paige et al. 1996). Historically, and prehistorically, Tufted Puffins were harvested by Native Americans in coastal areas from California to Aleutians and Bering Sea (e.g., Bent 1919, Gabrielson and Jewett 1940, Murie 1959). "Besides furnishing a welcome supply of fresh meat, the birds are skinned and the skins are cured and used for clothing. A parka made of puffin skins is not only warm but a very light and serviceable garment. About 45 skins are required to make one parka, which is made like a shirt with a hood and is worn with the feathers on the inside" (Bent 1919: 83). Bills of puffins were commonly used to make ceremonial hand rattles or gloves (approx. 50–75 bills/hoop or glove) by Aleuts, Aliituk, and Tlingit Indians for use in dance celebrations. "The dancers paint their faces and hold rattles in their hands; the rattles are made from two or three hoops of various widths, which are fastened by a band decorated with feathers, used in place of a handle. Many sea parrot beaks are tied to these hoops so that when they shake the rattle to the drum beats, a very loud sound is produced. . . ." (Dmytryshyn et al. 1988: 397). More than 200 puffins were harvested to provide



Figure 4. Ceremonial Tlingit dance apron, fringed with hundreds of Tufted Puffin bills that served as rattles (inset shows detail of puffin bills). The woven Chilkat blanket panel (made from goat wool and cedar-bark yarn) is mounted on buckskin. Dates approximately 1840-1850; collected 1939, Wrangell, AK, by Maj. Max C. Fleischmann. Photos and permission to reproduce them here provided by the Santa Barbara Museum of Natural History, courtesy of J. Timbrook, Curator of Ethnography.

enough bills for the ceremonial Tlingit dance skirt shown in Figure 4. While such hunting pressure is largely absent today, it seems reasonable to speculate that human harvest once had a significant impact on local puffin populations, particularly in southern areas where colonies are smaller and dispersed.

Sensitivity to disturbance. Investigator disturbance during incubation or hatching may cause desertion (Amaral 1977, Wehle 1980, Pierce and Simons 1986). Frequent visitation and activities reduced fledging success from an undisturbed rate of 94 to 18% in heavily disturbed area (Pierce and Simons 1986).

Toxic chemicals and oil pollution. Organochlorine and heavy-metal contamination of eggs and tissue widespread in Tufted Puffin, although generally low concentrations, and no known toxic effects (Ohlendorf et al. 1982, Tanaka 1989, Elliot and Noble 1993, Ohlendorf 1993). Vulnerable to oil pollution, especially in areas with small populations (i.e., south of British Columbia, Japan). No estimate of chronic mortality (Burger and Fry 1993). Most oil spills occur in winter when puffins largely absent from coastal and continental-shelf waters. About 570 Tufted Puffins were retrieved in aftermath of *Exxon Valdez* spill in Mar 1989 (Piatt et al. 1990b). Based on recovery rates, number killed may have been as high as 13,000 (JFP), although many apparently died of starvation long after spill (Piatt et al. 1990b). As much as 9% of Washington population of Tufted Puffins may have been killed in 1991 *Tenyo Maru* oil spill (Anon. 2000). Frequent oil spills implicated in historic population declines in California (Ainley and Boekelheide 1990).

Ingestion of plastic. Plastic particles frequently found in gizzards: 20% of 837 Tufted Puffins examined

from subarctic Alaska between 1969 and 1990 (Robards et al. 1995) and 88% of 8 birds examined from Central North Pacific in 1990–1991 (Robards et al. 1997). Plastics are of 2 main types: industrial pellets (40%) and “user plastics” (60%; fragments of containers, toys, etc.). Plastic pollution and ingestion widespread through subarctic Pacific and increased between 1970s and 1990s (Robards et al. 1995, 1997). Plastics could obstruct passage of food or affect physiology, but detrimental effects have not been demonstrated.

Fishing nets. Bycatch in gill-nets widespread in North Pacific. From 1950s to 1990s, tens of thousands killed in offshore salmon and squid drift-net fisheries (DeGange and Day 1991, DeGange et al. 1993). Squid drift-net fisheries alone killed an estimated $123,000 \pm 124,000$ (95% CI) Tufted Puffins annually during 1980s (DeGange et al. 1993). Catches declined to <500 birds by 1990 (Johnson et al. 1993) because high-seas drift-net fisheries were largely eliminated. Japanese drift-net fisheries for salmon continued, however, in Russian economic zone (Bering Sea, Kurils, Sea of Okhotsk), killing 15,000–30,000 Tufted Puffins annually during 1990s (Artyukhin and Burkanov 2000). Coastal gill-net fisheries continue to catch birds in Alaska, Russia, and Japan, but magnitude of bycatch unknown (and perhaps small, relative to high-seas bycatch; DeGange et al. 1993).

Introduced mammals. Mammalian predators once absent from most islands in Northeast Pacific, but arctic and red fox, Norway rats (*Rattus norvegicus*), and ground squirrels (*Spermophilus undulatus*) were intentionally or accidentally introduced to many seabird colonies in Alaska during 1800s and early 1900s. These predators decimated or eliminated sea-

bird populations on many islands, and Tufted Puffins were strongly affected because they nest in accessible dirt burrows (Bailey 1993, Bailey and Kaiser 1993). Impacts can be substantial. Eggs or young were lost from 34% of nests monitored at Shaiak I. (Petersen 1982). Hundreds of dead puffins found throughout island, and foxes cached eggs and adults all over the island. Removal of foxes can be equally dramatic; e.g., recovery of populations on Nizki I. (see Demography and populations: population status, above) started immediately following removal of introduced foxes. Introduced rats may be responsible for reduced populations and redistribution of breeding puffins on Langara I. and St. James I. in Queen Charlotte Is. (Bailey and Kaiser 1993). Introduction of European rabbit to Farallon Is. probably an important contributor to major decline of puffin population in early 1900s. Populations began to increase after removal of rabbits in 1974 (Ainley and Boekelheide 1990).

MANAGEMENT

Other than eradication of mammalian predators (above) and vigilance campaigns to prevent their introduction, which benefits all seabirds and Tufted Puffins in particular (Byrd et al. 1991, Bailey 1993), no specific management programs for this species. Bycatch in fishing gear is a localized management issue, infrequently addressed by local state or federal fishery-management organizations by closure of fisheries or change in fishing practices (DeGange et al. 1993). Subsistence harvest of puffins and their eggs is allowed for native peoples in Alaska, and harvests occasionally monitored but not restricted by state and federal wildlife agencies (Paige et al. 1996). Most colonies, and all large colonies, are protected: In U.S., within Fish and Wildlife Service's National Wildlife Refuge (NWR) system (in particular, Alaska Maritime NWR); in Canada, within Ecological Reserves system.

APPEARANCE

MOLTS AND PLUMAGES

Sexes alike in all plumages. Timing and duration of molt poorly known (Fig. 3). Two molts/yr. Following descriptions of molt and plumage of adult birds largely from Dement'ev and Gladkov 1951 and Kharitonov 1990.

Hatchlings. Covered with long down, 25–30 mm on back, shorter (up to 25 mm) on belly, head (10 mm), and wing (7–20 mm; Mikhtaryantz 1977). Upper mandible dark gray, lower mandible pink-gray. Egg tooth dull white, cere dark brown, tarsus and toes dark gray, foot web pinkish gray. Two color morphs in downy plumage (Wehle 1980, 1982b): all uniformly black or brownish black on back and about 95% same color or dark gray on belly; 5% pure white on belly. White patch varies from 20 mm in diameter to entire

belly white. Light-morph hatchlings sometimes change color to dark-morph juvenile and vice-versa.

Juvenal plumage. Feather development known from Talan I. (ASK). Primary and secondary remiges emerge as pin feathers on average between age 13–15 d (range 11–29) and burst from sheaths at 21 d (range 11–29). Tertiaries, back and belly pins erupt at 11–18 d (range 6–23), and feathers erupt at 20–27 d (range 10–30). Tail pins emerge at 18 d (range 17–19) and tail-feathers at 35.4 d (range 27–35).

Juvenal plumage similar to Definitive Basic plumage. Juvenal plumage fully developed at departure from nest; down sometimes remains on nape and rump.

Subadult plumages. Juveniles undergo molt in Feb through Apr (ASK, JFP, observing captive birds). Captive birds (see Breeding: immature stage, above) that were food-restricted and developed slower during chick stage initiate molt approximately 1 mo earlier than birds that were fed ad libitum (ASK). Require 15 and 10 d to lose their primaries and secondaries, respectively, and average of 21 d to lose all remiges (Thompson and Kitaysky unpubl.). Replace primaries in either of 2 discrete patterns: in 9 of 13 puffins, molt began at innermost primary, P1, and progressed distally to outermost primary P10; in 4 of 13 individuals, primary molt began in middle of primaries (P5–P7) and progressed both distally to P10 and proximally toward P1; before proximal wave reached P1, a second wave of molt was initiated at P1 and progressed distally, replacing P2 and P3 before reaching proximal wave. Tuft along side of crown, rictal rosette in gape, and basal ridge of culmen just beginning to show, and smaller than in adults. Cheeks grayish. Unclear whether molt activity described above includes overlapping Prebasic and Prealternate molts or involves only 1 molt. More study required.

Subsequently, at age 1 yr, immatures undergo apparently complete Prebasic molt early, perhaps in Jul–Aug (Dement'ev and Gladkov 1951). Molt sequence unknown. This molt results in acquisition of plumage similar to Definitive Basic (but lacks bill furrows; see Bare parts, below).

Definitive Basic plumage. Definitive Prebasic molt occurs postbreeding (perhaps Sep–Nov) by birds ≥ 2 yr old. Postbreeding molt apparently complete (Kharitonov 1990). Molt sequence unknown. About 15% of adult birds lost yellow head-plumes and began molt on head and face by late Aug 2000 at Triangle I. (C. Gjerdrum pers. comm.).

Entire head and underparts of body dark brown, occasionally with whitish flecks on belly. A lighter grayish-brown spot behind eye and grayish brown stripe extending back along side of crown. Head-plumes absent. Remaining upperparts (including upper wing and tail surfaces) brownish black.

Definitive Alternate plumage. Definitive Prealternate molt (late winter–spring) partial (Kharitonov 1990); molt sequence unknown.

Entire plumage blackish except large, triangular white patch extends from base of upper mandible back along side of head (passing through eye) to narrowest point on side or rear crown; uppermost section of patch beginning just above eye and extending back to rear of patch and beyond as a series of elongated plumes (tuft), pale golden yellow. White also extends from base of white patch up as a narrow white band around base of forehead and down as a narrow band around base of chin. Lower side of face and neck (all areas below tuft) and remaining underparts brownish black, contrasting with pure blackish color of crown, nape, back, scapulars, rump, tail, and upper wing surfaces. Narrow white stripe along leading edge of wing (extending from base to bend of wing). Under wing-coverts brownish gray.

BARE PARTS

Bill and gape. Young bird (<1 yr old) has triangular, blackish bill without developed keratinous cere. Breeding bird has stout, strongly compressed orange bill with dull-green horny plates at base of upper mandible. Bill furrows formed in reddish outer part of upper mandible. Gape flesh colored with coral-red shades. Bill continues to grow and change shape with age of bird, and it can be used as an age indicator (Tanaka and Ogi 1986). Likely, only upper mandible grows until bird at least 4–5 yr old, thus bill becomes deeper and thicker rather than changing in gape length with age. Number and size of bill furrows varies according to age of bird. In general, fledglings do not have furrows; 1-yr-olds have only a trace of 1 furrow; 1- to 2-yr-olds have 1 undeveloped furrow; 2- to 3-yr-olds have 1 well-developed furrow; 3- to 4-yr-olds have 2 well-developed furrows; and furrow number of ≥ 3 corresponds with sexual maturation (≥ 5 yr old).

Iris. In juvenile, dark charcoal black. In adults, dull yellow or pale cream color; not known at what age color changes.

Orbital ring. Black in young and coral red in breeding birds.

Legs and feet. In juvenile and sub-adult birds, legs and webs dark charcoal black, back side of tarsus and underparts of toes and webs light gray. In breeding adults, brilliant orange-red legs and webs with black nails; underparts of toes, webs and back side of tarsus orange-red.

MEASUREMENTS

LINEAR

Sexually dimorphic (Shiomi and Ogi 1991). Geographic variability not previously described (Gaston and Jones 1998). Data compiled on live or freshly collected specimens (Appendix 3) and skeletal measurements (Appendix 5) reveal both sexual and geographic variability in body-size measurements.

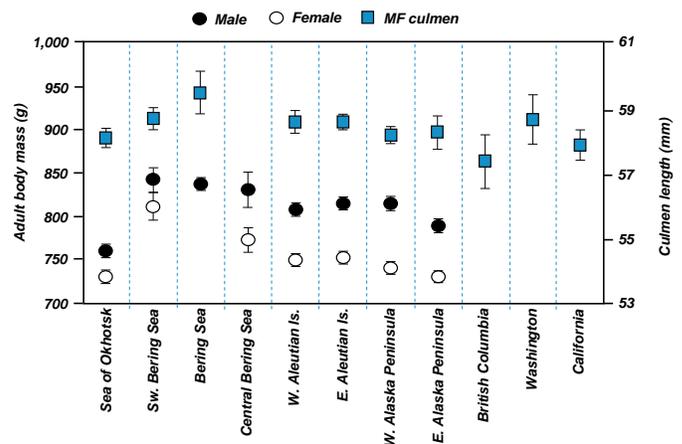


Figure 5. Geographic variation in body mass and culmen length of the adult Tufted Puffin. Male (M) and female (F) mass shown as circles, culmen length of males and females combined (MF) shown as squares.

Males significantly ($p < 0.01$) larger than females in bill length, gape length, bill depth, tarsus length, and wing length (Appendix 3). Measurement of skeletal characteristics offer more precise data on sexual dimorphism: Males significantly larger than females in 20 of 20 skeletal measurements (Appendix 5).

Bill (culmen) and wing lengths in males, females, or combined sexes did not vary significantly (using ANOVA) among study areas. Tarsus length did vary ($p < 0.001$), but largely owing to birds collected in sw. Bering Sea; which otherwise did not differ from other areas, and we suspect some systematic bias in measurement (tarsus measure difficult to standardize compared to culmen, e.g.). Other measures too limited for geographic comparison.

MASS

Average mass of sexes combined $774.2 \text{ g} \pm 67.2 \text{ SD}$ (range 520–1,000, $n = 976$). Using compiled data (Appendix 3), we found (Fig. 5) significant sexual dimorphism ($p < 0.001$) and geographic variability in mass for both males ($p < 0.001$) and females ($p < 0.001$). Overall, males ($805.5 \text{ g} \pm 61.8 \text{ SD}$ [$n = 483$]) 8.2% heavier than females ($743.7 \text{ g} \pm 57.5 \text{ SD}$ [$n = 493$]); slightly higher than dimorphism in Horned Puffins (7.5%). Some regional variability with puffins from sw. (Commander I., Kamchatka, Kurils), central (Pribilofs), and n. (St. Lawrence) Bering Sea larger than those in Aleutians or Gulf of Alaska. Puffins from Sea of Okhotsk (Talan) smallest.

PRIORITIES FOR FUTURE RESEARCH

In general, the species' biology is reasonably well described over much of its range. Populations in Japan are near extinction, and those in California, Oregon, and Washington all appear to be declining.

While population fluctuations are to be expected and some of these declines are probably due to natural changes in the marine environment, data are limited and need updating in many sites. It would be useful to assess adult survival in declining areas and address the question of why populations are declining by measuring, for example, impacts of human activities (oil pollution, gill-net mortality, colony disturbance, etc.). In some areas (Japan, San Juan Islands), extirpation of local populations is underway, and it might be more cost effective to find ways to protect and conserve these small populations than it will be to try to reintroduce them in the future. In Alaska, populations appear to be increasing everywhere except in the southeast. Populations and diets are being monitored at many sites. It would now be useful to start collecting survival data at key monitoring sites. Finally, Tufted Puffins are widely distributed throughout the eastern North Pacific and, like salmon and Steller sea lions, aspects of their biology appear to reflect large-scale oceanographic processes. It would, therefore, be useful to monitor the species at as many locations as possible, not only to better understand Tufted Puffin biology, but also to use this bird as a barometer of biological change in the North Pacific.

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Appendix 1. Diet of Tufted Puffin chicks at selected colonies ranging over about 6,500 km of coast from the far western Aleutians (Buldir I.) of Alaska to the central coast of California (Farallon Is.). Data shown as the percentage of total number of prey items observed in meals that were collected from adults as they delivered food to their young.

Region	Aleutian Is.		Alaska Peninsula				British Columbia	Oregon	California	
Island(s) Sources ¹	Buldir A	Bogoslof B	Aiktak B	Midun B	Ugaiushak C	Semidi B	Barren D	Triangle E	Goat F	Farallon G
Years of collections	1988–1999	1991–1994	1990–1998	1991–1994	1976–1993	1991–1994	1976–1999	1977–2000	1981–1982	1973–1982
Meal loads (n)	263	238	2,553	1,015	?	1,834	?	445	?	?
Prey items (n)	1,141	1,319	16,645	4,777	1,019	13,648	1,863	2,047	52	728
Fish										
Pacific herring	0.0	0.0	0.0	0.0	0.0	tr	0.0	1.1	14.1	0.0
Anchovy	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	46.9	38.9
Capelin	0.0	1.7	1.0	17.1	5.8	2.3	37.6	0.0	0.0	0.0
Myctophid spp.	1.8	15.7	0.0	0.0	0.0	tr	0.0	0.0	0.0	0.0
Pacific cod	0.0	0.0	9.0	5.8	1.1	1.5	1.8	0.0	0.0	0.0
Walleye pollock	18.1	24.2	66.1	46.8	11.8	28.6	17.7	0.0	0.0	0.0
Rockfish spp.	0.0	0.0	1.3	tr	0.0	0.2	0.0	33.6	1.3	46.8
Greenling spp.	19.6	0.5	4.5	tr	0.0	2.2	0.2	0.0	0.0	0.0
Sandlance	12.8	13.6	8.1	23.5	77.9	30.1	29.4	43.5	15.4	0.0
Other fish	7.1	4.8	7.9	5.3	3.4	6.8	4.5	18.8	17.1	2.6
Total fish	59.4	60.5	97.9	98.5	100.0	71.7	91.2	97.0	94.8	88.3
Invertebrates										
Squid	38.2	35.7	1.0	0.1	0.0	5.0	3.3	2.4	5.2	10.8
Other invertebrates	2.4	3.8	1.1	1.4	0.0	23.3	5.5	0.6	0.0	0.9
Total invertebrates	40.6	39.5	2.1	1.5	0.0	28.3	8.8	3.0	5.2	11.7

¹Sources: A = Williams and Daniels 2001; B = JFP, ASK, and S. Hatch unpubl.; C = 1976–1977 from Wehle 1980, 1983; 1992–1993 from JFP; D = 1976–1977 from Manuwal and Boersma 1977, 1978, 1979; 1991–1993 from P. D. Boersma unpubl.; 1995–1999 from Roseneau et al. 2000; E = Vermeer 1970, Gjerdrum 2001, K. Vermeer unpubl., A. Vallée unpubl., C. Cassidy St. Clair unpubl.; D. Bertram unpubl.; F = Boone 1986; G = Ainley and Boekelheide 1990.

Appendix 2. Diet of Tufted Puffins collected far offshore (source A) and near breeding colonies (sources B and C) during spring and summer. Data shown as percentage of mass (in grams for North Central Pacific Ocean locations) and number of items (for Aleutian Is., Alaska Peninsula, and Kodiak I. and n. Gulf of Alaska).

Location	North Central Pacific			Aleutians		Alaska Peninsula		Kodiak I. and n. Gulf of Alaska ²
	Kurils A	Aleutians A	Bering Sea A	Western B	Eastern B	Western B	Eastern B	
Sources ¹								
Years collected	1980s	1980s	1980s	1988–1998	1988–1998	1988–1998	1988–1998	1969–1978
Stomachs ² (n)	95	289	212	231	308	163	96	364
Prey items (n or g)	1,381.4	2,423.8	1,642.5	1,950	6,396	1,888	821	?
Fish								
Gadidae	—	—	—	0.3	17.5	18.0	27.5	2.7
Sandlance	—	—	—	4.1	0.4	3.0	26.8	5.1
Capelin	—	—	—	0.0	0.0	0.3	0.4	17.0
Pelagic	—	—	—	1.4	0.9	0.1	0.5	1.0
Benthic	—	—	—	0.0	1.9	0.4	1.8	0.1
Other	—	—	—	0.8	0.8	0.1	1.0	0.1
Total fish	22.0	41.2	33.6	6.7	21.4	21.8	58.0	26.0
Invertebrates								
Squid	58.3	41.5	60.5	82.7	16.8	17.1	14.9	22.1
Polychaete	0.0	0.0	0.0	9.4	3.1	1.9	0.9	0.2
Euphausiid	17.5	17.0	0.0	0.3	56.1	57.5	3.7	45.2
Mollusk	0.0	0.3	0.3	0.1	2.5	1.6	22.3	0.1
Other invertebrates	2.2	0.0	5.6	0.8	0.1	0.0	0.4	6.4
Total invertebrates	78.0	58.8	66.4	93.3	78.6	78.2	42.0	74.0

¹Sources: A = Tanaka 1989; B = JFP; C = Sanger 1986.

²Stomach sample size includes only those with food.

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Appendix 3. Linear measurements (mm) and body mass (g) of adult Tufted Puffins. Data shown as mean \pm SD (*n*).

Location/ Sources ¹	St. Lawrence I. A	Talan I. B	Sw. Bering Sea C	W. Aleutian Is. D	E. Aleutian Is. D	W. Alaska Peninsula D	E. Alaska Peninsula D	Triangle I. E	Washington F	California F
Bill length										
Male	59.7 (12)	59.2 \pm 2.4 (49)	59.4 \pm 2.3 (29)	59.7 \pm 2.6 (32)	59.8 \pm 2.0 (51)	59.0 \pm 2.2 (44)	59.2 \pm 1.8 (14)			57.8 \pm 0.9 (5)
Female		57.0 \pm 2.8 (43)	57.7 \pm 2.2 (22)	57.2 \pm 2.1 (28)	57.5 \pm 2.1 (57)	57.4 \pm 2.4 (41)	57.3 \pm 3.0 (13)			57.4 \pm 2.2 (4)
Combined	59.5 \pm 2.4 (13)	58.1 \pm 2.8 (92)	58.7 \pm 2.5 (51)	58.6 \pm 2.7 (60)	58.6 \pm 2.4 (108)	58.2 \pm 2.4 (85)	58.3 \pm 2.6 (27)	57.4 \pm 2.6 (10)	58.7 \pm 1.7 (5)	57.9 \pm 1.6 (12)
Gape length										
Male	48.0 (12)			51.9 \pm 2.8 (26)	47.0 \pm 2.8 (33)	52.4 \pm 2.5 (20)				
Female				50.1 \pm 1.9 (21)	45.9 \pm 2.7 (26)	51.0 \pm 2.2 (23)				
Combined				51.1 \pm 2.5 (47)	46.5 \pm 2.8 (59)	51.7 \pm 2.4 (43)				
Bill depth										
Male	43.6 (12)	43.6 \pm 4.5 (25)		45.2 \pm 3.7 (26)		42.2 \pm 2.4 (20)				45.7 \pm 1.6 (5)
Female		38.6 \pm 5.0 (19)		41.6 \pm 3.1 (21)	43.9 \pm 3.0 (10)	41.0 \pm 3.2 (23)				46.3 \pm 1.9 (4)
Combined		41.4 \pm 5.3 (44)		43.6 \pm 3.8 (47)	43.9 \pm 3.0 (10)	41.5 \pm 2.9 (43)			50.8 \pm 12.4 (5)	46.1 \pm 1.8 (12)
Bill width										
Male	14.3 (12)			11.7 \pm 0.9 (26)	11.6 \pm 1.2 (10)	11.0 \pm 0.7 (12)				
Female				10.9 \pm 0.8 (21)	11.6 \pm 1.2 (10)	10.6 \pm 0.9 (19)				
Combined				11.4 \pm 0.9 (47)	11.6 \pm 1.2 (10)	10.7 \pm 0.8 (31)				
Tarsus										
Male		36.1 \pm 2.3 (49)	38.9 \pm 1.3 (29)	35.9 \pm 2.3 (33)	37.9 \pm 3.3 (12)	37.3 \pm 3.2 (47)	35.9 \pm 1.5 (8)			34.4 \pm 1.1 (4)
Female		34.9 \pm 1.5 (43)	38.4 \pm 1.3 (22)	34.4 \pm 1.3 (29)	35.1 \pm 3.4 (40)	35.8 \pm 2.3 (45)	34.9 \pm 1.1 (8)			34.9 \pm 2.2 (4)
Combined	36.8 \pm 2.4 (13)	35.5 \pm 2.0 (92)	38.7 \pm 1.3 (51)	35.2 \pm 2.0 (62)	35.7 \pm 3.5 (52)	36.6 \pm 2.9 (92)	35.4 \pm 1.3 (16)	37.0 \pm 2.1 (10)	36.1 \pm 2.6 (5)	34.0 \pm 2.8 (11)
Wing length										
Male		203.8 \pm 6.8 (51)	196.8 \pm 8.4 (29)	205.0 \pm 5.8 (34)	204.2 \pm 5.3 (51)	204.6 \pm 5.8 (54)	201.8 \pm 4.1 (13)			193.8 \pm 5.9 (5)
Female		199.7 \pm 7.2 (42)	190.5 \pm 6.8 (22)	201.5 \pm 6.0 (30)	200.9 \pm 5.9 (58)	203.2 \pm 6.6 (49)	200.6 \pm 5.1 (17)			194.8 \pm 7.3 (4)
Combined	199.6 \pm 9.8 (13)	201.9 \pm 7.3 (93)	194.1 \pm 8.3 (51)	203.3 \pm 6.1 (64)	202.4 \pm 5.8 (109)	203.9 \pm 6.2 (103)	201.2 \pm 4.7 (30)	209.2 \pm 5.3 (10)	195.0 \pm 7.4 (5)	194.9 \pm 5.7 (11)
Body mass										
Male	838.2 (7)	761.5 \pm 52.0 (50)	842.8 \pm 72.5 (29)	809.0 \pm 62.8 (72)	815.9 \pm 59.5 (156)	815.5 \pm 57.8 (140)	788.6 \pm 65.0 (65)			
Female		730.8 \pm 51.4 (42)	811.8 \pm 70.8 (22)	750.2 \pm 51.7 (86)	753.3 \pm 54.8 (151)	741.6 \pm 59.6 (108)	731.9 \pm 63.4 (106)			
Combined	797 (11)	747.5 \pm 53.7 (92)	829.4 \pm 72.7 (51)	776.9 \pm 64.0 (158)	785.1 \pm 65.2 (307)	783.3 \pm 69.0 (248)	753.5 \pm 69.5 (171)	721.0 \pm 62.2 (10)		

¹Sources: A = Bedard 1969; Sealy 1973; J. Benson, A. Nielsen, and K. Winker unpubl.; B = Kitaysky 1996, ASK; C = Y. Artukhin unpubl.; D = JFP; E = G. Blackburn unpubl.; F = C. Thompson unpubl. N.B.: Vermeer and Cullen (1979) also reported body mass of 745.7 \pm 18.7 (27) for both sexes at Triangle I., British Columbia. Analysis (JFP) of unpubl. Fish and Wildlife Service data from the Pribilof Is. gives values for males 831.8 \pm 70 (12), females 773.7 \pm 52.7 (14), and combined 800.5 \pm 66.9 (26).

Appendix 4. Tufted Puffin colonies and populations in the North Pacific.¹

	Number of colonies	Number of individuals	Percentage of colonies	Percentage of individuals
West coast south of Alaska				
California	13	280	1.3	0.0
Oregon	31	5,030	3.0	0.2
Washington	16	22,300	1.6	0.8
British Columbia	31	76,730	3.0	2.6
Total south of Alaska	91	104,340	8.8	3.5
Gulf of Alaska				
Se. Alaska	28	18,200	2.7	0.6
N. Gulf of Alaska	104	63,650	10.1	2.1
E. Alaska Peninsula	232	475,660	22.5	16.0
W. Alaska Peninsula	83	394,820	8.1	13.3
Total Gulf of Alaska	447	952,330	43.4	32.1
Aleutians				
E. Aleutians	80	1,092,710	7.8	36.8
Central Aleutians	53	84,470	5.1	2.8
W. Aleutians	34	94,620	3.3	3.2
Total Aleutians	167	1,271,800	16.2	42.8
Bering/Chukchi Seas (U.S.)				
S. Bering Sea	23	96,170	2.2	3.2
N. Bering Sea	62	16,400	6.0	0.6
Chukchi Sea	12	80	1.2	0.0
Total Bering/Chukchi Seas	97	112,650	9.4	3.8
Total North America	802	2,441,120	77.8	82.2
Russia				
Chukchi Sea	13	320	1.3	0.0
N. Bering Sea	93	31,710	9.0	1.1
S. Bering Sea	66	45,500	6.4	1.5
Commander Is.	6	127,000	0.6	4.3
Kuril Is.	17	175,000	1.6	5.9
Sea of Okhotsk	29	150,580	2.8	5.1
Japan	5	30	0.5	0.0
Total Asia	229	530,140	22.2	17.8
Total world	1,031	2,971,260	100.0	100.0

¹Data compiled from: Alaska and Russia—Beringian Seabird Colony Atlas, U.S. Fish and Wildlife Service, Anchorage, AK, and Kondratyev et al. 2000. Note that estimates for Russia attempt to reconcile differences in numbers calculated from the Colony Atlas and Kondratyev et al. 2000. Japan—Watanuki et al. 1988, Brazil 1991, Osa and Watanuki 2002. British Columbia—Campbell et al. 1990. Washington—Speich and Wahl 1989, U. Wilson unpubl., R. T. Paine unpubl. Oregon: Hodder 2002. California—Carter et al. 1992, McChesney et al. 1995.

Appendix 5. Linear skeletal measurements (mm) and body mass (g) of adult Tufted Puffins (J. F. Pitocchelli unpubl.) Data shown as mean \pm SD (*n*).

	Male	Female	Probability
Premaxillary length	34.19 \pm 1.60 (70)	33.33 \pm 1.51 (87)	0.0006
Bill depth	18.30 \pm 0.92 (83)	17.66 \pm 0.91 (111)	0.0001
Interorbital width (max.)	11.26 \pm 0.51 (99)	10.81 \pm 0.55 (123)	0.0001
Interorbital width (min.)	5.82 \pm 0.46 (104)	5.70 \pm 0.48 (125)	0.0431
Skull width	35.06 \pm 0.82 (104)	33.15 \pm 0.89 (125)	0.0001
Skull length	90.41 \pm 6.99 (70)	88.62 \pm 1.90 (91)	0.0208
Upper mandible length	73.55 \pm 1.97 (80)	70.91 \pm 1.82 (111)	0.0001
Coracoid length	43.16 \pm 1.27 (105)	41.81 \pm 1.18 (126)	0.0001
Scapula length	67.91 \pm 2.13 (104)	66.24 \pm 1.97 (125)	0.0001
Sternum length	103.98 \pm 2.91 (102)	101.97 \pm 3.12 (123)	0.0001
Keel length	117.55 \pm 3.57 (103)	114.98 \pm 4.08 (122)	0.0001
Keel depth	37.56 \pm 1.17 (104)	36.76 \pm 1.15 (127)	0.0001
Synsacrum width (max.)	23.35 \pm 0.94 (105)	22.78 \pm 0.99 (126)	0.0001
Femur length	47.72 \pm 1.40 (103)	46.19 \pm 1.28 (123)	0.0001
Tibiotarsus length	75.03 \pm 2.14 (105)	73.26 \pm 2.11 (126)	0.0001
Tarsometatarsus length	34.23 \pm 1.13 (104)	33.00 \pm 1.15 (126)	0.0001
Humerus length	76.81 \pm 4.52 (104)	74.19 \pm 8.59 (124)	0.0055
Radius length	59.94 \pm 1.51 (105)	58.59 \pm 2.06 (127)	0.0001
Ulna length	61.30 \pm 1.52 (105)	59.84 \pm 1.61 (125)	0.0001
Carpometacarpus length	40.27 \pm 1.02 (104)	39.49 \pm 2.02 (125)	0.0004
Fresh mass	809.56 \pm 58.29 (79)	748.45 \pm 52.60 (93)	0.0001

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