

OPTIMAL FORAGING AND INTRASPECIFIC COMPETITION IN THE TUFTED PUFFIN¹

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Abstract. Diets of Tufted Puffin (*Fratercula cirrhata*) chicks and breeding and nonbreeding adults were compared between two years during the breeding season at Kodiak Island, Alaska. Fish dominated the diet of all groups. Nonbreeders ate more invertebrates than did breeders, and chicks were fed the lowest proportion of invertebrates of any group. Nonbreeders consumed more pelagic prey (e.g., cephalopods, euphausiids), than did breeders, which ate more inshore prey (osmerids, ammodytids). Chicks were fed the largest prey and prey with highest protein and energy values. These data are consistent with central place foraging and optimal foraging theory.

Key words: *Tufted Puffins; seabirds; feeding ecology; central place foraging; optimal foraging; Alaska.*

INTRODUCTION

Differences in diets between seabird chicks and adults have been widely documented from the Arctic to the Antarctic (e.g., Bédard 1969; Nettleship 1970; Sealy 1975; Croxall and Prince 1980; Vermeer 1980; Hunt et al. 1981a, 1981b; Baird and Gould 1983) and are believed to be related to differences in energetic and nutrient demands of birds of different ages and reproductive status (Belopol'skii 1961), and to the costs and benefits due to the constraints of central place foraging (Orians and Pearson 1979, Schoener 1979, Krebs et al. 1983, Houston 1987).

High quality packages of food (e.g., large prey, high in protein or energy) are often fed to chicks, and breeding adults may eat less nutritious prey (e.g., smaller fish or invertebrates; Belopol'skii 1961; Lind 1965; Royama 1966, 1970; Orians and Pearson 1979; Schoener 1979; Croxall and Prince 1980; Power 1980; Hergluson 1982; Krebs et al. 1983). This differential feeding may be absent in birds which feed their chicks by regurgitation. However, adult foraging behaviors differ depending on whether or not nestlings are present (Lind 1965; Royama 1966, 1970).

Breeding and nonbreeding adults might also consume different prey species or different proportions of other species (Ricklefs 1983), because breeders are limited by distance con-

straints of central place foraging. Prey may become scarce near large colonies of seabirds (Ashmole 1963; Goodman 1974; Stearns 1976, 1977; Furness and Birkhead 1984; Hunt et al. 1986; Birt et al. 1987), and when this happens, nonbreeders have the option of foraging in other areas where food might be more plentiful.

In many dietary studies, prey fed to chicks or consumed by adults have been compared using food collected at different times or in different areas (e.g., Corkhill 1973, Amaral 1977, Wehle 1978, Ainley and Sanger 1979, Springer et al. 1984). As some of these authors have pointed out, this could lead to invalid conclusions about differences in diets among species. To investigate resource partitioning and the basis of this partitioning among species within their entire annual cycle, prey of nonbreeding and breeding adults and chicks must be compared in the same general area over the same time period.

Alaska has a diverse seabird fauna, often concentrated in dense colonies, and nonbreeders often feed alongside breeders (Sanger and Baird 1977a, 1977b; Krasnow and Sanger 1982; Baird and Gould 1983; Baird, unpubl. data). These conditions are ideal to study both resource partitioning and optimal foraging theory by observing food brought to chicks as well as food eaten by breeders and nonbreeders. Tufted Puffins (*Fratercula cirrhata*), numerous and widespread in Alaska (Sowls et al. 1979, Baird and Gould 1983), are ideal birds for such investigations because nonbreeders and breeders alike often feed together (Krasnow and Sanger 1982, Baird and Gould 1983). Likewise, the chicks' food is car-

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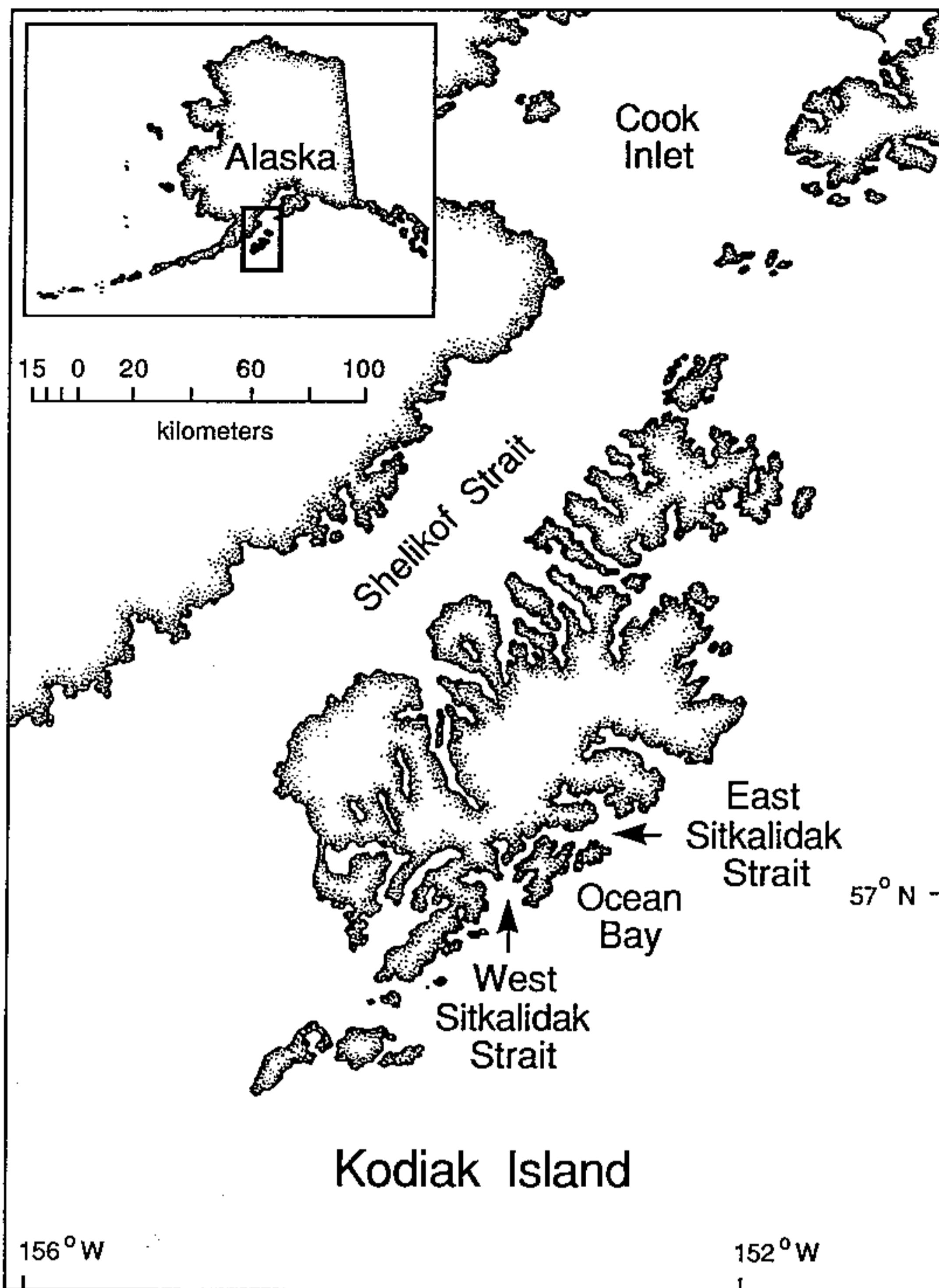


FIGURE 1. Sitkalidak Strait area of Kodiak Island.

ried back to the colonies in the adults' bills and can easily be distinguished from adult food contained in the stomach.

In this study I report diets of Tufted Puffin chicks, breeders, and nonbreeders gathered over the same time period (June–September) and in the same place (Southeast Kodiak Island). I suggest that diet differences found among these groups may be explained by lack of constraints imposed by central place foraging for nonbreeders, and by breeders providing food of high quality to chicks.

METHODS

I studied diets of Tufted Puffins at southeast Kodiak Island in the Gulf of Alaska (Fig. 1), collecting prey from nonbreeding and breeding adults, and from chicks throughout the breeding season from June to September, in 1977 and 1978. The Sitkalidak Strait and southeast Kodiak area in particular have rich feeding grounds (Krasnow and Sanger 1982, Sanger 1983), and Tufted Puffins are one of the most common species there (ca. 10,000 birds; Baird and Moe 1978). I collected prey from puffin groups at the following locations: (1) on the breeding colonies and

just offshore for adults and chicks, and (2) in bays, fjords, and at the distal, more pelagically influenced end-points of the strait for adults.

Adult puffins were shot as they fed. Adult breeders and nonbreeders could not be distinguished by sight. However, after collection I identified breeding birds as those having testes or ovary in breeding condition, or brood patches, or those carrying fish.

Food fed to chicks was collected by taping chicks' bills and retrieving food placed in the burrow (Baird 1986). Food samples from adults were collected regularly every three days over the entire breeding period. Chick food was collected every three days during the chick stage, which lasted approximately 50 days. Thus prey was collected at approximately the same time period for all groups ("simultaneous" collection).

Stomachs of collected adults and prey of chicks were preserved immediately in 10% formalin. Prey were subsequently sorted to lowest taxon, weighed, and measured. It has been strongly suggested that more than one method of analysis of food eaten should be used in order to obtain a complete picture of the diet of the group or species being studied (Hartley 1948, Reintjes and King 1953, Ashmole and Ashmole 1967). This multiple analysis is especially necessary if the feeding ecology of different species (or in this case different life stages or conditions of the same species) are being studied (Ashmole and Ashmole 1967).

Therefore, I analyzed diets among all bird groups using five different parameters. Each of these methods provides indications of different aspects of the feeding ecology of the different puffin groups (Ashmole and Ashmole 1967). *Weights* and *lengths* of prey were the two easiest and most direct measurements, and these parameters give estimates of biomass and age class of prey. Prey weights were taken directly from wet weights of whole specimens or estimated from conversion tables (Springer et al. 1984). Proportional masses of prey were determined by the method of Zaret and Rand (1971). Length of portions of fish was extrapolated from parasphenoid bone or vertebral column lengths (Baird, unpubl. data). Details of prey measurements, identification, and extrapolation equations appear in Appendix I.

I further compared prey using *frequency of occurrence* and *relative percent numbers* of prey. Frequency of occurrence (a measure of the reli-

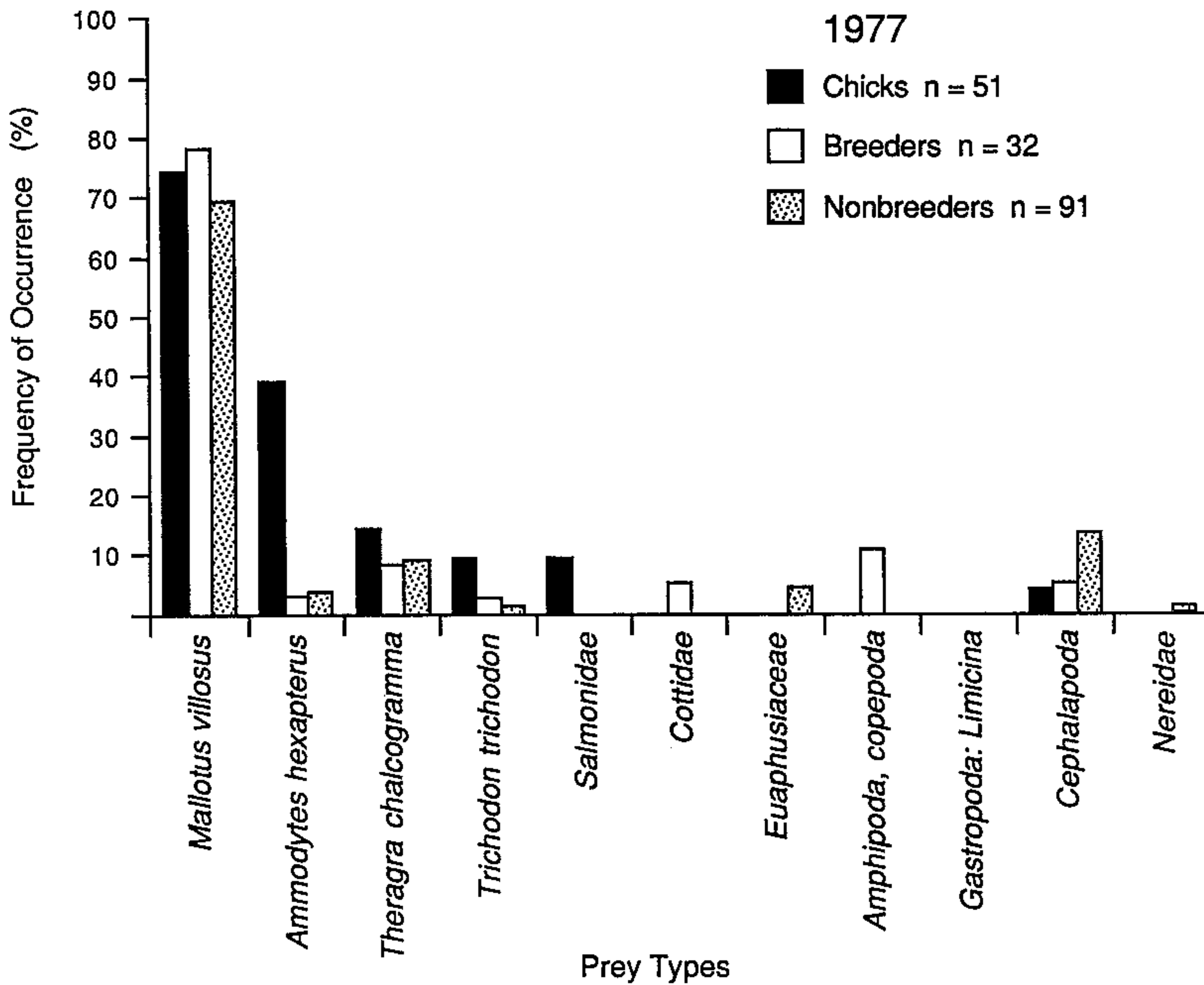


FIGURE 2. Frequency of occurrence of prey in Tufted Puffin groups, 1977.

ability or consistency of a food source throughout the season) is the proportion of samples in which a certain prey item is found. Relative percent numbers of prey is the number of items from a given taxon divided by the total numbers for all taxa. This measure will detect surges in temporal abundance of prey.

The combination of prey numbers, weight and length can provide gross estimates of energy or biomass available per meal. The additional knowledge of prey species and their respective body composition gives a crude index of energy, protein and fat composition for the prey items of each group (Hunt 1972, Harris and Hislop 1978, Sidwell 1979, Montevecchi and Piatt 1984). I used this index because bomb calorimetry was unavailable. The merits of each of these measurements are further discussed in Ashmole and Ashmole (1967) and in Diamond (1983).

RESULTS

Because the 1977 and 1978 breeding seasons were very different with respect to prey types taken, as well as with respect to reproductive success (Baird and Moe 1978, Baird 1979, Baird and Gould 1983, Baird 1990), I analyzed each year separately. Any inter-year differences are discussed in detail elsewhere (Baird 1979, 1990).

Fish were the most important prey group with respect to numbers, frequency, and mass for all puffin groups. Chicks were fed fish at every meal and they consumed the greatest proportion and biomass of fish among all puffin groups.

Frequency of occurrence per meal. Frequency of occurrence of prey items per stomach or bill load differed significantly among the three puffin groups in 1977 ($\chi^2 = 80.8$, $df = 18$, $P < 0.005$, Fig. 2), but not in 1978 ($\chi^2 = 32.8$, $df = 24$, $P < 0.1$, Fig. 3). The lack of significant differences in 1978 was due to the similarity of the diets of breeders and nonbreeders. (*A. posteriori* paired-sample tests showed highly significant differences within each pair group in 1977 [$P < 0.005$ to $P < 0.001$], but only significant differences between chicks and each adult group in 1978 [$P < 0.05$]).

In 1977, four species of fish were most frequent in meals of all groups, with capelin, *Mallotus villosus*, found in 70–80% of all meals. Sandlance, *Ammodytes hexapterus* were only frequent in chicks' meals. In 1978, capelin occurred less frequently and sandlance increased in frequency for all groups.

In 1977, nonbreeders' meals consisted of more invertebrates than did breeders' meals and contained more pelagic prey (e.g., gastropods such

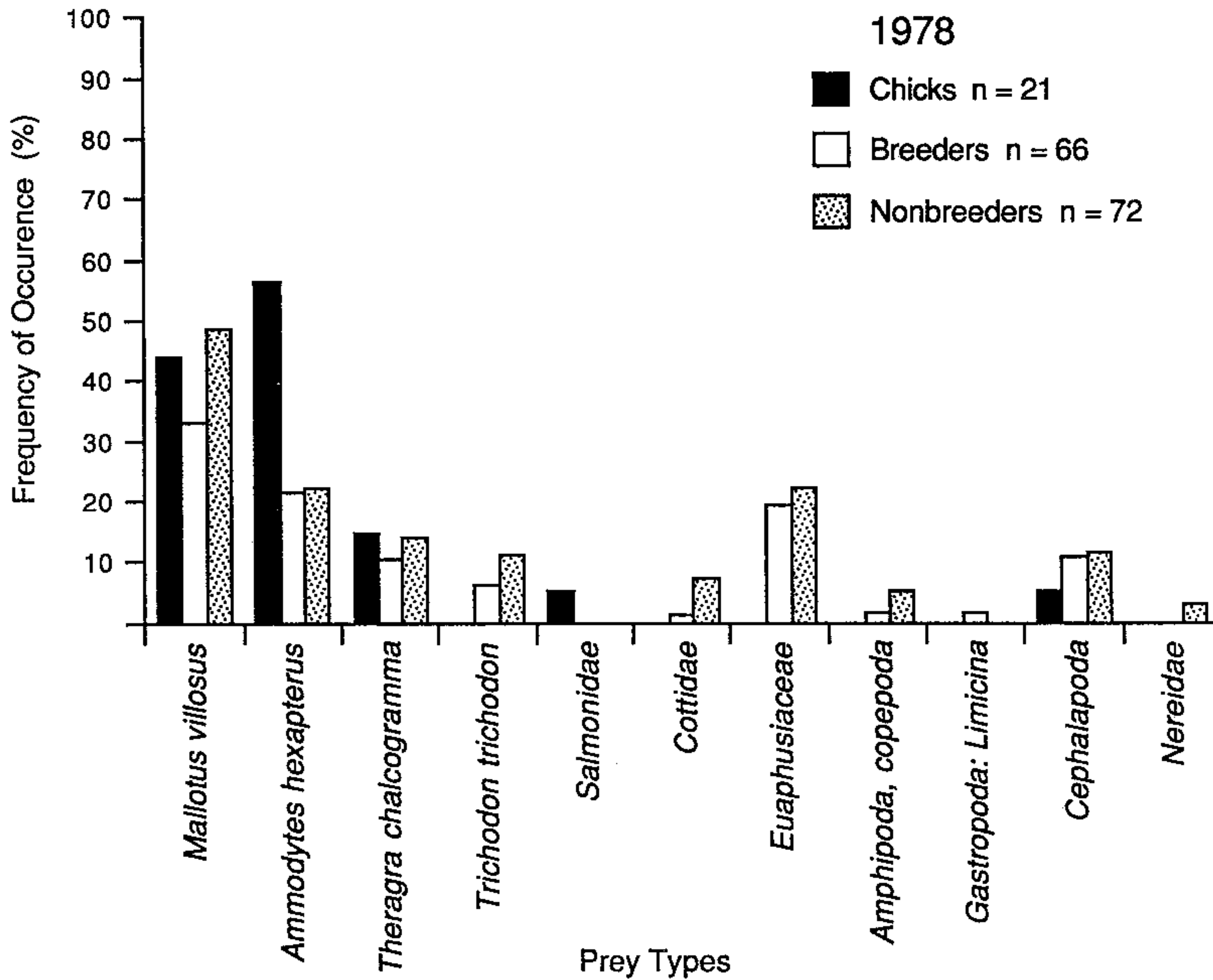


FIGURE 3. Frequency of occurrence of prey in Tufted Puffin groups, 1978.

as *Limicina lulicina* and polychaetes). In 1978, invertebrates and pelagic prey made up a greater proportion of meals of both breeders and non-breeders.

Relative percent numbers. Fish were also the most numerous groups in all diets for 1977 (Fig. 4) and in chick diets for 1978 (Fig. 5). Chi-square tests of differences in numbers of prey species for each prey type each year yielded significant differences among all puffin groups (1977: $\chi^2 = 326.7$, $df = 18$, $P < 0.005$; 1978, $\chi^2 = 496.8$, $df = 24$, $P < 0.005$). Pairwise comparisons of each prey within a year were all highly significant (all P values < 0.005). *M. villosus* predominated in 1977 for all puffin classes. *A. hexapterus* were only common in chick diets for both 1977 and 1978. Nonbreeders consumed significantly more invertebrates than did breeders. In 1978, invertebrates, mainly the euphausiid *Thysanoessa inermis*, and pelagic prey were most numerous for adults ($> 75\%$), yet were insignificant (ca. 3%) in chicks' diets.

Masses. Comparisons of mass or biomass proportions of whole prey, a more energetically meaningful measure of the contribution of each prey species, showed a high contribution of fish each year to diets of all groups (Fig. 6, 7). A Friedman Rank test comparing biomass contributions yielded significant differences among all

groups for each year (1977: $\chi^2 = 18.0$, $df = 8$, $0.02 < P < 0.05$; 1978: $\chi^2 = 120.0$, $df = 9$, $0.005 < P < 0.01$). Nonbreeders, breeders and chicks consumed significantly different species of fish with respect to biomass contributions. *A. hexapterus* was important only for chicks. In 1978, significantly different proportions of fish biomass were eaten by the different groups. Chicks were fed 98% fish, and breeders and nonbreeders took 83% fish by mass. There was a shift in proportion of biomass of different prey species, but there was still segregation among all groups. In 1978, contribution by mass of invertebrates (mainly euphausiids) increased for both breeders and nonbreeders.

Prey length. During both years, all fish eaten were second year fish (Jangaard 1974, Blackburn 1978, Craig and Halderson 1981), and all euphausiids among the prey of both breeders and nonbreeders were "immature." In 1977, the only species with a sufficiently large sample that was statistically valid was for *M. villosus*, the most important species for all groups that year.

The difference in length of *M. villosus* was significant among all groups (Kruskal-Wallis $H = 19.7$, $n = 265$, $P < 0.0001$), and nonbreeders took the smallest and chicks ate the largest. The apparent relationship between size of fish and age of puffin seemed to hold for most other fish

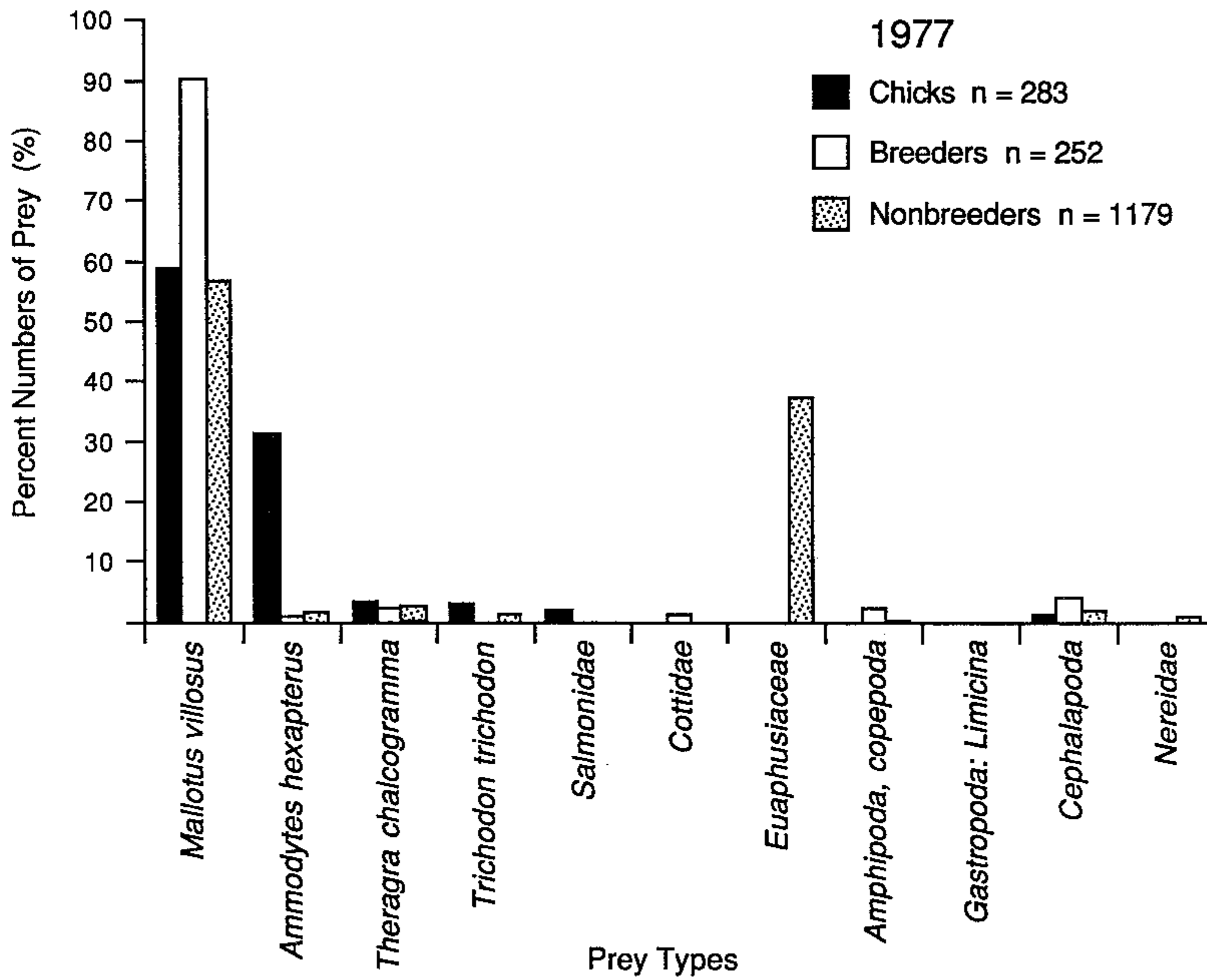


FIGURE 4. Percent numbers of prey consumed by Tufted Puffins, 1977.

species, even those species for which there was a small sample size (Table 2). Fish fed to chicks ranged from 3.2–6.6 mm longer than fish eaten by adults. The largest prey, salmonids ($\bar{x} = 11.8$

cm) were fed to chicks and the smallest prey, *Trichodon trichodon* ($\bar{x} = 7.6$ cm) were eaten by nonbreeders.

Sample sizes were larger in 1978 and more

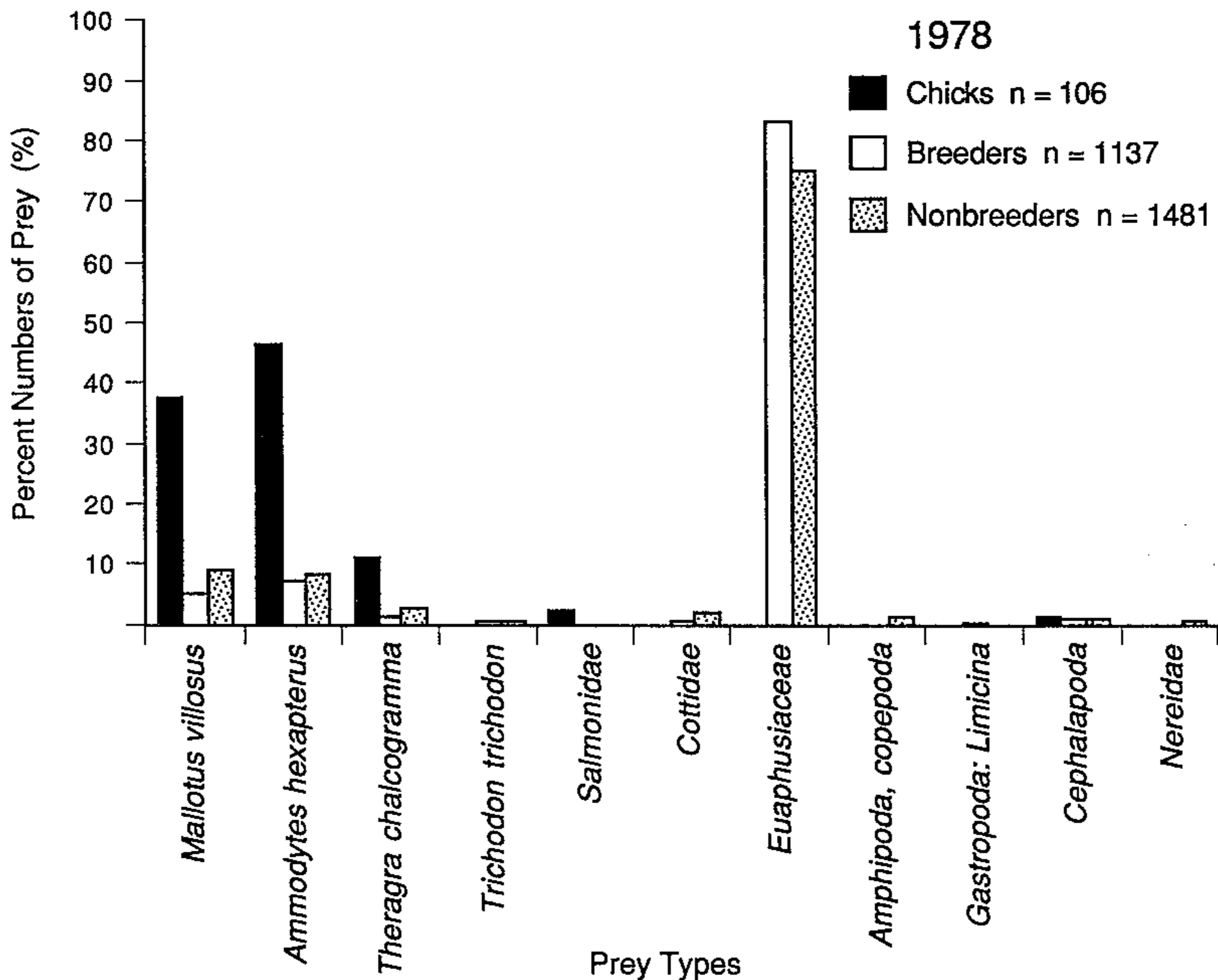


FIGURE 5. Percent numbers of prey consumed by Tufted Puffins, 1978.

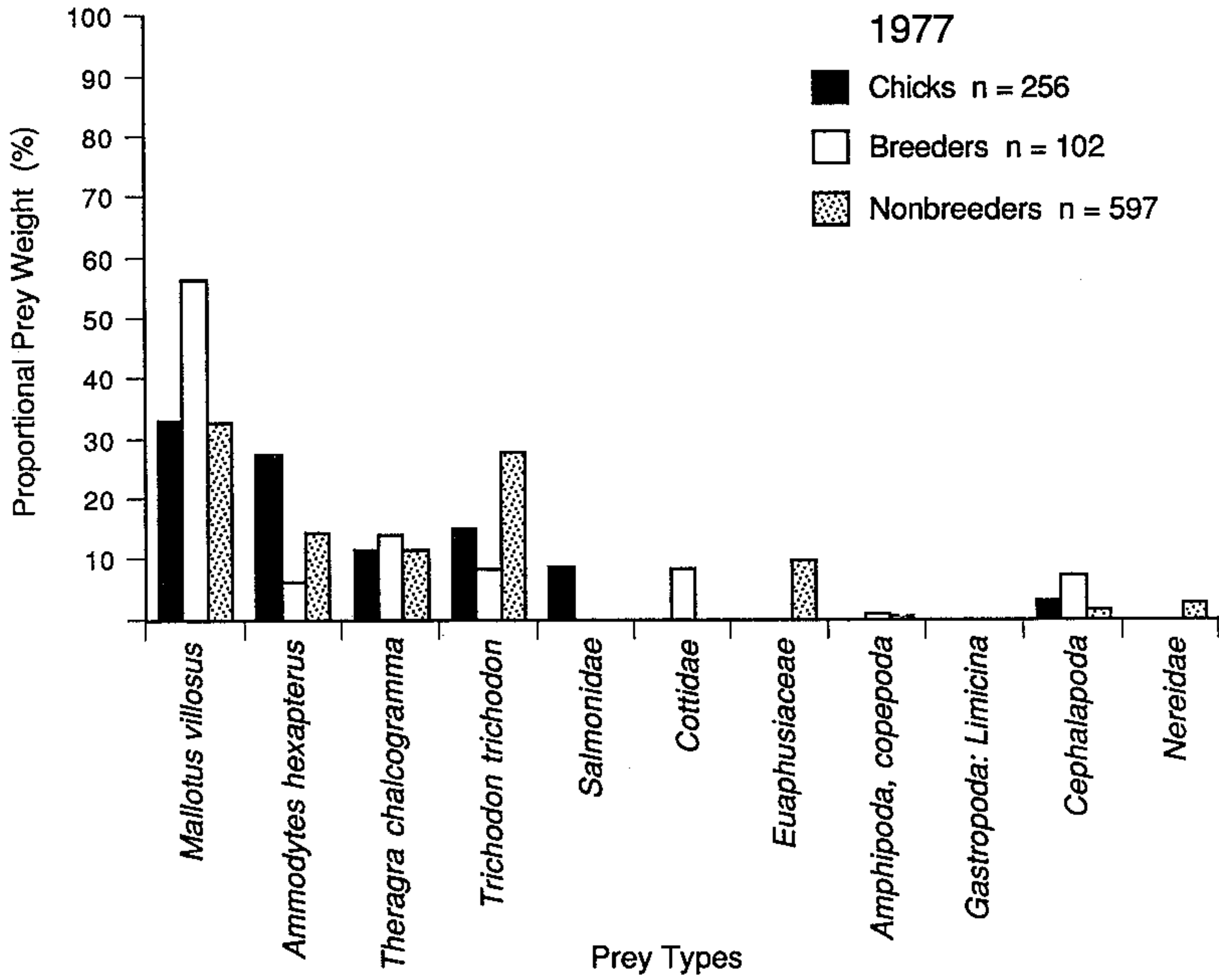


FIGURE 6. Proportional prey weights of Tufted Puffin Groups, 1977.

species could be compared among the puffin groups. Differences among lengths of *M. villosus* were significant for all puffin groups ($H = 6.7, n = 137, P = 0.035$), as were those among *A. hexapterus* ($H = 80.5, n = 195, P < 0.0001$). How-

ever, pairwise comparisons yielded no differences in length of *M. villosus* or *A. hexapterus* between adult groups. Lengths of chick prey (with the exception of *M. villosus*) were again longer than those of adult prey.

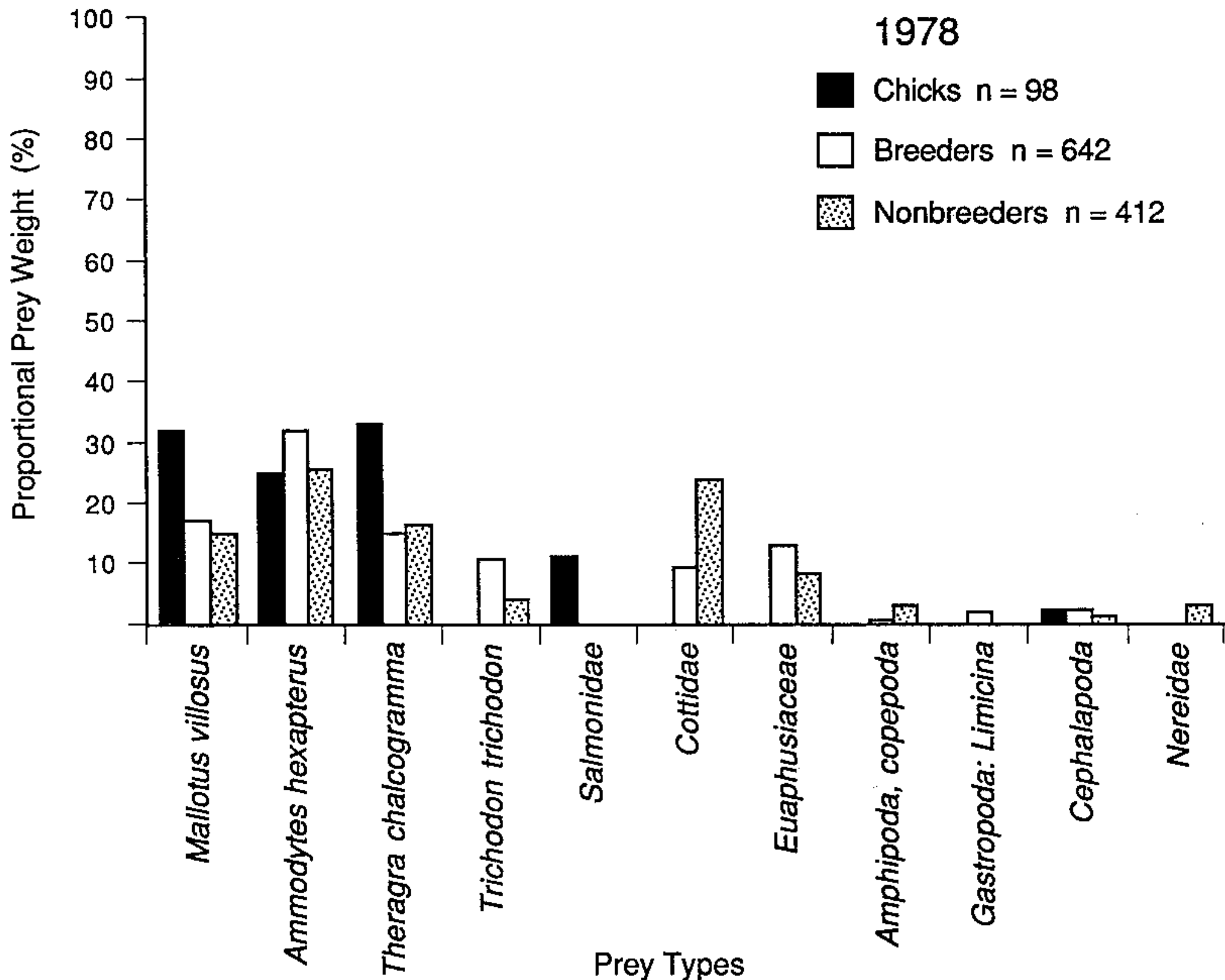


FIGURE 7. Proportional prey weights of Tufted Puffin Groups, 1978.

TABLE 1. A comparison of prey length (cm) for three sample groups of Tufted Puffins (significant differences = *).

Prey species	Year	Chicks			Breeder's			Nonbreeder's		
		\bar{x}	SE	<i>n</i>	\bar{x}	SE	<i>n</i>	\bar{x}	SE	<i>n</i>
<i>Mallotus villosus</i>	1977	9.0*	0.06	166	8.73*	0.15	64	8.34*	0.13	35
	1978	8.91*	0.22	29	9.87*	0.37	28	9.74*	0.24	80
<i>Ammodytes hexapterus</i>	1977	9.9	0.13	76	11.5	—	1	—	—	—
	1978	9.8*	0.27	50	7.96*	0.12	60	7.79*	0.08	85
<i>Theragra chalcogramma</i>	1977	8.77	0.43	10	—	—	—	8.45	0.05	2
	1978	7.13	0.29	8	—	—	—	—	—	—
<i>Trichodon trichodon</i>	1977	8.18	0.21	9	—	—	—	7.60	—	1
	1978	13.75	0.55	2	—	—	—	—	—	—
<i>Thysanoessa inermis</i>	1977	—	—	—	—	—	—	2.26	0.02	1
	1978	—	—	—	2.18	0.05	109	2.28	0.02	1
<i>Thysanoessa spinifera</i>	1977	—	—	—	—	—	—	2.36	0.0	2
	1978	—	—	—	2.35	0.19	2	2.49	0.06	2
Pooled all fish	1977	9.27*	0.11	265	8.77*	0.15	65	8.33*	0.1	38
	1978	9.36*	0.18	89	8.57*	0.21	88	8.61*	0.51	175
Pooled all plus euphausiid	1977	9.27*	0.11	265	8.77*	0.15	65	3.45*	0.02	195
	1978	9.36*	0.18	89	5.0	0.26	199	5.7	0.04	323

Salmonids, eaten only by chicks, were the largest species (\bar{x} = 13.8 cm) of all prey taken. All other fish eaten by adults were small (<8 cm); adults caught fish as small as 4.1 cm (a cottid, *Hemilepidotus jordani*). There was no significant difference between the two adult puffin classes with respect to lengths of either euphausiid. Chicks were never fed prey this small (2.3–2.4 cm).

Pooled lengths of fish showed that chicks consumed larger fish in both years ($P < 0.01$) and that in 1977, breeders ate larger fish than did nonbreeders ($P < 0.02$) and in 1978, lengths were not significant. When invertebrate lengths are added to the pooled lengths, the significant difference in prey length between chicks and adults increased ($P < 0.0001$) for both years, and the difference between breeders and nonbreeders increased in 1977 only ($P < 0.005$).

DISCUSSION

In both years at Sitkalidak Strait, all three Tufted Puffin groups ate more fish than invertebrates, breeders fed themselves less fish than they fed their chicks, and nonbreeders consumed relatively large numbers of invertebrates as measured by frequency of occurrence, numbers, and biomass. Nonbreeders, compared to other groups, ate a greater diversity of food, and more prey species in their diets were pelagic over both years. During 1978, a year when many fish prey were scarce in the Sitkalidak Strait ecosystem (low

abundance of *M. villosus* and patchy distribution of other fish species; Rogers et al. 1979, 1983), breeders consumed more pelagic and invertebrate prey, diets of both breeders and chicks were more varied than in the previous year, and, with respect to relative numbers, only chick prey was mainly fish.

In most diet studies of seabirds, one prey species usually predominates over others (Pearson 1968, Bédard 1969, Sealy 1975, Amaral 1977, Wehle 1983, Baird and Gould 1983, Diamond 1983, Furness and Barrett 1985, Ainley and Boekelheide 1990). For Tufted Puffins at Sitkalidak Strait in 1977, *M. villosus* predominated for all puffin groups with respect to all parameters. It was also found to be an important component of diets of puffins in the southeast of Kodiak Island during the same year (Nysewander and Hoberg 1978, Baird and Gould 1983), and in other nearby colonies (Amaral 1977). It is one of the more common fish species offshore of Kodiak Island and often there are large schools of this species (Blackburn 1978, Rogers et al. 1983).

In a year of low food availability and low abundance of *M. villosus* in particular (1978), no one prey species dominated all measures of dietary importance (frequency, numbers, weight). Greater diet breadth and lower dominance indices reflected this (Baird and Gould 1983).

Although *M. villosus* was found in a large proportion of stomachs and bill loads in 1978 (relatively high frequency), its low numbers and bio-

TABLE 2. Protein, fat, and calorific values of prey of Tufted Puffins¹ (range in parentheses).

Species	% wt protein	% wt fat	Calories/g
<i>Mallotus villosus</i> (capelin) May–August ²	$\bar{x} = 14.1$ (13.0–15.3) $\bar{x} = 13.7$ (13.0–14.0)	$\bar{x} = 4.1$ (2.1–10.3) $\bar{x} = 5.0$ (3.0–8.0)	93
<i>Ammodytes lanceolatus</i> (sandlance)	$\bar{x} = 18.2$ (17.9–18.5)	$\bar{x} = 0.9$ (0.3–1.5)	91
<i>Ammodytidae</i>	$\bar{x} = 17.8$	$\bar{x} = 6.0$	NA
<i>Theragra chalcogramma</i> (walleye pollock)	$\bar{x} = 16.0$ (15.3–17.2)	$\bar{x} = 2.4$ (1.2–3.0)	86
<i>Oncorhynchus kisutch</i> (silver salmon)	$\bar{x} = 21.1$ (19.9–22.0)	$\bar{x} = 5.7$ (1.3–9.9)	136
<i>Oncorhynchus nerka</i> (sockeye salmon)	$\bar{x} = 18.4$	$\bar{x} = 7.8$	144
<i>Loligo vulagris</i> (common squid)	$\bar{x} = 14.2$	$\bar{x} = 1.2$	78
<i>Mictiharus norvegica</i> (euphausiid)	$\bar{x} = 1.4$	$\bar{x} = 2.5$	78

no values for other invertebrates or fish

¹ From Hunt 1972, Harris and Hislop 1978, Sidwell 1979 (except where noted).

² From Montevicchi and Piatt 1984.

mass that year indicate that it was not a dominant prey even for adults that consumed more individuals and biomass of invertebrates and more of other species of fish. *M. villosus* in 1978 and *T. chalcogramma* in both years were what Ashmole and Ashmole (1967) called “supporting species,” that is, species found consistently throughout the season but in low numbers (perhaps reflecting their low availability in the environment). Data from other studies indicate that *M. villosus* was scarce throughout Sitkalidak Strait during 1978 (Rogers et al. 1983, Baird 1990).

Cephalopods served the same supportive function for nonbreeders, appearing in low numbers but found in nonbreeders’ stomachs fairly frequently. Euphausiids, in contrast, were found in a small percentage of stomachs in 1977, but when present, they contributed fairly high numbers to nonbreeders’ diets. This may indicate that they were present in large numbers only part of the season in the area where nonbreeders were foraging, or that the birds changed foraging areas (Ashmole and Ashmole 1967; Furness and Monaghan 1987; D. Ainley, pers. comm.). In 1978 they were both frequent and numerous in adult meals.

Dietary differences are expected between nonbreeders and central place foraging breeders because breeders are restricted to forage near the colony where they may be competing intensely for food, and where prey may be depleted (Orians

and Pearson 1979, Schoener 1979, Krebs et al. 1983, Furness and Birkhead 1984, Hunt et al. 1986, Birt et al. 1987, Briggs et al. 1987, Ainley and Boekelheide 1990). Because of competition, segregation of prey by adults may occur by species or size, and because of prey depletion, there may be proximate prey segregation by separation of foraging areas (Furness and Monaghan 1987, Ainley and Boekelheide 1990).

The greater species diversity and lower species evenness for nonbreeders (Baird and Gould 1983) indicates the consumption of a large variety of prey types caught with more equal frequency, reflecting their foraging in diverse habitats. Supporting this is the high incidence of pelagic prey (e.g., squids, euphausiids, polychaetes; Nemoto 1957, Brinton 1962, Barnes 1980, Ogi 1980) in their diets. Their ingestion of more invertebrates could also reflect their lack of need for high energy packets of food, since nonbreeders are not provisioning chicks and are not expending large amounts of energy flying from a patch to a central place. The consumption of more nearshore-schooling fish by breeders (*M. villosus*, *A. hexapterus*; Jangaard 1974, Blackburn 1978) suggests foraging in habitats different from those of nonbreeders.

The presence of pelagic invertebrates in breeders’ stomachs in 1978 (e.g., *Thysanoessa* and *Limicina lulicina*) suggests that in this year of lower fish availability, breeders ventured farther

from their colonies to the habitat usually frequented by nonbreeders. Greater species diversity for breeders in that year (Baird and Gould 1983) may also reflect lower food availability, sampling of diverse prey when preferred prey were unavailable, or foraging in different areas. Krasnow and Sanger (1982) confirmed the pelagic feeding of breeders when they reported equal distribution of both adult groups in Sitkalidak Strait during their 1978 collecting of birds at sea.

The differences in chick and adult diets with respect to type and size of fish is consistent with optimal foraging theory (MacArthur and Pianka 1966, Charnov 1976, Stephens and Krebs 1986, Houston 1987). Natural selection favors the parental foraging strategy that will maximize fitness. The survival of the young increases adult fitness as increasing energy is delivered to them. Risk of chick starvation is minimized, time in the nest may be decreased, and chicks may fledge heavier (Perrins et al. 1973, Nur 1984, Davies 1986, Houston 1987) perhaps giving them better survivability (Birkhead and Furness 1985). The energy delivered to the young depends on the energy provisioning rate (Houston 1987), which could be maximized by large prey size, prey of higher energy content, or quicker trip times.

Fish are not only larger than invertebrates but also have a higher energy content (Sidwell 1979, Croxall and Prince 1980) and thus are more profitable an item to consume. If prey are encountered often, all adults should theoretically bypass less desirable types (e.g., invertebrates) until a better prey item (e.g., fish) is found. Thus, all puffin groups should eat fish, and fish that are large.

However, since breeders are time- and distance-limited when feeding chicks and since provisioning chicks is a major demand on their time, they should eat for themselves whatever prey they encounter and then bring back the most nutritious and largest prey items that a chick can eat in order to maximize chick growth and fledging weight.

Tufted Puffins are multiple prey loaders, yet the amount of prey per bill load is limited. Thus it would be most efficient and least costly for adults not only to carry back fish rather than invertebrates, but also to bring bill loads of a few large fish rather than a bill load of many small fish. Harris and Hislop (1978) have shown that larger *Ammodytes* have greater fat content than do smaller ones (and thus a greater energy value). Likewise, many smaller fish of an equivalent to-

tal weight would yield more undigestible parts like fins, bones, and scales due to their greater surface: volume ratio. Thus, fish as large as chicks can handle should be expected. Chicks were indeed fed the longest fish of all puffin groups. The one exception was *M. villosus* in 1978, but the smaller length fed to chicks of this species may somehow be due to the apparent scarcity of larger sized *M. villosus* that year at Sitkalidak Strait (Rogers et al. 1983, Baird 1990). The feeding of large food items to chicks thus is consistent with optimal foraging theory.

Although I was not able to determine the body composition nor energy contained in the food items of my sample population, I was able to obtain protein, fat, and carbohydrate proportional amounts and energy for the same species of similar-sized prey from the literature (Table 3; Hunt 1972, Sidwell 1979, Montevecchi and Piatt 1984). Although these values are only representative, I believe that they hold for comparative purposes.

The choice of salmon and sandlance for chicks would maximize energy and protein delivered per meal. Protein content, in fact, may be more important than energy value for growing chicks (Harris and Hislop 1978, Montevecchi and Piatt 1984), aiding in rapid chick growth necessary for fledging at the end of the short subarctic summer. Salmon were only fed to chicks, and they have both the highest percent fat and protein and also the highest amount of energy of all prey consumed. However, they only appeared in Sitkalidak Strait late in the season.

The greater importance of *A. hexapterus* in chicks' diets, compared to adult diets, as measured by all parameters, was consistent for both years studied. This species was fed almost exclusively to chicks during the year of abundant food. Since amount of protein and energy increase with fish length, the taking of sandlance, the longest prey item besides salmon, would maximize energy gain by chicks and thus also adult fitness. Sandlance also have a very high percentage of protein per gram of fish so necessary for chick growth (Harris and Hislop 1978). Both the frequency of occurrence rate and percent numbers of sandlance were low for adults both years which may indicate both a low encounter rate and low numbers.

In other ecosystems, another alcid, the adult Thick-billed Murre (*Uria lomvia*), eats amphipods (*Parathemisto libellula*), which have higher energy content (due to more fat), than do Arctic

cod, *Boreogadus saida*. The latter are fed to chicks and have higher amounts of protein than do amphipods (M. Harris, pers. comm.).

Capelin were extremely abundant in Sitkalidak Strait in 1977 and probably their percent numbers, biomass and frequency were high because the encounter rate was high. When their numbers dropped off in 1978, it appeared that breeders were selecting *Ammodytes* for chicks, optimizing protein and energy.

Squid were the only invertebrates fed to chicks and they made up a very small proportion of chicks' diets; the most common invertebrate prey for adults were euphausiids. Squid and euphausiids both have the lowest amounts of protein and fewest calories of any other prey consumed by Tufted Puffins at Sitkalidak Strait.

The consumption by all puffin groups of only second year fish and only immature euphausiids, places all birds in the same trophic level and this age (size) choice is probably related to prey behavior and bird morphology. The size of fish and invertebrates found in my study is within the same range as in other studies of Tufted Puffin prey length (Amaral 1977, Ogi 1980, Baird and Gould 1983, Wehle 1983).

In other comparisons of diet among different species of birds, diets may be similar when food is plentiful because all are taking the most frequently encountered and abundant prey (Diamond 1983, Furness and Barret 1985). In poor food years, species often retreat in their diet breadth and may become more specialized with what they are most efficient at catching.

In my study, diets of breeding and nonbreeding adults converged in the poor food year, whereas adult diets differed considerably during the year of abundant food (Baird and Moe 1978, Baird 1979, Baird and Hatch 1979, Baird and Gould 1983). This convergence during a poor food year seems to run counter to what has normally been found. However, the different groups of birds I studied were from the same species, thus fed in the same way, and this apparent discrepancy in expansion or contraction of diet is readily explainable.

Chicks cannot forage for themselves and are completely dependent on what the adult brings them. Adults will always maximize large, high-quality packages of food for the young. Since the Sitkalidak colony was so large, in poor food years there probably was competition for food or even prey depletion around the colony, as in other

seabird colonies (Furness and Birkhead 1984, Hunt et al. 1986, Furness and Barrett 1985, Birt et al. 1987, Ainley and Boekelheide 1990). Breeding adults most likely had to search farther for food that year, feeding in areas often frequented by nonbreeders. Because of this far-ranging foraging, breeders ate prey similar to that of nonbreeders. In years of abundant food, nonbreeders still foraged over a wide area and breeders were able to remain near the colony where prey species different from those at the distal ends of Sitkalidak Strait were concentrated.

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APPENDIX I

Fish were identified by caudal assembly, otolith, or parasphenoid bone. Length of whole fish was measured from the most anterior tip to the fork of the tail. If partial fish were present, their fork length was extrapolated from parasphenoid bone or vertebral column regression equations (Table A1) for *A. hexapterus* and for *M. villosus*, the two most common prey species for birds at the Kodiak colonies.

Other prey items were also often whole. Cephalopods, mostly *Gonatus* squids, were identified by beak, if partially digested. Cephalopod length was measured as mantle length.

Euphausiids were identified by carapace and rostrum. Most samples were of whole or almost whole prey, and were measured from the tip of the rostrum to the tip of the telson. Occasionally, only eyestalks remained, and these, divided by two, gave numbers of euphausiid prey. *T. inermis* was the most abundant euphausiid, and some specimens of *T. spinifera* were found. It was assumed that all invertebrates were eaten directly by the birds and were not prey of fish that were eaten by the birds.

TABLE A1. Regression equations for extrapolating whole fish length from length of parasphenoid bone or partial vertebral columns.¹

Independent variable	Species	
	<i>Mallotus villosus</i>	<i>Ammodytes hexapterus</i>
Parasphenoid bone (PB)	Fish length = $8.1346 \times \text{PB} - 24.1697$ ($r^2 = 0.97$, $n = 63$)	Fish length = $7.1861 \times \text{P} + 14.4015$ ($r^2 = 0.85$, $n = 34$)
Vertebral column (VC)	Fish length = $1.3174 \times \text{VC} + 2.0398$ ($r^2 = 0.99$, $n = 67$)	Fish length = $1.2075 \times \text{VC} + 3.791$ ($r^2 = 0.96$, $n = 112$)

¹ From P. Baird, unpublished data.

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