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Puffins as samplers of juvenile pollock and other forage fish in the Gulf of Alaska

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ABSTRACT: We sampled the nestling diets of tufted puffins *Fratercula cirrhata* and horned puffins *F. corniculata* in 3 years at colonies from the north-central Gulf of Alaska to the eastern Aleutian Islands, Alaska, USA. Overall, tufted puffins consumed (by weight) 41 % sandlance *Ammodytes hexapterus*, 22 % capelin *Mallotus villosus*, 19 % walleye pollock *Theragra chalcogramma*, 13 % other fish, and 5 % invertebrates, whereas horned puffins took 85 % sandlance, 4 % capelin, 2 % pollock, 8 % other fish, and < 1 % invertebrates. All of the pollock consumed were young of the year, whereas 4 year-classes of capelin were present, from young of the year through spawning adults. Puffins took mostly first-year sandlance, but fish in their second year or older were also common at colonies near Kodiak, Alaska. The importance of juvenile pollock in the diet of tufted puffins varied geographically from little or no use in the north-central Gulf and Kodiak areas to moderate use (5 to 20 %) in the Semidi and Shumagin Islands to heavy use (25 to 75 %) in the Sandman Reefs and eastern Aleutians. An estimated 11 billion pollock were consumed by tufted puffins throughout the region in 1986. The proportion of pollock in puffin diets at the Semidi Islands was strongly correlated with independent estimates of cohort strength in 3 years. Puffins may thus provide a useful index of distribution and year-class abundance of first-year pollock, a species that currently supports an important commercial fishery in the Gulf of Alaska.

INTRODUCTION

Puffins feed mostly fish to their young, and they usually depend on one or a small number of prey species for the bulk of the chicks' diet. Not infrequently, those key prey species are also subject to commercial harvest by man, leading to potential conflicts between fisheries management and seabird conservation. For example, known or suspected conflicts have occurred involving Atlantic puffins *Fratercula arctica* and commercially exploited fish stocks such as herring *Clupea harengus* off northern Norway (Anker-Nilssen 1987, Barrett et al. 1987, Anker-Nilssen & Lorentsen 1990), sandlance *Ammodytes marinus* near the Shetland Islands, Scotland (Martin 1989), and capelin *Mallotus villosus* on the east coast of Canada (Nettleship 1991).

Capelin and Pacific sandlance *Ammodytes hexapterus* are important foods of puffins in Alaska (Wehle 1983, Hatch 1984, Baird 1990), but neither species is presently targeted by commercial fisheries. In contrast, walleye pollock *Theragra chalcogramma*, a species of considerable importance to puffins (see below), currently supports the world's largest single-species fishery, with annual landings exceeding 5 million metric t since the early 1980's (Lloyd & Davis 1989). A pollock fishery in the Gulf of Alaska developed rapidly after 1980, when a large spawning concentration was discovered in lower Shelikof Strait between Kodiak Island and the Alaska mainland (Fig. 1; Kendall et al. 1987). Spawning peaks in early April, and the southwesterly drift of eggs and larvae is such that juvenile pollock are potentially available to puffins and other seabirds along the Alaska Peninsula in midsummer (Kendall & Picquelle 1989, Hinckley et al. 1991).

We sampled puffins at colonies in this region over 3 years to determine patterns of prey use during the nestling period. The emphasis was on tufted puffins *Fratercula cirrhata*, but we also obtained material from horned puffins *F. corniculata* in 2 colonies. In this paper we document species, area, and annual variation in puffin nestling diets in the Gulf of Alaska, estimate

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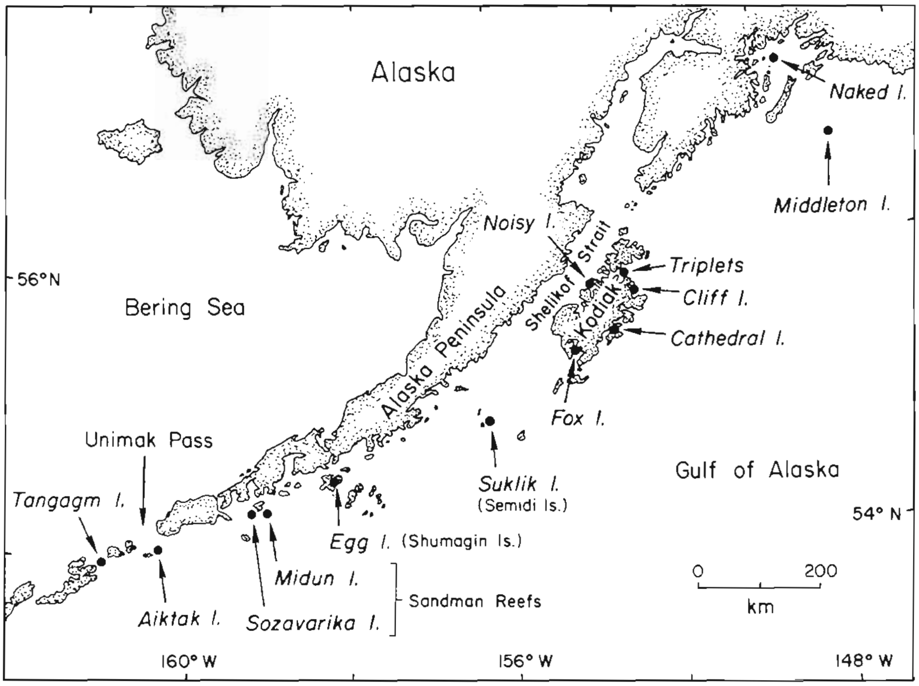

Fig. 1. Western Gulf of Alaska and eastern Aleutian Islands, indicating sampling sites for puffin diet studies and other locations mentioned in text

total consumption by puffins of juvenile pollock during the chick-rearing period, and evaluate whether the sampling of puffin diets is a useful method for estimating the year-class strength of walleye pollock.

METHODS

Between 1985 and 1987, we sampled the diets of nestling puffins in 13 colonies from Middleton Island, north-central Gulf of Alaska, to Tangagm Island in the Baby Islands near Unimak Pass (Fig. 1). Collections were limited in 1985 to Suklik Island (Semidi Islands), where both puffin species were available for sampling. The following year we visited Suklik and 11 additional colonies of tufted puffins. In 1987 we reduced the sampling scheme to emphasize sites in the region of heaviest pollock use in 1986.

Most sampling occurred over 2 to 3 wk from mid to late August (Table 1). Usually only 1 to 3 d were spent at a given colony each year, with 3 notable exceptions: Suklik Island in 1985 (10 d) and 1987 (29 d), and Aiktak Island in 1987 (9 d). Extended stays were used to document daily and seasonal variation in diet composition.

The principal method we used to collect chick meals was to block the entrances of puffin burrows to prevent food-carrying adults from entering. Many puffins returning to blocked burrows dropped their bill loads at the entrance. We made re-usable screens of galvanized hardware cloth (1.25 cm mesh), sized appropriately for tufted puffins (about 18 × 20 cm) or horned puffins (15 × 18 cm). The corners of a screen were pressed into the sod around a burrow entrance to make a firm barrier. Screened burrows were marked to aid in relocation. Food samples were collected and the screens removed after about 2 h. Since we could not be sure if a particular sample was a partial bill load, 1 full load, or more than 1 load, we refer to the samples as screen loads.

The usual procedure was to screen 50 to 200 burrow entrances at dawn, because puffins generally exhibit a morning peak in food deliveries (Corkhill 1973, Harris & Hislop 1978, Wehle 1983). Some sampling was done at other times of day to check for diurnal changes in diet composition. We tested for diurnal and seasonal variation in diet composition using 2-way ANOVAs on rank-transformed daily percentages of the major prey types. Thus, each factor (date or time) was controlled before testing the significance of the other. Times were grouped as forenoon or afternoon; the mean composition of each day's samples comprised a separate category of the factor 'date'.

The screen technique is effective for burrow-nesting species, but horned puffins usually nest in rock crevices. We were able to apply the method to both puffin species in this study because horned puffins used burrows extensively on 2 islands (Suklik Island and Sozavarika; Hatch & Hatch 1983). In addition to

Table 1. *Fratercula cirrhata, F. corniculata.* Sampling dates and sample sizes by colony

Location	Year	Sampling dates	Tufted puffin No. samples	Tufted puffin Total weight (g)	Horned puffin No. samples	Horned puffin Total weight (g)
Middleton I.	1986	2 Aug	3	23	–	–
	1987	3 Jul – 6 Aug	6	94	–	–
Naked I.	1986	13 Aug	2	11	–	–
The Triplets	1986	2 Aug; 2–3 Sep	32	260	–	–
Noisy I.	1986	11 Aug	12	74	–	–
Cliff I.	1986	4–5 Aug; 5–6 Sep	34	529	–	–
Cathedral I.	1986	29–31 Aug	39	384	–	–
Fox I.	1986	21–22 Aug	11	98	–	–
Suklik I.	1985	17–26 Aug	187	1455	131	1579
	1986	11–13 Aug	125	935	65	527
	1987	29 Jul – 26 Aug	310	1260	384	2009
Egg I.	1986	21–22 Aug	67	610	–	–
	1987	8–11 Aug	17	79	–	–
Midun I.	1986	24–25 Aug	106	716	–	–
	1987	14–17 Aug	54	374	–	–
Sozavarika I.	1987	18–20 Aug	16	118	39	223
Aiktak I.	1986	1–2 Sep	108	796	–	–
	1987	27 Aug – 5 Sep	335	2447	–	–
Tangagm I.	1986	30–31 Aug; 3 Sep	52	365	–	–

the screen loads, we collected a few bill loads from returning puffins that we startled and stray samples on the ground (Table 2).

All samples were washed, fixed in 5 % buffered formaldehyde solution for 12 to 24 h, then stored in 50 % isopropanol for later examination in the lab. A few individuals of common prey species were weighed and measured in the field to establish weight-length relationships in fresh material. Other samples were weighed fresh and reweighed in the lab to determine the effect of preservation. We found a mean change of −15 % in fish weights after preservation. Unless otherwise indicated, the data presented are preserved weights.

Prey were identified to the lowest possible taxon. Unidentified prey, and voucher specimens of species we tentatively identified were sent to taxonomic specialists at the Alaska Fisheries Science Center,

Table 2. Summary of return on sampling effort in puffin diet studies conducted in the Gulf of Alaska, 1985–1987

	Tufted puffin 1985	Tufted puffin 1986	Tufted puffin 1987	Tufted puffin All years	Horned puffin 1985	Horned puffin 1986	Horned puffin 1987	Horned puffin All years
Colonies visited	1	12	6	13	1	1	2	2
Samples obtained								
Screen	175	572	606	1353	55	62	340	457
Bill	12	5	0	17	64	0	0	64
Ground	0	14	132	146	12	3	83	98
Total	187	591	738	1516	131	65	423	619
Total prey items	1975	3923	3372	9270	1962	944	1829	4735
Prey species encountered								
Fish	6	15	27	32	5	5	13	13
Invertebrates[a]	3	4	7	7	1	0	2	2
Total sample weight (g)[b]	1455	4800	4371	10626	1579	527	2232	4338
Mean load size[c]								
Weight (g)	7.7	8.2	6.4	7.3	9.2	8.3	5.7	6.5
No. items	10.4	6.6	5.1	6.4	13.0	14.9	4.7	7.1
Mean prey species per sample	1.9	1.5	1.7	1.6	1.4	1.2	1.2	1.2

[a] Not all cephalopods were identified to species
[b] Preserved weights
[c] Screen samples only

National Marine Fisheries Service, Seattle, Washington, USA, for verification. Total lengths of individual prey were measured to the nearest mm; total samples and the portion of each prey type they contained were weighed to the nearest 0.1 g. To express the importance of a prey type from 1 site and year we used a pooled sample proportion – total weight of the prey divided by total weight of all samples collected. Where samples (n > 15) from different site-years are combined for comparisons, we used an unweighted mean of the proportions established for each site-year.

RESULTS

Diet composition – species, area, and year effects

Tufted puffins fed their chicks a greater variety of prey than horned puffins, the latter being primarily a sandlance feeder (Fig. 2). The difference was most pronounced on Suklik Island in 1985, when horned puffins fed 83 % sandlance to their chicks, whereas tufted puffins took 48 % sandlance and substantial quantities of several other fish species and invertebrates. In all, tufted puffins took 32 fish species and 7 kinds of invertebrates, including 2 species of polychaetes, 2 euphausiids, shrimp, octopus, and squid (Tables 2 & 3). We found 13 species of fish and 2 invertebrates (euphausiids and squid) in horned puffin food loads. The average screen load in both species weighed about 7 g and contained 6 to 7 prey items (Table 2).

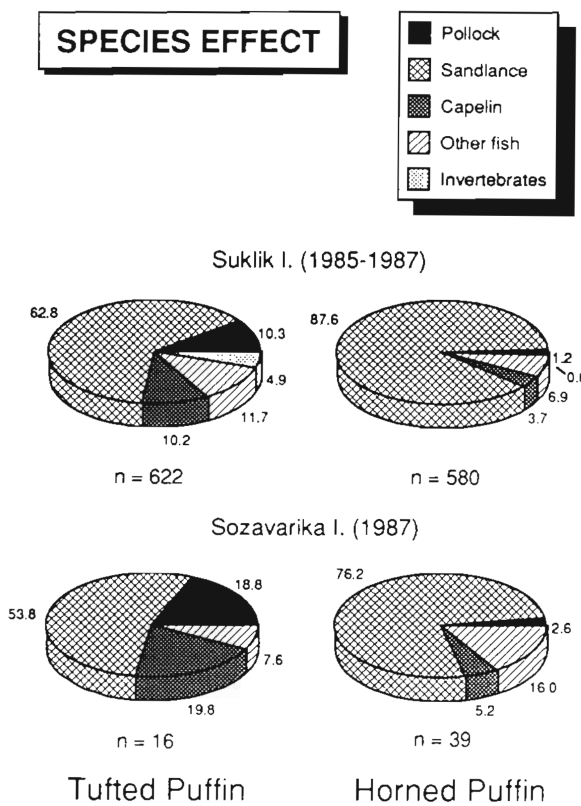

Fig. 2. *Fratercula cirrhata, F. corniculata.* Percent composition of tufted and horned puffin nestling diets at 2 colonies in the western Gulf of Alaska. Data from 3 yr on Suklik Island are pooled for comparison of species

The most important prey of tufted puffins were sandlance, capelin, and walleye pollock. The combination of those 3 species was a consistently high proportion (73 to 98 %) of the nestling diets sampled at 4 colonies in 2 yr (Table 4). The dominant prey species, however, differed markedly among sites (Fig. 3): sandlance at Suklik (Semidi Islands), capelin at Egg Island (Shumagin Islands), and pollock at Midun and Aiktak (Sandman Reefs and eastern Aleutians, respectively) (Fig. 3). The dominant prey species at a given colony was the same in different years, with the exception of Midun Island. Pollock was the major prey at Midun in 1986, whereas capelin predominated the following year (Table 4).

Sites northeast of the Semidi Islands were sampled less intensively, but our data indicate that sandlance and capelin were the main prey in 1986; pollock generally occurred in only trace amounts (Table 5). Because of small sample sizes from some colonies, pooled sample estimates are preferred for characterizing tufted puffin diets in the region.

Combining data from 4 colonies (Suklik, Egg, Midun, and Aiktak Islands) in 1986 and 1987, we found shifts in the relative amounts of sandlance, capelin, and pollock consumed by tufted puffins (Fig. 4). Although these 3 species comprised about 87 % of the diet in both years, the decrease in the proportion of pollock taken (20 % in 1987 versus 40 % in 1986) was compensated for by increased amounts of sandlance (10 %) and capelin (10 %).

Changes in the proportions of fish species at different colonies were not entirely concordant between years. Whereas sandlance increased in importance between 1986 and 1987 at Egg, Midun, and Aiktak Islands, they declined at Suklik Island in the Semidis (Table 4). Pollock declined at Midun and Aiktak between years but were relatively unchanged at the Semidis and Egg Island. Finally, capelin increased at 2 sites (Semidis and Midun Island), declined at 1 site (Egg Island), and remained unchanged at 1 site (Aiktak Island).

Composite results from different sites and years suggest there is an east to west gradient of increasing pollock consumption by puffins in the Gulf (Fig. 5)

Table 3. *Fratercula cirrhata, F. corniculata*. Overall occurrence, % weight and lengths of prey in nestling diets of tufted and horned puffins, Gulf of Alaska, 1985–1987

Species[a]	Tufted puffin						Horned puffin					
	Occurrence		% Weight[b]	Length (mm)			Occurrence		% Weight[b]	Length (mm)		
	Colony-yrs (n = 19)	% of samples[b]		Mean	(n)	Range	Colony-yrs (n = 4)	% of samples[b]		Mean	(n)	Range
Pacific sandlance *Ammodytes hexapterus*	18	53.1	41.3	72	(3530)	28–200	4	92.4	84.8	70	(3746)	25–164
Capelin *Mallotus villosus*	16	22.0	21.6	84	(445)	26–147	4	9.4	4.1	72	(91)	23–124
Walleye pollock *Theragra chalcogramma*	14	30.7	19.1	63	(1807)	33–112	4	6.8	1.6	58	(50)	34–82
Pacific cod *Gadus macrocephalus*	11	9.9	4.3	61	(203)	39–88	2	1.0	0.3	73	(1)	–
Prowfish *Zaprora silenus*	6	1.9	2.1	92	(32)	53–122	0	–	–	–	–	–
Squids (Gonatidae)	6	3.3	2.1	54	(75)	19–235	2	3.0	0.5	37	(22)	22–100
Pacific sandfish *Trichodon trichodon*	8	3.0	1.8	73	(32)	57–90	1	2.6	1.4	76	(4)	67–88
Rock/kelp greenlings *Hexagrammus* spp.[c]	6	2.5	1.4	66	(182)	43–82	3	11.8	6.1	70	(116)	35–107
Atka mackerel *Pleurogrammus monopterygius*	2	0.1	0.4	139	(2)	138–139	0	–	–	–	–	–
Euphausiids *Thysannoessa* spp.[d]	6	2.2	0.3	24	(338)	12–41	1	0.1	<0.1	31	(2)	29–33
Octopus (Octopoda)	8	1.3	0.3	38	(30)	16–54	0	–	–	–	–	–
Rockfishes *Sebastes* spp.[e]	4	0.6	0.1	37	(20)	23–57	1	0.3	<0.1	34	(5)	27–45
Flatfishes (Pleuronectidae)[f]	7	2.1	0.1	40	(18)	29–50	2	1.0	<0.1	44	(1)	–
Pacific herring *Clupea harengus*	1	0.3	<0.1	39	(22)	34–45	1	0.5	<0.1	39	(22)	31–43
Northern ronquil *Ronquilus jordoni*	1	<0.1	<0.1	31	(6)	27–35	0	–	–	–	–	–
Daubed shanny *Lumpenus maculatus*	1	<0.1	<0.1	73	(1)	–	0	–	–	–	–	–
Quillfish *Ptilichthys goodei*	2	<0.1	<0.1	156	(4)	153–160	0	–	–	–	–	–
Sablefish *Anoplopoma fimbria*	2	0.8	<0.1	83	(5)	44–110	2	0.5	0.2	61	(7)	39–98
Whitespotted greenling *Hexagrammos stelleri*	1	<0.1	<0.1	59	(1)	–	0	–	–	–	–	–
Lingcod *Ophiodon elongatus*	1	<0.1	<0.1	78	(1)	–	0	–	–	–	–	–
Sailfin sculpin *Nautichthys oculofasciatus*	1	<0.1	<0.1	29	(1)	–	0	–	–	–	–	–
Tadpole sculpin *Psychrolutes paradoxus*	2	<0.1	<0.1	33	(4)	24–56	0	–	–	–	–	–
Ribbed sculpin *Triglops pingeli*	2	0.1	<0.1	60	(3)	58–62	0	–	–	–	–	–
Smooth alligatorfish *Anoplagonus inermis*	1	<0.1	<0.1	108	(1)	–	0	–	–	–	–	–
Gray starsnout *Asterotheca alascana*	1	<0.1	<0.1	86	(1)	–	0	–	–	–	–	–
Pacific spiny lumpsucker *Eumicrotremus orbis*	1	<0.1	<0.1	26	(1)	–	0	–	–	–	–	–
Unid. smelt (Osmeridae)	1	0.1	<0.1	150	(1)	–	0	–	–	–	–	–
Unid. poacher (Agonidae)	1	<0.1	<0.1	–	–	–	0	–	–	–	–	–
Unid. prickleback (Stichaeidae)	1	<0.1	<0.1	58	(1)	–	0	–	–	–	–	–
Unid. lanternfish (Myctophidae)	1	<0.1	<0.1	–	–	–	0	–	–	–	–	–
Unid. salmon *Onchoryhnchus* sp.	1	<0.1	<0.1	117	(1)	–	0	–	–	–	–	–
Polychaetes (Polychaeta)	2	0.1	<0.1	36	(22)	23–64	0	–	–	–	–	–
Shrimp (Caridea)	2	<0.1	<0.1	46	(1)	–	0	–	–	–	–	–
Chum salmon *Onchorhynchus keta*	0	–	–	–	–	–	1	1.3	1.5	109	(2)	105–112
Sockeye salmon *Onchorhynchus nerka*	0	–	–	–	–	–	1	0.7	0.7	104	(1)	–

[a] Species listed in order of decreasing importance (% weight) in the diet of tufted puffins; fish nomenclature follows Hart (1973)
[b] Unweighted mean percentage of prey type across all colony-years
[c] Rock greenling *Hexagrammos lagocephalus* and kelp greenling *H. decagrammus* not consistently identified to species
[d] Includes *Thysannoessa inermis* and *T. spinifera*
[e] Includes black rockfish *Sebastes melanops* and an unidentified rockfish *Sebastes* sp.
[f] Includes 3 species not consistently identified to species: arrowtooth flounder *Atheresthes stomias*, rex sole *Glyptocephalus zachirus*, and flathead sole *Hippoglossoides elassodon*

Table 4. *Fratercula cirrhata*. Composition of tufted puffin nestling diets at 4 locations in the western Gulf of Alaska, 1986–1987

Colony, year	% Weight Sandlance	Pollock	Capelin	Other fish	Invertebrates	Sum of sandlance, pollock, capelin	No. samples	Total sample weight (g)
Suklik, 1986	84.3	5.2	2.2	7.3	1.0	91.7	125	935
Change (1986–1987)[a]	–[b]	ns	+[c]					
Suklik, 1987	56.0	5.1	19.7	9.8	9.4	80.8	310	1260
Egg, 1986	7.0	6.3	74.1	12.6	0	87.4	67	610
Change (1986–1987)[a]	+[b]	ns	–[d]					
Egg, 1987	34.5	0	63.1	0	2.4	97.6	17	79
Midun, 1986	2.6	70.2	15.2	11.8	0.2	88.0	106	716
Change (1986–1987)[a]	+[b]	–[b]	+[c]					
Midun, 1987	28.6	26.4	41.6	3.2	0.1	96.6	54	374
Aiktak, 1986	8.6	74.5	0	16.7	0.2	83.1	108	796
Change (1986–1987)[a]	+[b]	–[b]	ns					
Aiktak, 1987	27.6	45.3	0.4	18.9	7.8	73.3	335	2447

[a] '+' indicates increase between years, '–' indicates decrease
[b] $p < 0.001$; *t*-test of difference between 1986 and 1987 (comparing means of arcsine-transformed percentages of prey type per food load)
[c] Test performed as in footnote [b]: $p < 0.01$
[d] Test performed as in footnote [b]: $p < 0.05$
ns: not significant

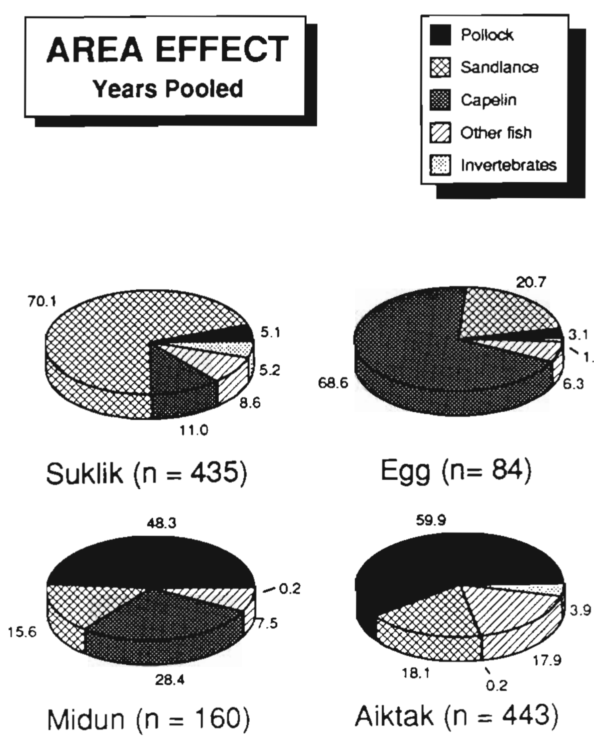

Fig. 3. *Fratercula cirrhata*. Percent composition of tufted puffin nestling diets at 4 colonies sampled in 2 years. Data from 1986 and 1987 are pooled for the comparison of sites

Time of day and seasonal effects

We examined data for tufted puffins from Suklik and Aiktak Islands in 1987 for evidence of diurnal and seasonal variation in diet composition (see 'Methods'). The proportion of sandlance showed significant daily variation at Suklik Island ($F_{23,274} = 1.58$, $p < 0.05$), as did sandlance ($F_{8,323} = 9.74$, $p < 0.001$) and pollock ($F_{8,323} = 4.99$, $p < 0.001$) at Aiktak. The only significant outcome for time of day was a higher proportion of capelin obtained in morning than afternoon hours on Suklik ($F_{1,274} = 6.28$, $p < 0.05$).

Correlations of sandlance, pollock, and capelin with calendar date at both sites were uniformly low (maximum $r^2 = 0.16$) and nonsignificant. Thus, although the composition of samples was subject to change from day to day, we found no evidence of seasonal trends in respective sampling periods of 10 and 29 d.

Lengths and age classes of prey

Puffins generally took fish in the size range of 30 to 150 mm (Table 3). Occasionally they delivered smaller prey such as larval capelin (25 to 40 mm) or euphausiids (12 to 41 mm). We found little difference between puffin species in prey lengths from samples collected in the same years and locations. Lengths of sandlance

Table 5. *Fratercula cirrhata*. Composition of tufted puffin nestling diets at 7 locations in the northern Gulf of Alaska and Kodiak archipelago in 1986

Prey species	% Weight							All areas (% weight)	
	Middleton	Naked	Triplets	Noisy	Cliff	Cathedral	Fox	Pooled samples	Mean percentage
Sandlance	94.4	0	53.2	32.5	40.1	84.5	42.6	55.3	49.6
Pollock	4.7	24.1	0	1.6	0	1.3	0	0.7	4.5
Capelin	0	0	37.0	35.1	57.7	1.1	16.9	32.5	21.1
Other fish	0.9	75.9[a]	9.7	6.3	2.3	12.6	40.6	10.1	21.2
Invertebrates	0	0	0.1	24.5	0	0.5	0	1.4	3.6
No. samples	3	2	32	12	34	39	11	133	
Total weight (g)	23.4	11.2	260.3	73.6	529.4	383.7	98.2	1379.8	

[a] Unidentified salmonid

taken at Sozavarika Island in 1987 were similar, as were sandlance, capelin, and greenlings (Hexagrammidae) taken at Suklik from 1985 to 1987. There was, however, a small difference in the lengths of pollock taken at Suklik (means of 55.4 mm in tufted puffins and 58.5 mm in horned puffins; $F_{1,469} = 4.70$, $p = 0.031$).

There were small but significant differences in the mean lengths of pollock in tufted puffin samples from different collection sites and years (range of means 51.6 to 70.6 mm; $F_{8,1783} = 122.83$, $p < 0.001$). Sample means varied more noticeably in sandlance (range of means 64.1 to 111.5 mm; $F_{12,7220} = 327.50$, $p < 0.001$) and capelin (range of means 66.6 to 126.1 mm; $F_{6,472} = 68.98$, $p < 0.001$). Mean pollock lengths were correlated with mean collection dates at 5 sites in 1986 and at 3 sites in 1987 (Fig. 6), suggesting the variation in that species could be explained by growth of individual pollock (see below).

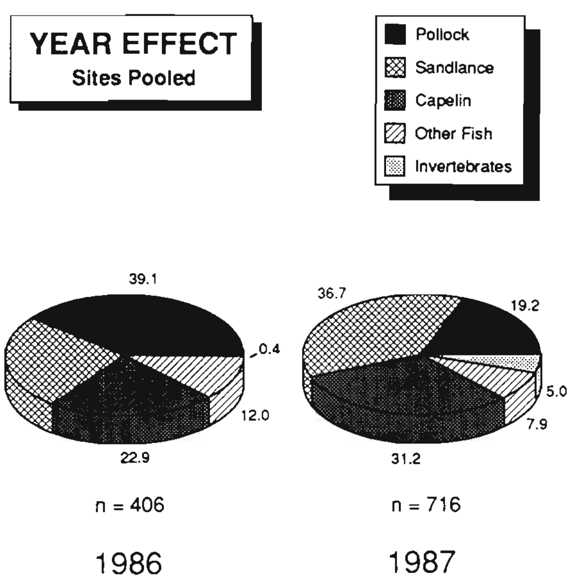

Fig. 4. *Fratercula cirrhata*. Percent composition of nestling diets during 2 years in the western Gulf of Alaska. Data from 4 sites (Suklik, Egg, Midun, Aiktak) are pooled for comparison of years

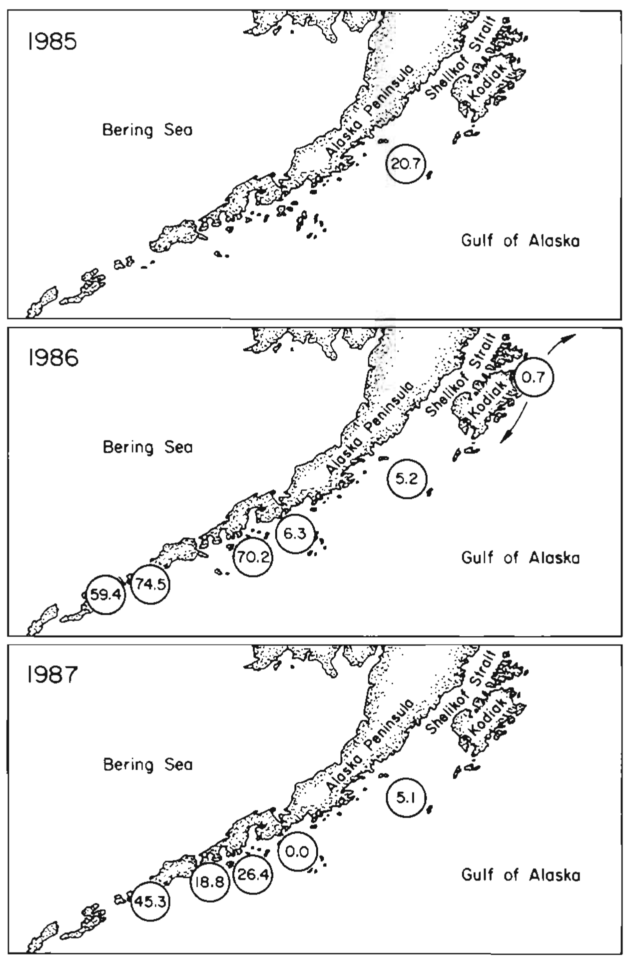

Fig. 5. *Theragra chalcogramma*, *Fratercula cirrhata*. Proportions of pollock in tufted puffin nestling diets, illustrating an east-west gradient of pollock use in the Gulf of Alaska

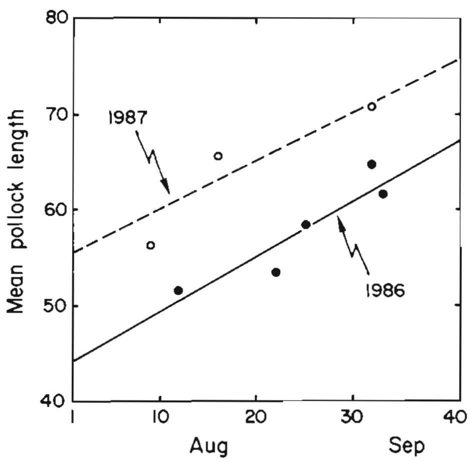

Fig. 6. *Theragra chalcograma*. Mean lengths of juvenile pollock in relation to mean sampling dates at puffin colonies in the Gulf of Alaska during 1986 and 1987

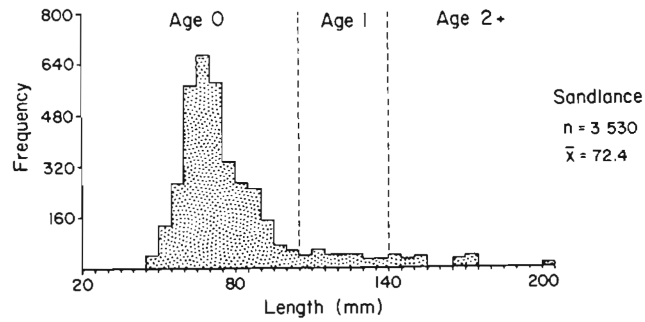

Fig. 8. *Ammodytes hexapterus*. Length-frequency distribution and age classes of Pacific sandlance in tufted puffin diets in the Gulf of Alaska. Combined data from 18 colony-years, 1985-1987. Age determinations based on age-at-length data in Dick & Warner (1982)

All pollock taken by puffins were Age 0 juveniles (Fig. 7). At least 3 age-classes of sandlance were present, although hatching-year juveniles far outnumbered older fish (Fig. 8). Four modes in the length-frequency distribution of capelin correspond to Ages 0 to 3 (Fig. 9). Capelin in Alaska become sexually mature at Age 2 or 3 (Pahlke 1985), so puffins fed extensively on adults as well as juveniles of that species.

Puffins in the Kodiak area (Cliff and Cathedral Islands and the Triplets) took older capelin and sandlance more frequently than those along the Alaska Peninsula (10 colonies from Suklik Island to Tangagm). The result was sharply contrasting age distributions of prey biomass. Whereas Age 1 or older fish made up 95% of the sandlance biomass delivered in Kodiak colonies, the largest component was Age 0 fish along the Alaska Peninsula (Fig. 10). Similarly, about 80% of the capelin biomass near Kodiak was Age 3 fish, while Age 2 capelin contributed most of the bulk in the other colonies we sampled (Fig. 11).

Pollock growth rates

Because all the pollock collected in a given year were of a single cohort (Age 0 juveniles), it is possible to estimate their daily growth increments. We used 2 methods, the first being a linear regression of area mean lengths and mean collection dates for sites visited in 1986 and 1987 (Fig. 6). This assumes that fish from all areas were hatched at the same time and that conditions for growth were similar throughout the region. Secondly, we computed regressions of daily mean lengths and calendar date for 2 sites with extended sampling periods (Suklik Island in 1985 and 1987, and Aiktak Island in 1987). Estimates from either method pertain to the size range of juvenile pollock taken by puffins, which may differ from the size distribution in the population at large. Five estimates of pollock growth ranged from 0.49 to 1.15 mm day^{-1}, the 2 highest values being the longitudinal estimates from Suklik (Table 6).

About 85 % of the variation in area mean lengths was explained by sampling date, consistent with the

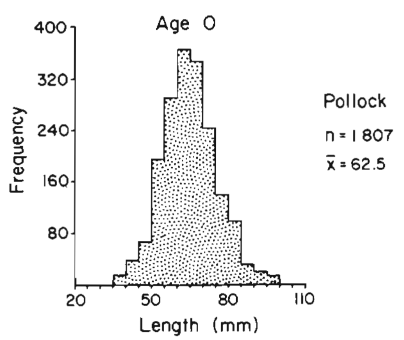

Fig. 7. *Theragra chalcogramma*. Length-frequency distribution of walleye pollock in tufted puffin diets in the Gulf of Alaska. Combined data from 14 colony-years, 1985-1987. Assignment of juvenile pollock to Age 0 group based on age-at-length data in Walline (1983)

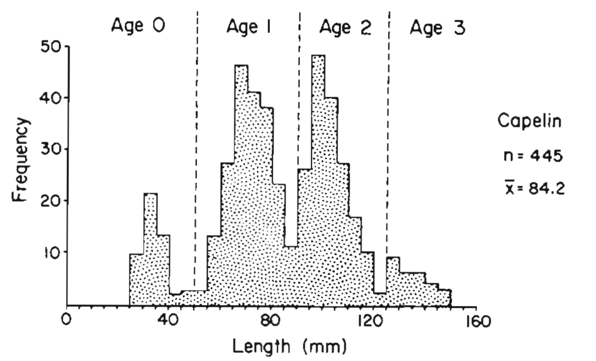

Fig. 9. *Mallotus villosus*. Length-frequency distribution and age classes of capelin in tufted puffin diets in the Gulf of Alaska. Combined data from 16 colony-years, 1985-1987. Age determination based on age-at-length data in Pahlke (1985)

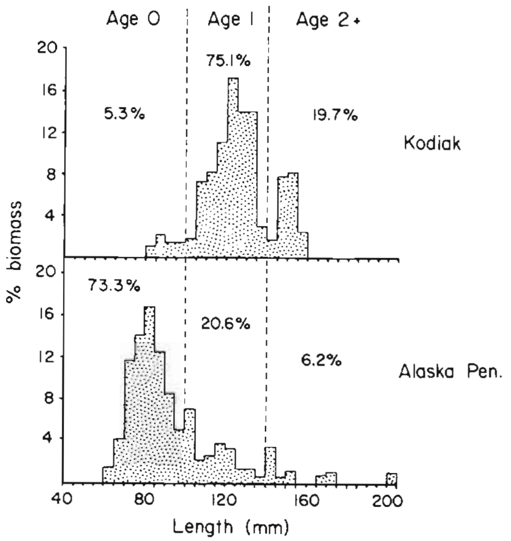

Fig. 10. *Ammodytes hexapterus*. Age distribution of sandlance biomass in tufted puffin diets compared between colonies near Kodiak and those along the Alaska Peninsula. Length-frequency data converted to biomass using weight-length relationships obtained from fresh specimens measured in this study [$W = 7.603\ L^{3.296} \times 10^{-7}$; W: weight (g); L: total length (mm)]

possibility that pollock from all areas comprised a unit stock. In an analysis of covariance, however, significant differences among areas remained after adjusting for calendar date ($F_{4,839} = 6.87$, $p < 0.001$ in 1986; $F_{2,590} = 5.66$, $p < 0.01$ in 1987).

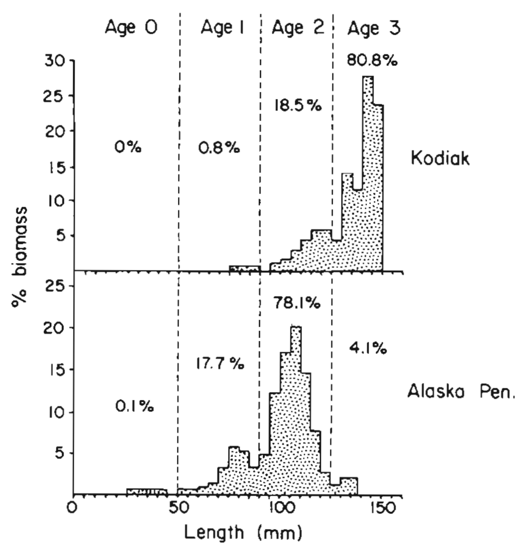

Fig. 11. *Mallotus villosus*. Age distribution of capelin biomass in tufted puffin diets compared between colonies near Kodiak and those along the Alaska Peninsula. Length-frequency data converted to biomass using weight-length relationships obtained from fresh specimens measured in this study [$W = 4.024 L^{3.522} \times 10^{-7}$; W: weight (g); L: total length (mm)]

Estimating pollock consumption by puffins

To estimate pollock consumption by tufted puffins during chick-rearing in the Gulf, we divided the region into areas of light, moderate, and heavy pollock use (Fig. 12). Area 1 includes colonies from the north-central Gulf and Prince William Sound through the Kodiak archipelago. Area 2 is bounded approximately by the Semidi Islands and Shumagin Islands, and Area 3, with the heaviest pollock use and largest puffin population, extends from the Sandman Reefs through the eastern Aleutians.

Our calculation of pollock consumption rests on the following assumptions: (1) The diets of adult and nestling puffins during chick rearing are the same. (2) The composition of the diet is constant over the whole chick-rearing period, which in the Gulf of Alaska lasts about 60 d from mid July to mid September. (3) An adult puffin weighs 775 g (Wehle 1980) and has a daily energy requirement consistent with the allometric equation for cold water seabirds using flapping flight (Birt-Friesen et al. 1989): $\log y = 3.24 + 0.727 \log x$, where y = field metabolic rate (kJ d^{-1}) and x = body mass (g). We computed mean energy densities of puffin diets by area using summer values for capelin (4.9 kJ g^{-1}), lesser sandlance *Ammodytes marinus* (4.9 kJ g^{-1}), and whiting *Merlangius merlangus*, an Atlantic gadoid, (4.0 kJ g^{-1}) (Montevecchi & Piatt 1984, Hislop et al. 1991). (4) A tufted puffin chick consumes 6400 g of food from hatching to fledging. The estimate is based on food consumption (3634 g) by young Atlantic puffins adjusted for the larger size of tufted puffin chicks (496 g vs 284 g at fledging; Harris 1978, Wehle 1980). (5) On average, about 80 % of the puffins in Alaskan colonies produce eggs, mean hatching success is 64 %, and fledging success averages 74 % (Byrd et al. in press).

Data on pollock use in all 3 areas are available from 1986. The calculations for Area 3 are summarized in Figure 13. We use a value of 68 % pollock in the puffins' diet, which is the mean percentage observed at 3 colonies in the area (Midun, Aiktak, and Tangagm). About 25 000 metric t of food were consumed in Area 3 over the chick-rearing period, of which about 17 600 metric t were pollock. Based on the mean fresh weight of individual pollock observed in this study (1.6 g), that is equivalent to 10.7×10^9 juvenile pollock removed by puffins. Similar calculations for Area 1 (1 % dietary pollock; Table 5) and Area 2 (6 % pollock observed at Suklik and Egg Islands in 1986) give respective estimates of 84 metric t and 440 metric t of pollock consumed from mid July to mid September. Total pollock mortality from tufted puffin predation throughout the Gulf is estimated at 11.0 billion juveniles.

Table 6. *Theragra chalcogramma*. Growth rate estimates for Age 0 pollock in the Gulf of Alaska, 1985-1987

Year	Dates	Regression estimates				Method
		Slope (mm d^{-1})	n	r^2	p <	
1985	17 Aug - 26 Aug	1.15	400 fish	0.09	0.000	Suklik I. longitudinal estimate
1986	12 Aug - 2 Sep	0.59	5 sites	0.86	0.02	Regression of area mean lengths
1987	31 Jul - 26 Aug	1.09	43 fish	0.21	0.002	Suklik I. longitudinal estimate
1987	27 Aug - 5 Sep	0.49	492 fish	0.03	0.000	Aiktak I. longitudinal estimate
1987	9 Aug - 1 Sep	0.58	3 sites	0.85	0.25	Regression of area mean lengths

Predicting pollock year-class strength

The proportion of pollock in tufted puffin diets at the Semidi Islands was relatively high (21 %) in 1985 and low (5 %) in 1986 and 1987. Trawl surveys for young of the year conducted by the National Marine Fisheries Service in September 1985-1987 provide similar estimates of relative cohort size (Table 7). There is agreement as well with the results of a 1989 bottom trawl survey indicating the relative abundance of fish aged 2 to 4 yr. Finally, there is close correspondence with model estimates of pollock cohort size based on survey results and information on fishing mortality (Hollowed & Megrey 1990). Models give different estimates of absolute abundance depending on the type of survey data (hydroacoustic or bottom trawl) used for calibration. In either case, the relative measures of fishable stock size were accurately predicted by puffin diets at the Semidis.

DISCUSSION

Variation in puffin nestling diets can be interpreted from both the avian and fisheries points of view. From the standpoint of puffin ecology, differences among colonies in the age composition of prey are noteworthy because of the fluctuations in cohort size that occur in fishes like capelin and sandlance (Hart 1974, May 1974). We sampled colonies around Kodiak in 1 year only, but an earlier study (Baird 1990) also showed a prevalance of older sandlance and capelin at Cathedral Island in 1977 and 1978. If that pattern is typical, it implies that a strong or weak year-class of prey would potentially affect all colonies, but not in the same years. As a corollary, one would expect puffin colonies with a greater variety of species and age groups of prey available to show less variability in chick-rearing success than those with a simpler prey base. The difference between puffin species - tufted puffins

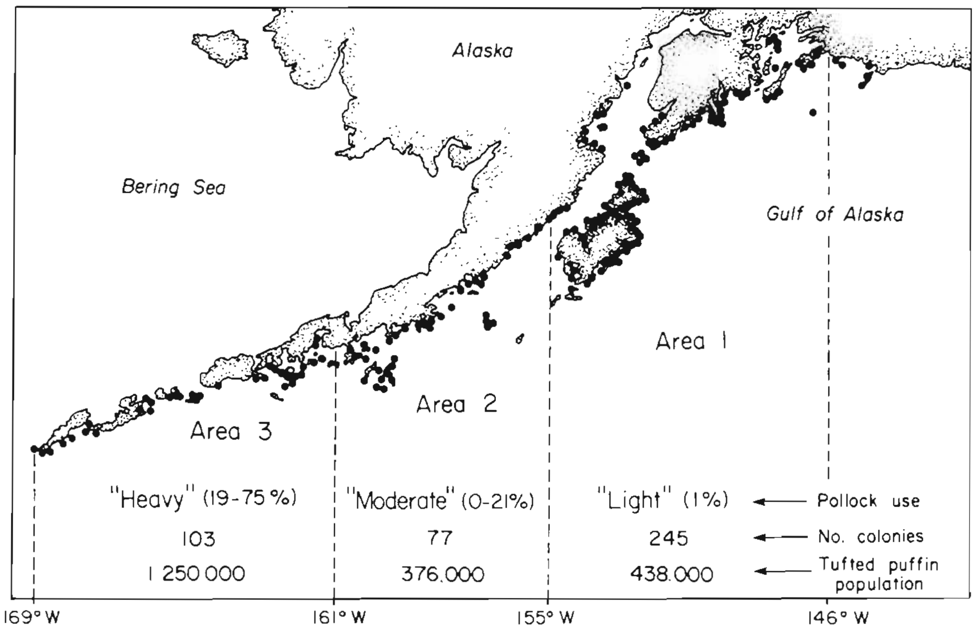

Fig. 12. *Fratercula cirrhata, Theragra chalcogramma*. Distribution of colonies, abundance, and pollock use by tufted puffins in the western Gulf of Alaska. Information on puffin numbers from Sowls et al. (1978) and unpubl. data of the U.S. Fish and Wildlife Service

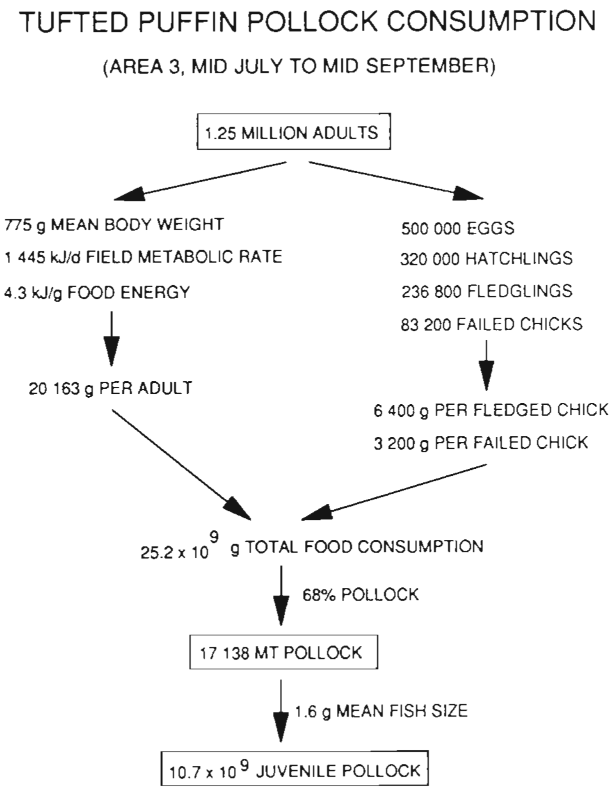

Fig. 13. *Fratercula cirrhata, Theragra chalcogramma.* Computation of pollock consumption during chick rearing by tufted puffins in 1986, Area 3 – Sandman Reefs through the eastern Aleutians. Chicks that fail are assumed to eat half the food supplied over a 46 d fledging period

taking a greater variety of prey, including invertebrates, and horned puffins specializing on forage fish – implies that tufted puffins may be similarly buffered against changes in prey resources.

The energy densities of different prey also have implications for puffin breeding biology. Pollock and other gadids typically have lower calorific values than fattier fish such as capelin and sandlance (Perez 1990, Hislop et al. 1991). Other factors being equal, puffins in colonies that rely on pollock would have to work harder to deliver a given amount of energy to their young. That possibility is consistent with intercolony differences in diet and field metabolic rates in other avian piscivores (Montevecchi & Barrett 1987) and planktovores (Montevecchi et al. in press).

The interactions between seabirds and commercial fishing are usually considered by asking (a) whether fisheries adversely affect seabirds through competition for a common prey resource, (b) whether seabirds remove a significant portion of potentially harvestable fish stocks, and/or (c) whether seabirds can furnish information of use to fishery managers. As for (a), there are several affirmative examples worldwide (Schaefer 1970, Crawford & Shelton 1978, Barrett et al. 1987, Vader et al. 1990), but puffins are probably not threatened by pollock fisheries in Alaska for 3 reasons. First, our information indicates that puffins eat only juvenile pollock, which are not harvested. Second, adult pollock are consumers of juvenile pollock (Dwyer et al. 1987) and also eat other seabird prey such as capelin and sandlance (Straty & Haight 1979). Finally, the spawner-recruit relationship for pollock may be inverse over a wide range of adult pollock densities (Hollowed & Megrey 1990). Short of a severe depletion of spawning females, then, the fishery could benefit puffins by removing potential competitors for juvenile pollock and other forage fish.

We estimated that puffins consumed about 11 billion pollock during chick-rearing in the Gulf of Alaska and eastern Aleutians in 1986. That is possibly an overestimate because it assumes there were similar proportions of pollock in adult and chick diets and that pollock use was constant from mid July to mid September. Although we detected no trends during extended visits to Suklik Island and Aiktak Island in 1987, seasonal shifts in prey use have been noted in other studies of puffin chick feeding (e.g. Hatch 1984, Vermeer & Westrheim 1984).

The amount of predation attributable to puffins may or may not be substantial in relation to other sources of

Table 7. *Theragra chalcogramma.* Estimates of pollock year-class strength for the Gulf of Alaska, 1985-1987[a]

Year-class	Tufted puffin diet Semidi Is. (% weight)	Fall Y-O-Y survey (abundance index, $\times 10^9$)[b]	1989 bottom trawl survey (% at age)[c]	Stock synthesis model estimates ($\times 10^9$)[c]	
				Model A[d]	Model B[e]
1985	20.7 (0.668)	22.1 (0.580)	21.4 (0.686)	2.010 (0.707)	0.589 (0.738)
1986	5.2 (0.168)	6.2 (0.163)	4.2 (0.135)	0.426 (0.150)	0.120 (0.150)
1987	5.1 (0.165)	9.7 (0.257)	5.6 (0.179)	0.406 (0.143)	0.089 (0.112)

[a] Standardized values in parentheses obtained by dividing each measurement by its respective column total
[b] Young of the year (Y-O-Y) survey data from Bailey & Spring (in press)
[c] From Hollowed & Megrey (1990)
[d] Model emphasis on bottom trawl survey results
[e] Model emphasis on hydroacoustic survey results

juvenile pollock mortality. For perspective, it is estimated that 400 billion juveniles are consumed annually by adult pollock in the eastern Bering Sea (Dwyer et al. 1987). Predation by puffins is perhaps of greater relative importance in the Gulf of Alaska, where there are fewer pollock and lower rates of cannibalism (Hollowed & Megrey 1990). As a rough estimate, puffins may remove about one-tenth of the Age 0 stock existing in the Gulf during early July, or 10 times the number of fish surviving the following March (Fig. 14). There are indications that puffins in winter continue to prey on juvenile pollock, and that other seabirds are also consumers of pollock in summer and fall (J. F. Piatt unpubl.). In the aggregate, seabirds may thus have a considerable influence on the early life history of pollock in the Gulf. In a comparable system, cormorants *Phalacrocorax carbo* and shags *P. aristotelis* were found to be a possible limiting factor for the recruitment of cod *Gadus morhua* into severely reduced but commercially important stocks in the Norwegian and Barents Seas (Barrett et al. 1990).

The use of seabirds as indicators of fish stocks is frequently suggested (Anderson et al. 1980, Sunada et al. 1981, Crawford et al. 1983, Cairns 1987, Montevecchi & Berruti 1991) but difficult to carry beyond the conceptual stage (Berruti 1985). We are optimistic that puffins can provide useful information on walleye pollock in at least 3 categories – the regional distribution of late summer juveniles, daily growth increments, and early indications of year-class strength. Because puffin colonies are numerous throughout the Gulf (Fig. 12), there is no shortage of sampling sites to choose for monitoring the spatial distribution of juvenile pollock. By mid July, the emergence of schooling behavior makes it difficult to monitor juvenile fish by conventional acoustic or net sampling methods (Hinckley et al. 1991). In contrast, puffins appear to be effective samplers at this stage, and indeed may not begin to exploit pollock until they aggregate in schools. Genetic studies of the pollock delivered by puffins in different colonies could help in discriminating spawning stocks and delineating their nursery areas.

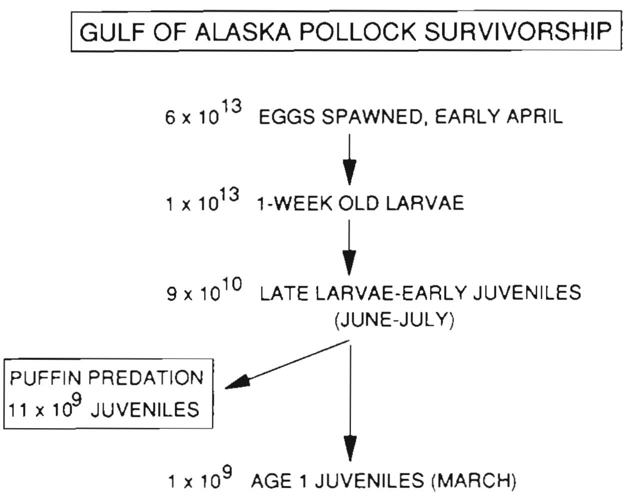

Fig. 14. *Theragra chalcogramma*. Relative role of puffin predation in the early life history of walleye pollock in the Gulf of Alaska. Estimates of pollock abundance, which pertain to the spawning stock of Shelikof Strait, are from Kendall & Incze (unpubl.) and Hinckley et al. (1991)

We have greater confidence in our estimates of pollock growth from fixed locations than those based on multiple sites (Table 6). Both values from Suklik Island (1.09 and 1.15 mm day^{-1}) are considerably higher than any reported by Walline (1983) for Alaskan pollock in 4 years, 1978 through 1981 (range 0.34 to 0.69, mean 0.55 mm day^{-1} from hatching to 25 to 100 mm standard length). Our values, of course, do not incorporate the slower growth that occurs in the larval stage. For age-specific measures of growth, repeated sampling of pollock in puffin food loads from one location would seem to be a valid technique that avoids the tedious determination of daily growth increments in otoliths (Walline 1983).

The heaviest use of pollock was in the westernmost colonies, which are downstream from the Shelikof Strait spawning area and may be drawing from the juvenile stock produced there. Recent surveys have indicated the nursery area for late larval and early juvenile Shelikof pollock (June-July) is primarily between the Semidi and Shumagin Islands and that older juveniles (August-September) are abundant west of the Shumagins in some years (Hinckley et al. 1991). It is possible, however, that pollock taken in the area from the Sandman Reefs to Unimak Pass arise from other spawning aggregations, smaller than the Shelikof stock but locally important to puffins. For example, a sizeable spawning stock was discovered recently on the Davidson Bank, south of Unimak Pass (V.G. Westpestad pers. comm.).

Our provisional test of puffin diets as an indicator of juvenile pollock abundance uses data from the Semidi Islands, the only site visited in all 3 years. The Semidis are thought to be within the main nursery area for pollock produced in Shelikof Strait, and estimates of seasonal pollock abundance are available from recent fishery research in the area (Kendall et al. 1987, Kendall & Picquelle 1989, Schumacher & Kendall 1989, Hinckley et al. 1991).

The apparent correlation of year-class strength and pollock deliveries by puffins at the Semidis is encouraging, but further study is needed to show whether puffin diets can provide a reliable index of Age 0 pollock abundance. The relationship would not necessarily be expected. If puffins take prey in proportion to

their relative abundances, a decrease in pollock could signal either a decline in the absolute abundance of that species or an increase of alternative prey such as capelin or sandlance. Preferential feeding by puffins over a range of prey densities might further complicate the problem of inferring prey dynamics (Berruti 1985, Piatt 1987). Some of those potential problems could be overcome by quantifying rates of food delivery as well as diet composition (e.g. Ashcroft 1979). The time frame for sampling afforded by puffins is good because Bailey & Spring (in press) found that of 2 alternative abundance indices they examined (larvae and Age 0 juveniles) the cohort strength of first-year pollock in late summer was most effective for predicting recruitment at Age 2.

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