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ADSTRACT	approvea:	 _	_		
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The breeding biology and early life history of the Tufted Puffin (Fratercula cirrhata) were studied for two years on Goat Island, Curry County, Oregon. Artificial nest boxes were used to minimize disturbance and provide easy access to puffin eggs and chicks. Utilization of these boxes was 47.5% and 57.5% in 1981 and 1982, respectively. Egg laying began each year in early May and continued until mid-June; a total of 46 eggs was produced and 31 eggs hatched. Four precisely known incubation periods had a mean of 42.8 days; the estimated mean for the remaining 27 eggs was 43.6 days. Eight chicks fledged each year. In 1981, the mean estimated nestling period was 57.6 days; in 1982, it was 50.5 days. Precise laying, hatching and fledging dates were obtained for 2 chicks in 1982. These gave total incubation and nestling periods of 91 (41+50) and 92 (43+49) days.

Chicks were fed primarily during the morning hours

shortly after dawn and again several hours before dark; very little feeding activity was observed during afternoon hours. Food items collected from nest boxes consisted of three species in 1981 and seven species Northern anchovy (Engraulis mordax) 1982. uр approximately 50% of the items collected during both Chicks received an average daily food intake of 71.3 gms in 1982 based on 4.7 deliveries/day X 2.3 items/delivery X 6.6 qms/item. Chicks in 1981 gained an average of 6.6 qms/day and fledged at a mean weight of 437.1 gms. Ιn 1982, chicks gained an average of 9.0 gms/day and fledged at 516.9 gms. Weight and growth measurements for culmen, manus and tarsus were taken on a Mean weekly culmen, manus and tarsus weekly basis. measurements provided more consistent information with regard to age of the chick than did weight. Weight may better serve as an indicator of food availability. Nesting success, based on total chicks fledged for the number of active nest boxes, was 38% for the two years of this study.

# Breeding Biology and Early Life History of the Tufted Puffin ( $\underline{Fratercula}$ $\underline{cirrhata}$ )

bу

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in partial fulfillment of the requirements for the degree of

Master of Science

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# BREEDING BIOLOGY AND EARLY LIFE HISTORY OF THE TUFTED PUFFIN (FRATERCULA CIRRHATA)

#### INTRODUCTION

Tufted Puffins (Fratercula cirrhata) are colonial, burrow nesting members of the Alcidae. Colonies commonly are located on precipitous coastal islands or inaccessible headlands where burrows are excavated in steep. slopes. Tufted Puffins have high wing loading (1.49 gm/cm) and therefore have difficulty becoming airborne (Vermeer, 1979). By launching from steep elevated slopes, wind and altitude are used to gain the airspeed necessary for sustained flight. Colony sites usually require soil adequate to support vegetation and to permit burrow excavation, although infrequent nesting in rocky crevices occurs (Gabrielson and Lincoln, 1959: Swartz, 1966). The absence of mammalian predators also is an important characteristic of colony sites (Vermeer and Cullen, 1979).

Tufted Puffins are found throughout the North Pacific with a center of dispersal in the western Aleutian Islands (Udvardy, 1963; Sowls et al, 1978). Historically, puffins nested along the California coast of as far south as Santa Barbara Island (33 33'N) (Willet, 1915); however, at present, only remnant colonies remain in California. For example, Tufted Puffins on the

Farallon Islands once numbered several thousand (Ainley and Lewis, 1974), but today the population is approximately 100 (Sowls et al, 1978). Ainley and Lewis (1974) attributed the initial decline to oil pollution, but hypothesized that the failure of puffins to recover was related to the dramatic, long-term reduction of Pacific sardine (Sardinops caerulea) stocks.

Along the Oregon coast, Tufted Puffin colonies were reported from 31 locations with the total population estimated at 6,500 (Varoujean and Pitman, 1980). The Three Arch Rocks colony was the largest (4,200) and populations of 300-400 birds each occurred at Haystack Rock (Clatsop Co.), Haystack Rock (Tillamook Co.), Island Rock and Goat Island; all remaining colonies consisted of 150 birds or less (Varoujean and Pitman, 1980).

Tufted Puffins are sensitive to human disturbance and frequently abandon all nesting activities if disturbed during egg laying or incubation (Frazer, 1975; Manuwal, 1978; Sowls et al., 1978; Hatch, 1984). Within the last decade, studies were initiated in some of the large colonies in Alaska and British Columbia to collect basic biological information (Frazer, 1975; Amaral, 1977; Wehle, 1980; Vallee, pers. com.). Studies in Oregon, however, have consisted primarily of locating and censusing Tufted Puffin colonies.

Responsible exploitation of natural resources requires a basic understanding of the environmental

impacts. Oil exploration along the Oregon coast is not yet a reality, but tanker traffic is. A major oil spill in the coastal zone during the nesting season could be disastrous for many of Oregon's more than 400,000 marine birds (Varoujean and Pitman, 1980). Further, as hypothesized by Ainley and Lewis (1974), exploitation of a primary prey species may result in a long term population depression for predators. If resource managers are to manage under such circumstances, a knowledge and standing of the basic biology for each species is a necessity. This study was conducted to add to the knowlege of the breeding biology and early life history of Tufted Puffins in Oregon and had the following objectives:

- 1) to determine the length of Tufted Puffin incubation and nestling periods;
- 2) to conduct a quantitative and qualitative analysis of food provided to Tufted Puffin chicks;
- 3) and to examine the relationship of food consumption to growth and weight gain for Tufted Puffin chicks.

#### STUDY AREA

Island (42 03'N 124 19'W) is an 8.5 ha island approximately 2 km northwest of Brookings, Curry County, Oregon and 500 m offshore. Steep rocky cliffs form the perimeter; the upper portion of the island has a slope rising to a maximum elevation of 56 m. Weissenborn and Snavely (1968) considered Goat Island to be underlain by the Dothan Formation, a sandstone shale association described by Diller (1907). Soil accumulation was undetermined depth, but supported a diverse plant com-Browning and English (1972) reported a 2-3 munity. area on Goat Island dominated by Phalaris spp. Phalaris spp. was not found on Goat Island during this study. A 2-3 ha area on the upper slopes was covered with a dense stand of grasses and, although no one species was dominant, Pacific reedgrass (Calamagrostis nutkaensis) and Holcus lanatus were common. A variety of forbs and several shrubs also were found throughout the island, but

An estimated 200 pairs of Tufted Puffins nested on Goat Island in 1979 (Varoujean and Pitman, 1980). Burrows were excavated on a steep grassy slope on the north end of the island approximately 20-25 m above sea level. A dense growth of Pacific reedgrass adjoined the puffin colony above, however puffins avoided this area except for the immediate edge (1-2 m).

no trees were present (Appendix I).

A climatological profile for Goat Island was synthesized from Climatological Data, Annual Summary, Oregon The climate is mild maritime (Anonymous, 1981). 1981 average annual temperature of 11.8 C. with with southerly gale force winds and heavy rainfall, occur regularly during the winter. Temperatures in January, the coolest month, average 8.3 C, but freezing can expected several times each winter. Precipitation heaviest during November, December and January with nearly one half of the yearly total (205 cm) falling during this period. The driest months are June, July and August which average just over 2.5 cm of rain per month. Summer temperatures occasionally reach 32 C; September is the warmest month with an average temperature of 15.3 C. Northwesterly winds of 25-30 km/h are common during the afternoon throughout much of the summer (Anonymous, 1968).

#### METHODS AND MATERIALS

This study was conducted in 1981 and 1982 with limited observations in 1983, the latter prompted by the strong El Nino anomaly. During a preliminary investigation in 1980. Tufted Puffins only used nest boxes Therefore, artificial nest boxes wooden tunnels. and tunnels used during this study were constructed from cedar fencing material. Boxes and tunnels were constructed with sides and tops, but no floors. and right angle or "L" shaped tunnels were used (Fig. Forty nest boxes and tunnels were placed 1). existing burrows or dug into the puffin colony and covered with soil and sod. A monitoring schedule of 3-4 days per week was established in April each year continued through the nesting season. Boxes inspected daily until an egg was present and weekly there-As anticipated hatch dates neared, boxes again checked daily. Nest box utilization was determined by the presence of an egg. In 1981, four nest boxes were repositioned after the nesting season had begun; were not repositioned in 1982. Inspection boxes of unused boxes was discontinued in late June each year.

Eggs were weighed to the nearest gram with a 500 gm Pesola scale; length and diameter measurements were taken with a vernier calipers to the nearest 0.1 mm. Eggs that failed to hatch were collected for pesticide analysis.

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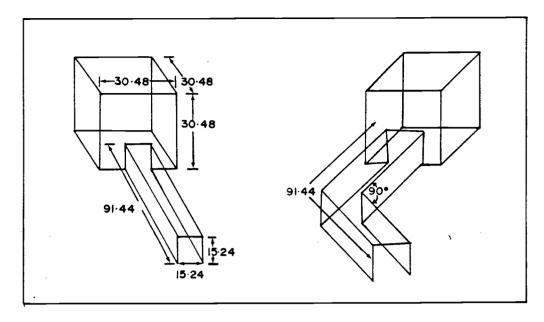


Fig. 1. Design of nest boxes used during the Tufted Puffin study on Goat Island, 1981 and 1982.(dimensions in cm)

Chicks were weighed and measured as soon after hatching as possible and weekly thereafter. Weights to the nearest gram, were determined with 500 gm and 1,000 gm Pesola scales. Culmen and tarsus measurements to the nearest 0.1 mm were taken with vernier calipers. The manus was measured with a millimeter rule to the nearest 1 mm.

Information regarding feeding of chicks was gathered during 5 24-h observation periods. Observations were conducted weekly from 17 July 1982 through 15 August 1982 during daylight hours from a semi-permanent plywood blind. A generalized feeding schedule for the chicks was determined by counting all adult puffins seen carrying food during randomly selected 10-min periods (N=86) each

hour. It was assumed all that such sightings were attempts to deliver food to chicks. During these observation periods, 2 nest boxes were monitored continuously. All food deliveries were recorded, food items were preliminarily identified (fish or squid) and counted. Food items were collected from active nest boxes and frozen; food collected was replaced with a similar quantity of northern anchovy (Engraulis mordax). At the end of each season, identification of collected food items was confirmed; items were weighed to the nearest 0.1 gm on a Mettler Balance (PN1210) and total length determined with a millimeter rule to the nearest 1 mm.

All comparisons for significant differences were conducted with Student's t-test, p<0.05 (Sokal and Rohlf, 19.81).

#### RESULTS

# <u>Utilization</u> of nest boxes

Nest box utilization in 1981 was 47.5% (19/40), including 2 of the repositioned boxes; during 1982, nest box utilization was 57.5% (23/40). Fourteen nest boxes (35%) were used both years.

## Egg description

Tufted Puffin eggs from Goat Island were ovate-pyriform in shape. Color and markings were difficult to determine because eggs acquired a dirty brownish appearance with darker mottling. A few blades of Pacific reedgrass or eelgrass (Zostera spp.) were commonly found in the nest chamber, but eggs were frequently in contact with the soil.

Twenty puffin eggs were measured and weighed in 2 1981; the formula V=kld was used to determine egg volumes (1)(Harris, 1964). Mean length, diameter, volume and weight were 71.3 mm, 48.8 mm, 81.0 cc and 91.0 gm, respectively (Tables 1 and 2). Twenty-five eggs were measured and weighed during 1982 and mean values were 73.0 mm, 49.3 mm, 84.5 cc and 90.3 gm. Mean values did not differ significantly between years.

(1) V=volume; k=constant 0.476; l=length; d=diameter

Table 1. Length, diameter and volume of Tufted Puffin eggs from various North Pacific locations, including Goat Island in 1981 and 1982.

Location	Length (mm)	(mm)	(cc)	N
	Max. <u>M</u> in. X s	Max. Min. X s	Max. Min. X S	
Not reported	72.0	51.5 45.0 49.2	83.0	43 (a)
Not reported	71.0 68.0	50.0 45.0		(b)
Not reported	78.2 69.2	51.8 48.0		(b)
East Amatuli Is, AK			81.5	51 (c)
East Amatuli Is, AK	72.8		82.9	11 (d)
Ugaiushak Is, AK	72.9 3.18	52.0 46.5 49.3 1.47	84.3	41 (e)
Ugaiushak Is, AK	79.8 68.6 73.5 2.53	51.9 46.3 49.0 1.57		46 (e)
St Lazaria Is, AK		48.5	82.5	20 (f)
Buldir Is, AK	72.5 3.05	52.0 46.4 49.3 1.48		37 (e)
Destruction Is, WA	72.8	49.6 47.0 48.1	80.2	6 (g)
Goat Is, OR	71.3 3.15	51.1 45.9 48.8 1.61	81.0 7.4	20 (h)
Goat Is, OR	77.6 66.6 73.0 2.82	51.7 44.6 49.3 1.80	96.3 69.8 84.5 7.0	25 (i)
(a) Bent, 1919 (b) Dement'ev and Glac (c) Amaral, 1977 (d) Manuwal and Boers (e) Wehle, 1980		(g) Fra: (h) Thi:	nnell, 1900 zer, 1975 s study, 19 s study, 19	81

Table 2. Weight of Tufted Puffin eggs from various North Pacific locations, including Goat Island, 1981 and 1982.

Location		Weight	(gm)		N	
	Max.	Min.	$\overline{\chi}$	S		
East Amatuli Is, AK East Amatuli Is, AK Ugaiushak Is, AK Ugaiushak Is, AK Buldir Is, Ak Goat Is, OR Goat Is, OR	107.0 106.0 110.0 107.0 107.5 105.0 101.0	80.4 86.0 81.0 81.5 81.0 77.0 75.0	92.8 95.1 94.7 93.9 94.4 91.0 90.3		32 11 41 39 37 20 25	(a) (b) (c) (c) (c) (d) (e)

- (a) Amaral, 1977(b) Manuwal and Boersma, 1978
- (c) Wehle, 1980
- (d) This study, 1981
- (e) This study, 1982

Mean length and diameter measurements of puffin eggs Goat Island differed significantly from data from other geographic locations in only one instance (Table Mean length of eggs from Goat Island (71.3 mm, 1981) 1). significantly less than the mean length of eggs from Ugaiushak Island, Alaska (73.5 mm, 1977). Approximate volumes for eggs from other colonies were determined from mean length and diameter measurements (Table 1). data were inadequate for tests of significance, but were similar to data from Goat Island in 1981 and 1982.

Eggs from Goat Island weighed less than eggs from several locations in Alaska. The mean weight of from Goat Island in 1982 (90.3 gm) was significantly less mean weights from Buldir Island in 1975 (94.4 gm) and Ugaiushak in 1976 (94.7 gm) and 1977 (93.9 gm).

## Egg laying

Exact dates for initiation of egg laying were not obtained, however approximate dates were determined. Laying began in early May; eggs were first observed on 7 May 1982 and 8 May 1981. Although laying continued until mid-June, egg production was concentrated in May, 85% (N=20) in 1981 and 88% (N=26) in 1982. During 1981 laying occurred uniformly throughout the month, but in 1982, 69% (18/26) of the eggs were laid during a 2-week period from 8 May through 21 May. Eight eggs were produced outside of this 2-week period, 2 prior to 8 May and 6 after 21 May. A total of 6 eggs (13%, N=46) was produced in June, 3 each year.

# Egg replacement

Tufted Puffins produce a single, one-egg clutch each breeding season; however, replacement of lost or abandoned eggs was reported (Wehle, 1980). Several instances of probable egg replacement were recorded during this study. In 1981, an artificial nest box was repositioned over an active burrow in which an egg was present. Several days after repositioning, the egg was in the tunnel and the following week only shell fragments remained. Approximately 2 weeks later another egg was present; a chick eventually fledged from this second egg. In 1982,

eggs in 2 boxes disappeared early in the incubation period and within 15 days an egg was again present in each nest box. In one box, the second egg hatched and the chick fledged. The replacement egg in the second box was buried in the soil and failed to hatch. The initial egg in a third nest box was also buried. A second egg hatched, but the chick disappeared after about 10 days.

Weight and measurement data (Table 3) indicated that initial eggs (N=3) were slightly larger than replacement eggs (N=4). However, comparison of mean values indicated these differences were not significant.

Table 3. Weight, length, diameter and volume measurements for initial and replacement Tufted Puffin eggs from Goat Island, 1981 and 1982.

		Initia	al Egg		Replacement Egg				
	Wt. (gm)	Len. (mm)	Dia. (mm)	Vol. (cc)	Wt. (gm)	Len. (mm)	Dia. (mm)	Vol. (cc)	
	102 97 89 *	76.1 70.6 70.8	50.1 51.0 49.8	90.9 87.4 83.6	98 86 89 77	73.1 70.8 69.2 74.5	49.7 50.0 48.8 46.3	85.9 84.3 78.4 76.0	
X s	96	72.5 3.1	50.3 0.6	87.3 3.7	87.5 8.7	71.9	48.7 1.7	81.2	

<sup>\*</sup>Egg disappeared prior to being weighed and measured.

# Incubation period

Exact laying and hatching dates were difficult to obtain because nest boxes were checked only 4 days each

However, minimum and maximum incubation periods were determined for each egg; extremes observed during this study were 32-39 and 46-53 days, respectively. Fifteen eggs hatched in 1981. An exact incubation period of 42 days was recorded for one egg. For the remaining 14 eggs, a mean incubation period of 42.4 +4.8 days was estimated from combined minimum and maximum periods. Exact laying and hatching dates were obtained for 3 eggs during 1982, incubation periods were 41, 43, and 45 days. The estimated mean for 13 remaining eggs was 45.1 +4.7 days. Comparing known incubation periods with estimated periods, no significant differences were observed for 1981, 1982 or for both years combined. The mean for all precisely known incubation periods was 42.8 +1.7 days and the mean for all estimated periods from both years was 43.8 +4.9 days.

Wehle (1978) calculated mean incubation periods of 46.8 days and 46.2 days on Ugaiushak Island in 1976 and 1977, respectively. Both known and estimated mean incubation periods from Goat Island were significantly less than the periods from Ugaiushak Island.

# Nestling period

Minimum and maximum nestling periods were determined for each chick and exact dates were obtained for 2

chicks. In 1981, the estimated mean nestling period for 8 chicks was 57.6 +7.5 days. No precise nestling periods were determined, but extreme minimum and maximum periods were 46-54 and 72-75 days, respectively. Ιn chicks fledged; the estimated mean nestling period for these chicks was 50.5 +6.6 days with extreme minimum and maximum periods of 39-42 and 53-64 days. Although the estimated mean nestling periods differed by more than 7 days between years, this difference was not significant. The estimated mean nestling periods on Goat Island fered significantly from nestling periods reported Ugaiushak Island, 44.8 days (1976) and 41.8 days (1977) (Wehle, 1980). Exact hatching and fledging dates obtained for 2 chicks during 1982; one fledged at 50 days and the other at 49 days. Precise egg laying dates also were known and total incubation and nestling periods were 91 and 92 days, respectively.

# Feeding of chicks

During 1982, 2 peak feeding periods were observed each day (Fig. 2). The major feeding period began each day shortly after dawn, peaked quickly, then declined gradually until mid-day. A second major feeding period, of lesser magnitude, began about 1800 hours and continued until dark. Very few chicks were fed during the afternoon hours.

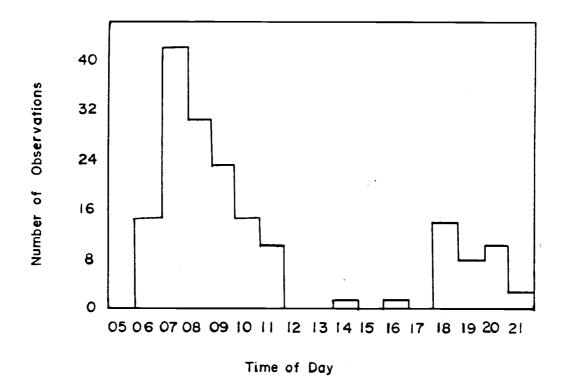


Fig. 2. Observations of adult Tufted Puffins carrying food near the colony on Goat Island, July and August, 1982.

On Goat Island, the number of food deliveries per nest box during a 24-h period ranged from 0 to 12 with a mean of 4.7. Precise quantity was difficult to determine, but an average of 2.3 items per delivery was estimated.

The mean weight of food items collected from nest boxes in 1982 was  $6.6 \pm 7.5$  gm (N=39). With an average of 4.7 deliveries per day and 2.3 items per delivery, the estimated average daily food intake was 71.3 gm.

During 1981 only 3 prey species were collected, northern anchovy, Pacific herring (<u>Clupea harengus</u>) and Pacific sand lance (<u>Ammodytes hexapterus</u>)(Appendix II). A greater variety of food items was collected in 1982;

in addition to the 3 species recorded in 1981, rockfish, (Sebastes sp.), Pacific sanddab (Citharichthys sordidus), rex sole (Glyptocephalus zachirus) and squid (Loligo opalescens) were collected (Appendix III). Northern anchovy made up approximately 50% of the diet of puffin chicks both years (Table 4). Pacific herring and Pacific sand lance also were recorded in the diet each year. However in 1981, the importance of herring may have been exaggerated by 3 large specimens and a small sample size (N=13), which indicated 70% (wet weight) of the diet was herring. Of the four species collected only in 1982, squid made the largest wet weight contribution to the diet of the chicks (16%), but Pacific sanddab occurred more frequently.

Table 4. Food items collected from Tufted Puffin nest boxes on Goat Island, 1981 and 1982.

	19	81	198	2
Food Item	No. of Items	% Wet Weight	No. of Items	•-
Pacific herring (Clupea harengus)	3	70	2	25
Northern anchovy (Engraulis mordax)	7	27	16	54
Pacific sand lance (Ammodytes hexapterus)	3	3	3	3
Rockfish ( <u>Sebastes</u> sp.)			1	*
Pacific sanddab (Citharichthys sordidus)			11	2
Rex sole (Glyptocephalus zachirus)			2	*
Squid (Loligo opalescens)	<b></b>		4	16

<sup>\*</sup> less than 1%.

# Weight gain by chicks

Initial weights for Tufted Puffin chicks were recorded within 3 days of hatching. In 1981, the mean initial weight was 63.5 gm (Table 5); in 1982, mean initial weight increased to 67.9 gm. Both mean maximum and mean fledging weights were less in 1981 than in 1982. In 1981, weights were 476 gm and 437.1 gm, respectively; in 1982, these weights increased to 530 gm and 516.9 gm. Pre-fledging weight loss was recorded for 88% (N=8) of the chicks in 1981, but only 38% (N=8) in 1982. The mean weight loss was 27.6 gm in 1981 and 31.3 gm in 1982. Mean weight gain per day was 6.6 gm during 1981, but

increased in 1982 to 9.0 gm/day.

Mean values for initial, maximum and fledging weights for 1981 and 1982 were compared. Pre-fledging weight loss and weight gain per day for 1981 and 1982 also were compared. Only mean weight gain per day differed significantly; all other comparisons were not significant.

Limited observations indicated that puffin chicks grew slowly in 1983; one chick lost 4 gm between 1 August and 30 August. The average weight on 30 August was 307 gm (N=3); by comparison, chicks of similar age weighed 432 gm (N=8) and 517 gm (N=7) in 1981 and 1982, respectively. Nest boxes were vacant when checked on 13 September and all chicks were assumed to have fledged.

Table 5. Weight gain for Tufted Puffin chicks on Goat Island, 1981 and 1982.

	Initial Wt. (gm)	Maximum Wt. (gm)	Fledging Wt. (gm)	Pre-Fledging Wt. Loss (gm)	Wt. Gain Per Day (gm/day)
1981					
X	63.5	476	437.1	27.6	6.6
S	7.9	65.9	72.0	15.8	1.7
N	15	8	8	7	8
1982					
X	67.9	530	516.9	31.3	9.0
S	10.3	73.3	88	39.6	2.1
N	7	8	8	3	8
N 	/ 	8 	8	3	8

# Culmen, manus and tarsus growth by chicks

Mean initial culmen measurements were 22.6 mm in both 1981 and 1982; mean culmen measurements at fledging were 39.6 mm and 40.2 mm, respectively (Table 6). During 1981, the mean culmen growth rate was 0.300 mm/day, but in 1982 it increased to 0.349 mm/day. In 1981, mean initial manus measurements were incorrectly taken; in 1982, the mean was 23.7 mm. Mean manus measurements at fledging were 156.1 mm in 1981 and 152.5 mm in 1982. Manus growth was not computed in 1981, but the growth rate was 2.6 mm/day in 1982. Mean initial tarsus measurements were 26.3 mm both years. Mean tarsus measurements at fledging were 41.9 mm (1981) and 42.5 mm (1982) and mean tarsus growth rates were 0.276 mm/day and 0.311 mm/day.

Mean values for initial and fledging culmen, manus and tarsus measurements were compared for 1981 and 1982. Mean growth rate values for 1981 and 1982 also were compared. Only culmen growth rates differed significantly; all other comparisons were not significantly different.

Table 6. Culmen, manus and tarsus growth for Tufted Puffin chicks on Goat Island, 1981 and 1982.

	CULMEN		MANUS			TARSUS			
	Int. (mm)	Fledge (mm)	Gth. Rate (mm/day)	Int. (mm)	Fledge (mm)	Gth. Rate (mm/day)	Int. (mm)	Fledge (mm)	Gth. Rate (mm/day)
	22.6 1.3 8	39.6 2.2 8	.300 .046 8	*	156.1 9.0 8		26.3 1.4 8	41.9 2.0 8	.276 .049 8
1982	22.6 0.7 7	40.2 2.0 8	.349 .035 8	23.7 2.4 7	152.5 8.3 8	2.6 .17 8	26.3 2.2 7	42.5 1.1 8	.311 .029 8

<sup>\*</sup> Measurements taken incorrectly

Mean growth and weight measurements from this study were compared with similar data from Alaska (Table 7). Mean initial and fledging measurements were similar for culmen, manus, tarsus and weight with the exception of fledging weight. Although data were inadequate for tests of significance, culmen, manus and tarsus measurements provided more consistent information regarding growth than did weight.

Table 7. Mean growth and weight measurements for Tufted Puffin chicks from the Barren Islands, Alaska, 1978 and Goat Island, 1981 and 1982.

Culmen		Manus		Tarsus		We	ight
Int.	Fledge	Int.	Fledge	Int.	Fledge	Int.	Fledge
(mm)	(mm)	(mm)	(mm)	(mm)	(mm)	(gm)	(gm)
22.0	39.2	25.3	152.2	26.6	44.3	68	550 (a)
22.6	39.6	*	156.1	26.3	41.9	63.5	437.1(b)
22.6	40.2	23.7	152.5	26.3	42.5	67.9	516.9(c)

<sup>(</sup>a) Manuwal and Boersma, 1978

Combined 1981 and 1982 mean weekly growth measurements for puffin chicks from Goat Island provided base line information for future comparisons (Table 8).

Table 8. Mean weekly culmen, manus, tarsus and weight measurements for Tufted Puffin chicks from Goat Island, 1981 and 1982.

Week	1	2	3	4	5	6	7	8
Culmen(mm) Manus (mm) Tarsus(mm) Weight(gm)	25.6 27.4	37.8 32.7	53.7 36.8	91.5 39.3	117.5 41.1	135.4 42.0	150.0 42.0	157.0 42.5

## Nesting success

Fifteen of 46 eggs (N=20, 1981; N=26, 1982) failed to hatch during this study. When opened, 6 eggs showed no sign of embryonic development; another contained a partially developed embryo. Two eggs were pipped, but

<sup>(</sup>b) This study, 1981

<sup>(</sup>c) This study, 1982

<sup>\*</sup> Initial measurements incorrect

the chicks died before hatching was complete and 6 eggs disappeared for unknown reasons. Sixteen of the 31 chicks fledged, 8 each year. Nesting success was based on total chicks fledged for the number of active nest boxes, human disturbance notwithstanding. In 1981, nesting success was 42% (8/19), but in 1982 the success rate declined to 35% (8/23). The combined success rate for both years was 38% (16/42).

#### Nesting season

The nesting season for Tufted Puffins on Goat Island was approximately 6 months, mid-April through mid-September. Puffins were first seen near Goat Island on 17 April 1981 and 24 April 1982. The last chicks to fledge from nest boxes departed on 13 September 1981 and between 24 and 28 August 1982. In 1981, very few adult puffins were seen near the colony on 13 September, an indication that the nesting season was nearly complete. However, on 28 August 1982, the nesting season was still on going; adults were present on the colony and one was seen taking food into a natural burrow.

#### DISCUSSION

Nestling periods and growth of Tufted Puffin Goat Island differed considerably between years and with chicks from other areas. Length of the nestling growth seem to be closely related. period and (1980) correlated faster growth and shorter nestling periods with the abundance of sand lance and capelin in the diet of chicks. Vermeer and Cullen (1979) associated variations in growth of chicks with food availability. Mean nestling periods of 44.8 and 41.8 days on Ugaiushak Island (Wehle, 1978) were significantly less than the 57.6 and 50.5 days from Goat Island. Frazer (1975) reported a nestling period of 51 days Destruction Island. Washington and on East Amatuli land, Alaska, the average age at fledging was 47 (Amaral, 1977). The shortest nestling periods were reported from Nelson Lagoon. Alaska where 6 chicks fledged at 38 to 41 days. These chicks also gained an average of gm/day, more than twice the rate of chicks on Goat Island; this rapid growth was attributed to"...an abundant and non-competitive food supply" (Gill et 1978).

The phenomenon of upwelling may provide an explanation for the variation in availability of food resources and consequently the variable patterns of growth experienced by puffin chicks on Goat Island. Nutrients,

temperature, productivity and food resources are all closely associated with upwelling. Marine ecosystems where upwelling occurs are relatively cold, nutrient rich and highly productive with abundant food resources (Barber and Chavez, 1983).

1981, upwelling along the southern Oregon coast similar to the long-term average during the (Table 9); however, in July strong upwelling occurred. By 1 August, 50% (4/8) of the puffins chicks had lost weight and weight gain remained slow throughout month. Pacific herring collected from nest boxes during this period may have been too large chicks to swallow. Several chicks also were observed with fish tails protruding from their beaks. These fish, probably herring, were eventually ingested. Loss o f weight by some chicks and prey that were difficult to ingest suggest less than optimal feeding conditions.

Table 9. Bakun upwelling index for the Oregon coast for the period April through August 1981-1983 and 1948-1967 averages for the same months.

Location	Month	Average 1948-1967(a)	1981(b)	1982(b)	1983(b)
o o 42 N 125 W	April May June July August	33 79 103 132 91	44 66 78 201 78	3 189 66 97 57	8 56 77 61 45

<sup>(</sup>a) Bakun, 1973

<sup>(</sup>b) Bakun, unpub.

Upwelling during 1982 was strong in May but moderated in June, July and August (Table 9). Nestling periods were shorter and chicks fledged heavier than in 1981, an indication that food resources may have been more available.

Reported nesting failures associated with El Nino anomalies (Boersma, 1978; Schreiber and Schreiber, 1983) prompted continuation of this study in 1983, albeit with limited observations. The effect of the 1982-1983 El Nino was apparent along the Oregon coast during the summer of 1983. Upwelling was below the long-term average throughout the spring and summer (Table 9) and puffin chicks grew slowly. Chicks were assumed to have fledged, but fledging weights were probably below weights from previous years. Nestling periods in 1983 were approximately 9 weeks, somewhat longer than in 1981 and 1982.

Although the area around Triangle Island, British o Columbia (50 52'N; 129 05'W) is not an area of strong upwelling, reproductive success of Tufted Puffins may be affected by the phenomenon. Vermeer (1979) reported poor reproduction for Tufted Puffins on Triangle Island in 1976, 1977 and 1979; these were years of poor upwelling or downwelling (Bakun, unpub.). In 1975, upwelling fluctuated throughout the season (Bakun, unpub.) and reproductive success was "marginal" (Vermeer, 1979). Stronger than average upwelling occurred in June and July of 1978

(Bakun, unpub.) and reproductive success was good (Vermeer, 1979).

Slower growth, lower fledging weights and extended nestling periods for puffins during periods of anomalous upwelling suggest a relationship between the upwelling phenomenon and the availability of food resources. trients are not recycled into the photic zone when welling fails to develop or is weak and consequently overall production is reduced dramatically (Barber Barber and Chavez (1983) reported that Chavez, 1983). the 1982-1983 El Nino had profound detrimental effects on reproduction and survival of the Peruvian anchovy (E. ringens). If northern anchovies were effected similarly in 1983, Tufted Puffins may have had difficulty securing adequate food for their young. Timing of upwelling also may be important. Water from an upwelling event may be nutrient rich, but biomass poor. In addition, offshore transport of surface waters was reported during periods of strong upwelling (Small and Menzies, 1981; 1980); food resources also may be transported offshore. When strong upwelling occurs during the spring, there is sufficient time for biomass, including food resources for puffins, to increase before the chicks hatch. However, strong upwelling during the summer may transport food resources offshore creating a temporary food shortage for puffin chicks.

Vermeer and Cullen (1979) suggested that because of

the variation in weight among chicks of similar age, wing length might provide a more reliable indicator of growth. presentations by Manuwal and Boersma (1978) Wehle (1978) supported this hypothesis. For chicks unknown age, culmen, manus and tarsus measurements (Table 8) can be used to determine an approximate age; weight at the indicated age might then suggest the availability of resources. Growth data obtained during this study food would be most applicable to chicks from Goat Island may have some general application for chicks elsewhere the Oregon coast, but not for puffin chicks along areas where climatic conditions and/or food differed radically from Goat Island.

Incubation periods on Goat Island were shorter incubation periods on more northerly colonies, Ugaiushak in particular. Frazer (1975) reported a maximum period of 43 days on Destruction Island incubation proposed a range of 38-48 days. On East Amatuli Island, Amaral (1977) estimated a mean incubation period of 45.2 days (range 43-53, N=11). A correlation between egg size and length of the incubation period was reported: larger eggs required longer incubation (Parsons, 1972; Rahn and Ar, 1974). Egg weight data suggest that puffin eggs from Island weighed less and consequently were smaller Goat eggs from other colonies. However, Wehle than (1980)only weights from eggs less than 3 days old so the gave

data may not be directly comparable; he also reported an average weight loss of 12.6 qm/egg during incubation. Collection of measurement and weight data from eggs Goat Island was delayed (1-4 weeks) in 1982 because it suspected that handling of eggs might have caused desertions. Eggs lost weight due to dehydration during this period and a comparison of weights between incubated eggs would be inappropriate. To further and fresh clarify possible differences in mean egg size between colonies, egg volumes were determined (Table 1). data were inadequate for tests of significance, but egg volumes from all colonies were similar.

Sealy (1984) suggested that extended incubation periods in some alcids resulted from interrupted incubation caused by disturbance. Information was not available to evaluate differences in disturbance between Goat Island and other puffin colonies. Thus, neither egg size nor possible disturbance provide an explanation and the reason for a shorter incubation period on Goat Island is unclear.

Tufted Puffin chicks on Goat Island were fed twice daily, morning and evening. Similar feeding schedules were reported previously (Amaral, 1977; Baird and Moe, 1978; Wehle, 1980). In addition, Amaral (1977) and Wehle (1980) reported afternoon peaks, but no such peak was observed on Goat Island. On Triangle Island in 1977, Vermeer et al. (1979) noted only the early morning peak;

however, this was a year when Tufted Puffins had difficulty securing adequate food for their young. In 1980, chick feeding activities on Triangle Island were high during the morning and evening with smaller peaks during the day (Vallee', per. com.).

Amaral (1977) reported 2 to 6 feedings for each chick per day with an average of 3.8. On Triangle Island, chicks were fed once or twice a day during 1977, a poor reproductive year, but 3 to 4 times per day in 1978 when improved reproductive success was observed (Vermeer and Cullen, 1979).

Puffin chicks on Goat Island received an average of 71.3 gm of food per day. By comparison, chicks from the Barren Islands, Alaska received an estimated 80 gm/day (Manuwal and Boersma, 1978). Vermeer (1979) reported an average food intake of 75-80 gm/day for puffin chicks in August 1978, but only 28 gm/day in August 1977.

A total of 7 prey species were collected from Goat Island during this study; however, approximately 50% of the diet of the puffin chicks was northern anchovies. More than 40 prey items have been identified from adult puffins (Wehle, 1976 and 1980; Hatch et al., 1978; Vermeer, 1979; Sanger, 1983), but small schooling fishes frequently made up a majority of the diet. Pacific sand lance was overwhelmingly the predominant prey fed to chicks on Ugaiushak Island (Wehle, 1980, 1982). Sand

lance also were frequent prey on Buldir Island, but squid were important as well (Wehle, 1980,1982). Capelin (Mallotus villosus) was the principle food item in the Sitkalidak Strait/Barren Island area (Amaral, 1977: Baird and Moe, 1978; Manuwal and Boersma, 1978), but sand lance were again the most important prey on Triangle Island (Vermeer, 1979). However, the bluethroat argentine (Nansenia candida) was utilized extensively on Triangle Island in 1978. Argentines, a deep-water species, may have become available because of strong upwelling during the summer of 1978 (Vermeer, 1979). The diet of Tufted chicks appears to consist primarily of Puffin schooling fishes such as Pacific sand lance, capelin and northern anchovy, but adults also are opportunistic and exploit most readily available food resources their young.

In conclusion, Tufted Puffins on Goat Island have shorter incubation periods, but slower growth rates and longer nestling periods than puffins on more northerly colonies. Growth rates and nestling periods also differed considerably between years; apparently the flexible growth pattern of Tufted Puffins has evolved to cope with fluctuations availability of food resource.

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APPENDICES

Appendix I. Plants from Goat Island, Curry County, Oregon.

Common Name

Scientific Name

Carnet weed Family ATTOACEAE

Carpet-weed Family Sea-fig or Ice-plant

Honeysuckle Family Black Twinberry

Pink Family
Beach Sandspurry
Red Sandspurry
Common Chickweed

Sunflower Family Yarrow Chilian or Common California Aster Chapparal Broom

Seaside Daisy Purple Cudweed Spotted Cats-ear or False Dandelion Hairy Lasthenia

Pineapple Weed
Coast Microseris
Tansy Ragwort
Common Groundsel
Milk-thistle
Goldenrod
Common Sow-thistle
Dune Tansy

Stonecrop Family
Sea-cliff Stonecrop
Broadleaf Stonecrop

Mustard Family Wartcress Wild Radish

Sedge Family Sedge

Heath Family Salal

AIZOACEAE Mesembryanthemum chilense

CAPRIFOLIACEAE Lonicera involucrata

CARYOPHYLLACEAE
Spergularia macrotheca
Spergularia rubra
Stelleria media

COMPOSITAE
Achillea millefolium
Aster chilensis

Barcharis pilularis
consanguinea
Erigeron glaucus
Gnaphalium purpureum
Hypochaeris radicata

Lasthenia minor

maritima

Matricaria matricarioides

Microseris bigelovii

Senecio jacobaea
Senecio vulgaris
Silybum marianum

Solidago sp.

Sonchus oleraceus

Tanacetum douglasii

CRASSULACEAE

<u>Dudleya</u> <u>farinosa</u>

<u>Sedum spathulifolium</u>

CRUCIFERAE
Coronopus
Raphanus sativus

CYPERACEAE Carex sp.

ERICACEAE

Gaultheria shallon

GARRYACEAE Silk-tassel Family Wavy-leaf Silk Tassel Garrya elliptica Geranium Family
Dove's-foot Geranium GERANIACEAE Geranium molle Grass Family GRAMINEAE Hall's Bentgrass Wild Oat Agrostis hallii Avena fatua Bromus carinatus mollis California Brome Soft Brome or Chess Calamagrostis nutkaensis
Elymus glaucus
Festuca bromoides Pacific Reedgrass Western Rye-grass Barren or Six-weeds Fescue Red Fescue Festuca rubra Holcus lanatus Velvet-grass Hordeum brachyantherum Lolium multiflorum Meadow Barley Italian Ryegrass Annual Bluegrass San Francisco Bluegrass Poa annua Poa unilateralis Waterleaf Family Tracy's Mist-maiden HYDROPHYLLACEAE Romanzoffia tracyi Iris Family IRIDACEAE Douglas' Iris Iris douglasiana oregonensis Pea Family LEGUMINOSAE Seashore Lupine Lupinus littoralis Trifolium wormskjoldii Springbank Clover Evening Primrose Family Watson's Willow-herb ONAGRACEAE Epilobium watsonii Plaintain Family English Plaintain Seaside Plaintain PLANTAGINACEAE Plantago lanceolata Plantago maritima Plumbago Family Sea Thrift PLUMBAGINACEAE Armeria maritima

Purslane Family PORTULACACEAE
Red Maids Calandrinia ciliosa menziesii

Phlox Family

Gilly-flower

Blue Field Gilia or Field

POLEMONIACEAE

Gilia capitata

Buckwheat Family Black Knotweed or Nailwort Polygonum paronychia Knotweed Sheep Sorrel or Sour Duck Curly Duck

Fern Family Leather-leaf Fern Sword-fern Bracken Fern

Rose Family Coastal or Chilean Strawberry Thimbleberry Salmonberry Pacific Blackberry

Saxifrage Family Large Fringe-cup

Figwort Family California Figwort

Parsley Family Sea-coast Angelica Pacific Hemlock-parsley Footsteps of Spring or Bear's-foot Snake-root

POLYGONACEAE

Rumex acetocella Rumex crispus

POLYPODIACEAE Polypodium scouleri Polystichum munitum Pteridium aquilinum pubescens

ROSEACEAE Fragaria chiloensis

Rubus parviflorus spectabilis ursinus

SAXIFRAGACEAE Tellima grandiflora

SCROPHULARIACEAE Scrophularia californica

UMBELLIFERAE Angelica hendersonii Conioselium chinense Sanicula arctopoides

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Appendix II. Food items collected on Goat Island in
1981.
Pacific Herring (Clupea harengus)
Length* Weight
              (gm)
  (mm)
 168
              32.9
 180
              46.2
 183
               40.8
Northern Anchovy
(Engraulis mordax)
Length
           Weight
 (mm)
              (gm)
  94
               2.1
 112
               6.4
 125
               11.3
 108
               7.2
 111
               6.7
 108
               7.2
 105
                5.9
Pacific Sand Lance
(Ammodytes hexapterus)
Length Weight
              (gm)
  (mm)
  86
               1.4
  86
               1.2
  82
                1.7
```

<sup>\*</sup> total length

Appendix III. Food items collected on Goat Island in 1982.

Pacific Herring Rex Sole (Clupea harengus) (Glyptocephalus zachirus)

Tucille ne	11119	NEX JUIC		
(Clupea ha	rengus)	(Glyptocephalus	zachirus)	
<u>Length</u> *	Weight	Length	Weight	
( m m )	(gm)	( m m )	(gm)	
160	32.7	**	0.16	
169	32.9	**	0.24	

Northern A	nchovy	Pacific Sand	dab ***
(Engraulis		(Citharichth	ys sordidus)
Length	Weight	Length	Weight
( mm )	(gm)	( m m )	(gm)
119	11.7	43	0.59
121	10.7	47	0.75
120	10.8	50	0.80
123	12.1	49	0.87
104	6.8	4 7	0.67
120	11.6	4 2	0.44
107	6.1	40	0.54
96	4.9	43	0.41
107	6.3	**	0.42
100	6.1	**	0.41
108	7.4	**	0.66
106	7.3		
114	9.3	Rockfish	
117	10.4	(Sebastes sp	p.)
104	6.6	Length	Weight
106	6.7	( mm )	(gm)
		4 7	.52

Pacific Sa	nd Lance		
(Ammodytes	hexapterus)	Squid	
Length	Weight	(Loligo	opalescens)
(mm)	(gm)	Length	Weight
Ì02	2.9	(mm)	(gm)
105	2.7	131	14.1
105	2.6	130	12.0
		110	8.0
		115	7.1

<sup>\*</sup> total length

<sup>\*\*</sup> partial specimen, length not determined

<sup>\*\*\*</sup> larvae

Appendix IV. Egg measurements, incubation and nestling periods plus weight data for Tufted Puffin chicks from Goat Island in 1981.

		EGG		INCU	BATION	FLE	DGING	СН	ICK WE	GHT	BOX NO.
	Wt. (gm)	Len. (mm)	Dia. (mm)		. Max. ays)					Max. (gm)	
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20	85 83 95 94 98 80 105 95 102 83 96 77 90 81 91 95 98 91 102 80	71.3 68.7 70.8 74.9 73.1 70.5 77.4 70.6 74.1 67.6 71.9 69.4 76.0 68.3 68.0 70.3 71.8 66.8 76.1	47.0 48.0 49.9 48.6 49.7 46.2 50.5 50.4 51.1 47.5 49.7 45.9 47.4 50.0 50.1 47.6	39 36 42 39 37 38 39 48 39 38 44 46 	47 40  46 47 42 46 47 ?? 46 43 48 39 53 	46 51 59 72 52 57 52 52 	54 56 63 75 55 61 59 57 	69 54 53 61 63 70 69 65 71 73 69 50 58 55 73	445 433 405 381 537 369 553 374 (199) (145) (50) (133) (55) (49)	519 466 467 399 544 389 574 450 (245) (145) (76) (50) (173) (55) (73)	1 6 14 17 30 36 38 40 2 4 13 16 21 24 27 10 15 18 30 33
\frac{1}{\tilde{X}}		71.3	48.8	(1) (2) (3)	0.0 42.4 4.8	(1) (2) (3)	ND 57.6 7.5	*63.5 7.9	437.1 72.0	476.0 65.9	

<sup>??</sup> Replacement egg

<sup>(1)</sup> Known

<sup>(2)</sup> Estimated (3) Combined

ND No Data

All chicks weighed within 3 days of hatching

Appendix V. Egg measurements, incubation and nestling periods plus weight data for Tufted Puffin chicks from Goat Island in 1982.

		EGG		INCU	BATION		DGING		CK WE		BOX NO.
	Wt. (gm)	Len. (mm)	Dia. (mm)	Min . (da		Min	. Max. ays)		Last (gm)	Max. (gm)	
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26	77 89 94 96 101 96 82 97 86 90 94 81 79 86 89 95 75 80 91 95	74.8 75.5 74.5 71.6 72.8 72.2 75.1 76.6 70.7 73.0 72.6 69.1 70.8 69.2 74.9 73.7 74.8 76.2 76.1 77.6	52.0 50.7 46.3 50.0 50.2 51.7 51.1 48.4 50.3 48.0 51.5 47.8 50.0 49.8 48.9 44.6 47.4 48.1 49.7 49.1	43 41 45 41 41 43 41 39 45 46 36 39 43 45 43 45 45 46 36 37 47 47 47 47 47 47 47 47 47 47 47 47 47	53 47 53  47 46  53 46 46 53 49 47 46 	46 46 39 50 53 49 52 46 	57 52 42  64  58 53    	111 101 *75 *80 74 260 99 *71 146 *76 79 94 *54 *563 *	567 415 512 618 363 532 527 610 (205) (300) (150) (150) (144) (150) (144) (63)	567 492 512 618 383 540 527 601 (205) (427) (150) (150) (150) (250) (63) 	2 5 8B 9 14 19 30 38 6 15 16 17 18 28 36 40B 1A 1B 3 11 12 21 24 39 40A 8A
X   S   X   S   X   S   S   S   S   S		73.0	49.3	(2)	43.0 2.0 45.1 4.7 44.9 4.5	(2)	49.5 .0.7 50.7 7.2 50.5 6.6			530.0 73.3	

<sup>\*</sup> Chicks weighed within 3 days of hatching
(1) Known
(2) Estimated
(3) Combined

Appendix VI. DDE and PCB contamination in Tufted Puffin eggs.

Sublethal accumulations of organochlorine pesticides and polychlorinated biphenyls (PCBs) have been implicated in the decline of reproductive success among some birds. DDE, a metabolite of the organochlorine pesticide, DDT was found to cause production of fragile thin-shelled eggs (Keith and Gruchy, 1972: Lincer, 1975: Pearce et al., 1979), many of which were broken during incubation. Predatory birds are particularly vulnerable because DDE accumulates and becomes more concentrated at higher trophic levels (Harrison et al, 1970). Experimental evidence indicates that PCBs also may be responsible for some reproductive failures (Dahlgren et al, 1972: Jensen, 1972; Risenbrough and Anderson, 1975); however, wild populations are frequently contaminated with both DDE and PCBs, thus confounding individual effects. decline in reproductive success becomes evident eggshell thinning approaches 20% (Keith and Gruchy, 1972; Hunt and Hunt, 1973; Lincer, 1975); 20% thinning has been associated with DDE contamination of 10-20 ppm (Pearce et al, 1979).

To determine if Tufted Puffin eggs from Goat Island were contaminated with DDE and/or PCBs, 5 Tufted Puffins eggs which failed to hatch were collected. The contents of these eggs were frozen in chemically clean glass bottles and shipped to the Patuxent Wildlife Research

Center for analysis. Residue levels were determined according to procedures described by Henny et al. (1982). Shell thickness is represented by the average of 3 measurements taken near the equator of the egg with a graduated micrometer (.01 mm). Representative shell thickness for eggs collected on Goat Island varied from .381 mm to .432 mm with a mean of .409  $\pm$ .021 (Table 10). DDE residues were found in all eggs, but PCB contamination was detected in only one (Table 11).

Compared with pre-1947 measurements, mean shell thickness for eggs from Goat Island declined 4.2%; however, this reduction was not significant. DDE and PCB residues were well below the levels where reproductive success has been reported to decline in other species of birds (Henny, pers. com.).

Table 10. Comparative values for thickness (mm) of Tufted Puffin eggshells.

Period	N	х	s	Change from Pre-1947	
Pre-1947 1949-53 1979 1982	23 5 3 5	.367	.042 .013 .016 .021	1.9% 14.1% 4.2%	Henny et al., 1982 Henny et al., 1982 Henny et al., 1982 This study

Table 11. Concentrations of DDE and PCBs found in Tufted Puffin eggs.

		(PPM	DDE wet wt.)	PCBs (PPM wet wt.)		
Site	N	X	Range	<del></del> X	Range	
Hinchinbrook Is.(a) Barren Is.(a) Kodiak Is.(a) Ugaiushak Is.(a) Semidi Is.(a) Shumagin Is.(a) Buldir Is.(a) Shaiak Is.(a)	10 8 10 3 7 6 2 6	.408 .287 .339 .205 .162 .368 .135	.2754 .0739 .1557 .1436 .0631 .1265 .1215	.625 .574 .533 .531 .263 .524 .395	.4685 .1486 .03 - 1.1 .10 - 1.9 .0356 .3878 .3940 .0682	
Haystack Rock(b) Goat Is.(c)	3 5	.620 .286	.6063 .2232	•510 *	.4855 *42	

<sup>(</sup>a) Ohlendorf et al., 1982(b) Henny et al., 1982(c) This studyDetected only once

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