A comparison of seabird diets and foraging distribution around the Pribilof Islands, Alaska

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1. Abstract

We compared the diet and foraging distribution of five species of seabirds nesting at the two largest Pribilof Islands, which differ in the distribution of water masses around each island. We report significant asymmetry in the distribution of birds on the water around the islands. We also report significant differences in diet between members of the same species on the two islands, which are less than 100 km apart. In most cases, differences in volume of prey per bird were due to differences in the proportion of birds taking a prey, rather than due to differences in volume or number of prey per successful bird. The Walleye Pollock (*Theragra chalcogramma*) was taken by a higher proportion of birds on St. Paul than on St. George. A higher proportion of euphausiids was taken by birds on St. George than on St. Paul. The diets of breeding seabirds depended on the location of a colony in a physically heterogeneous ocean.

2. Résumé

Nous avons comparé le régime alimentaire et la répartition des aires d'alimentation de cinq espèces d'oiseaux de mer nichant dans les deux plus grandes îles Pribilof dont la distribution des masses d'eau entourant chaque île diffère. Il existe une importante asymétrie dans la distribution des oiseaux posés sur l'eau autour des iles. Nous signalons également l'existence de profondes différences dans le régime alimentaire de certains membres de la même espèce nichant dans les deux îles distantes de moins de 100 km. Dans la plupart des cas, les différences dans le volume de la proie par oiseau sont attribuables à des différences dans la proportion d'oiseaux qui capturent une proie plutôt qu'à des différences dans le volume ou le nombre de proies par oiseau opportuniste. La morue du Pacifique occidental (*Theragra chalcogramma*) est capturée par une plus forte proportion d'oiseaux sur l'île St. Paul. Toutefois, les euphausiidés sont capturés en plus grand nombre sur l'île St. George. Durant la saison de reproduction, les régimes alimentaires des oiseaux sont tributaires de la dispersion d'une colonie dans un océan physiquement hétérogène.

3. Introduction

During the breeding season most seabirds must find food in limited areas around breeding colonies, and must bring food back to colonies at sufficiently short intervals to support adequate growth of chicks. Previous studies of the diets of breeding seabirds have shown that the species at any one colony differ in prey selection, with somewhat greater differentiation of diets among species at tropical colonies (Ashmole 1968) than among species at higher latitude colonies (Pearson 1968, Hunt *et al.* 1980). Differences in diet have been attributed to foraging technique (Bedard 1969) and to interspecific variation in foraging range (Pearson 1968, Prince 1980, Croxall and Prince 1980). There have been few attempts to relate seabird diets to biologically significant features of the waters around colonies, although some comparisons of diet have been made for non-breeding birds at different locations (Hartley and Fisher 1936, Bradstreet 1980).

We here compare the foraging distribution and diets of seabirds at the two largest Pribilof Islands, which are surrounded by water masses that differ in ecologically significant ways. We describe the physical and biological environment, with an emphasis on those factors most likely to affect food distribution and foraging behaviour. We then show that significant differences in diet exist at a scale of less than 100 km, despite large variation in volume, number, and types of prey taken by individual birds. We show that dietary heterogeneity between the two islands is due primarily to individual variation in the type of prey taken, rather than variation in the amount of each prey taken. Finally, we discuss our results in light of recent oceanographic studies in the southeast Bering Sea.

4. Physical and biological setting

The Pribilof Islands, located at the edge of a relatively wide continental shelf, are isolated from the nearest land by 330 km of open ocean (Fig. 1). St. George is the higher of the two large islands, with a cliff area of 3.5 km² along its perimeter (Hickey and Craighead 1977). St. Paul is lower and has a cliff area of 0.5 km² along its perimeter. St. Paul is located 100 km from the shelf break, whereas St. George is only 25 km from the shelf break. Associated with the shorter distance to the shelf break is a steeper gradient in bathymetry around St. George. As a result of differences in bathymetry and location, the islands differ in two oceanographic features: distance to a water mass boundary (inner front) associated with the 50-m isobath, and distance to another front at the shelf break.

During the summer, a vertically homogeneous water mass forms around both islands (Kinder *et al.*, in press). A thermocline forms in water deeper than about 50 m, but fails to form in shallower water because wind mixing reaches to a depth of 30 m, while tidal forces stir water upwards to 20 m off the bottom. Because mixing occurs down to the bottom, rather than just to a thermocline at

about 30 m, heating of surface water occurs more slowly in the homogeneous water mass around the island than in the stratified water offshore. Because of local bathymetry this water mass extends farther to the northeast than to the southwest of St. Paul, and it extends farther outward from St. Paul than from St. George. The front that marks the transition from stratified to well-mixed water around the islands is relatively sharp (Kinder et al., in press). Enhanced vertical mixing occurs at similar fronts in other continental seas (Swallow et al. 1981, Simpson and Pingree 1978).

The two islands also differ in their proximity to a northwestward flowing boundary current at the shelf edge. This current is weak relative to other boundary currents (Kinder and Coachman 1978), but like other shelf-break currents at similar latitudes, this current is associated with a permanent front that marks the transition from shelf waters (less haline, greater seasonal variation in temperature) to oceanic waters (more haline, less seasonal variation in temperature). This front shelf break begins at the 170-m isobath (Fig. 1).

A third front lies shoreward of the shelf-break front east of the Pribilof Islands. This front is associated with the 100-m isobath (Coachman and Charnell 1979) and it marks the transition from a two-layer system over the mid-shelf zone, to a three-layer system over the outer shelf zone. This front has not been delineated from hydrographic data near the Pribilofs, but from bathymetric considerations, coastal (<50 m) and middle shelf (50–100 m) waters can be expected to the north of St. Paul Island (Fig. 1). Outer shelf waters (100–170 m) are limited to the area southeast and southwest of St. George Island (Iverson et al. 1979).

Little is known about the distribution of plankton and nekton in the immediate vicinity of the two islands. Studies of zooplankton (Motoda and Minoda 1974) and juvenile pollock (Smith 1981) suggest that higher standing stocks of these groups occur on the outer shelf (greater than 100-m depth) and hence are most abundant to the southwest of the Pribilof Islands. The outer shelf in the Bering Sea is dominated by a pelagic food web, whereas the middle shelf (roughly 50 to 100-m depth) is dominated by a benthic food web (Iverson et al. 1979, Schneider and Hunt 1982). It is thus likely that food available to birds is different around the two islands, because coastal or middle shelf waters extend north and northeast of St. Paul, whereas outer shelf

waters cover much of the area to the south and southeast of St. George (Fig. 1).

5. Methods

5.1. Data collection

Bird counts were made around the Pribilof Islands on cruises in July 1977, May 1978, August 1978, and September 1978. All bird counts were made while the ship was underway at speeds ranging from 10 to 20 km/h. All sitting birds in a sector extending to 300 m directly abeam of the vessel off the side with the best visibility were recorded during 10-min watches. Counts were standardized by excluding ship-following birds, and by dividing the count by the area scanned during each watch. Counts were made almost continuously during daylight hours, except during periods of fog. Cruise tracks were oriented along radii extending outward from both islands. For this analysis, only birds on the water were counted, as they were either observed to be feeding or were assumed to have been feeding recently in the area where they were seen.

Food samples were obtained from birds that were shot while they were returning to the island from sea. Birds were collected from a skiff within 2 km of land, or at points of land crossed by returning birds. Collections were made every 2–4 days. Collections were made throughout the day, but the majority of birds (60%) were collected during the 4-h period before noon, local time. Most of the collecting was done in June, July, and August 1975–78 (Table 1). Ethanol (70–80%) was injected down the esophagus to arrest digestion. Most carcasses were opened within 12 h of collection. All food in the proventriculus, gular pouch, and stomach was removed and placed in a plastic bag in 80% ethanol.

Samples were sorted in the laboratory by identifying each item to the lowest taxon possible, then recording displacement volume for each taxon. The number of items per taxon was estimated by counting identifiable parts (heads, eyes, beaks, or tails) and dividing by the number of such parts in an intact organism. This measure is a standing stock estimate, rather than a rate measurement (ingestion per unit time).

5.2. Data analyses

Analyses were confined to the five piscivorous bird species for which a statistically adequate sample was available on both islands. Only two stomachs were available for Red-faced Cormorants from St. George, so regurgitations were used in the analysis. A preliminary comparison of cormorant stomach and regurgitation samples collected on St. Paul Island, where our sample of stomachs was larger, showed that prey composition (% occurrence) did not differ significantly between the two methods of collection. Stomach samples were analysed for the four remaining species. Samples were pooled to provide adequate replication.

We designed statistical analyses to control problems that arose: differential digestion of prey taxa and the effects of high individual variation in diets when comparing the average numbers or volumes of prey in two or more groups.

The problem of differential digestion in analysing diets was controlled by making statistical comparisons within prey categories. The variance due to differential digestion among prey taxa is thus eliminated from the analysis, which

Figure 1
Location of Pribilof Islands in the southeastern Bering Sea. St. Paul Island is to the north, and St. George Island is to the south
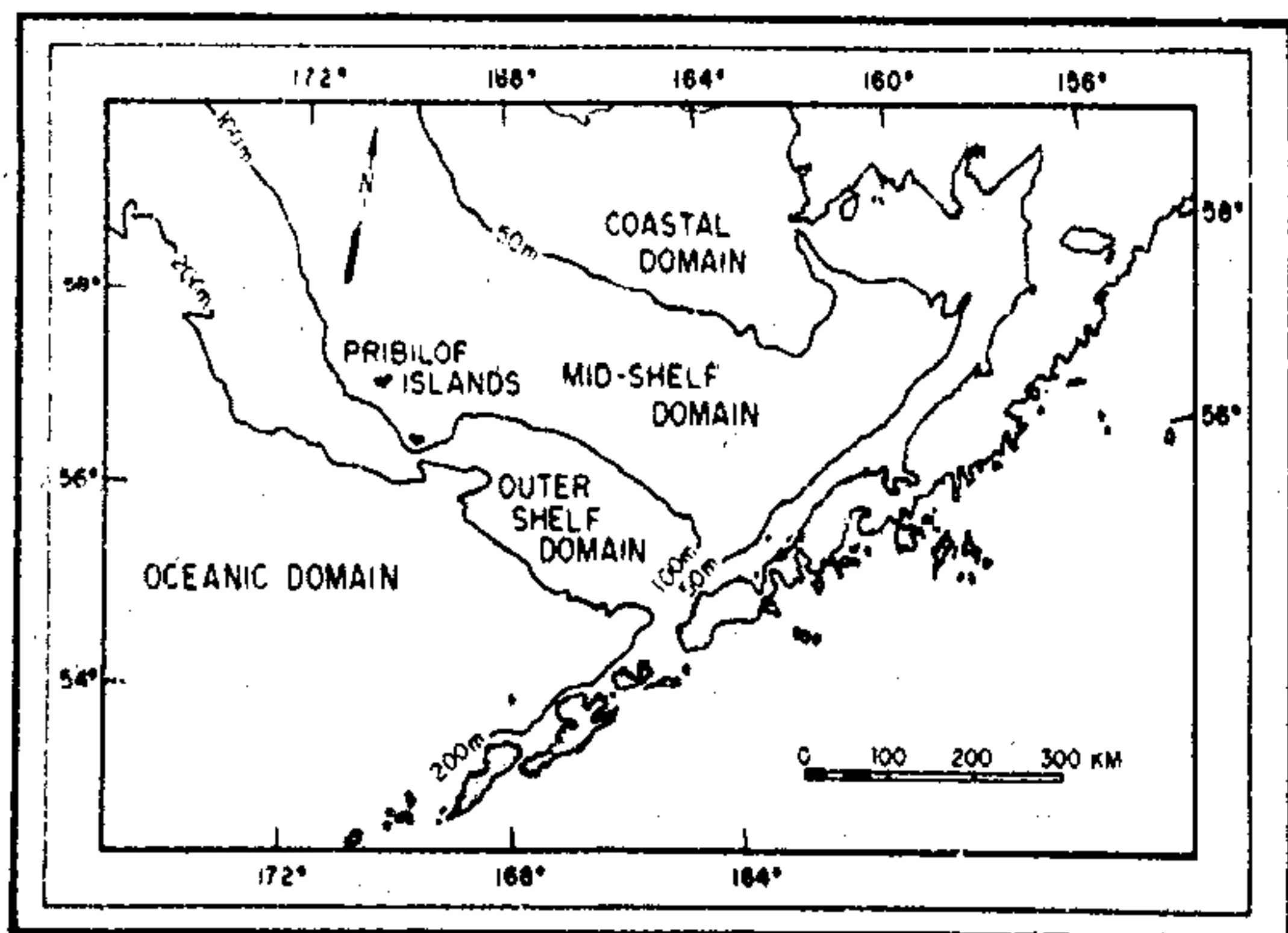
assumes only that digestion rates of any given prey are equal on the two islands. Two-sample ANOVAS were made on prey number and prey volume per bird, for any prey taxon that accounted for more than 5% of the number or volume of prey taken by St. Paul birds or by St. George birds.

If the average number or volume of prey per bird differed significantly between St. Paul and St. George, the analysis was carried further to see if the variation was due to differences in the proportion of birds taking a prey (percent occurrence of a prey taxon in the sample of birds) or whether the variation was due to differences in number or volume of prey taken by successful birds. G-tests (Sokal and Rohlf 1969) were used to test for differences in proportion (i.e. differences in % occurrence). Two-sample ANOVAS were used to test for differences in number or volume of a taxa per capture (i.e. birds without the prey taxa were excluded from the analysis). No test was performed if the sample size was zero for an island (no instances of capture). Criterion levels were set at a conservative level ($P = 0.01$) since a large number of tests were performed. If two samples were heteroscedastic (had unequal variances at $P = 0.01$), a non-pooled estimate of variance was used.

We divided the area around the islands into circumferential zones set at 20 km, 60 km, and 110 km from the islands (Fig. 2). Distances correspond roughly to major bathymetric features (50-m isobath, 100-m isobath, shelf break) that govern mixing regime and water mass distribution. If water masses are important, then the distribution of birds between these zones will be asymmetrical. Asymmetries in bird distribution were tested by comparing corresponding zones in the northeast and southwest (shelf-break) sides of the study area (Fig. 2).

6. Results

6.1. Colony composition

St. George Island has seven times the cliff area of St. Paul Island (Hickey and Craighead 1977). Population sizes of cliff-nesting species deviated strongly from this ratio. St. George harboured a disproportionate number of "pelagic" species, which have long flight ranges and which tend to be found in a few large colonies near deep water (Hunt et al. 1981b): Northern Fulmar (*Fulmarus glacialis*), Red-legged Kittiwake (*Rissa brevirostris*), and Thick-billed Murre (*Uria lomvia*). The ratio of these species between St. George and St. Paul was 100 to 1, 100 to 1, and 14 to 1 respectively (Sowls et al. 1978). St. Paul harboured a disproportionate number of more ubiquitous coastal nesters, found in small to intermediate colonies throughout the eastern Bering Sea: the Red-faced Cormorant (*Phalacrocorax urile*), Black-legged Kittiwake (*Rissa tridactyla*), and Common Murre (*Uria aalge*).

Table 1
Food samples collected at the Pribilof Islands, 1975–78

Species	St. Paul Island				St. George Island		
	1975	1976	1977	1978	1976	1977	1978
Red-faced Cormorant (regurgitations)							
June				1		5	1
July	14	19	7	6	6	17	8
August	17	12			14		1
September		1					
Totals	31	32	7	7	20	22	10
Black-legged Kittiwake (stomachs)							
April				3			
May			4	9		3	1
June	2		11	2		24	5
July	16	10	16	43	2	14	5
August	1	3	6	14	1		1
September	4					1	
Stomachs with food	23	13	37	71	3	42	15
Stomachs examined	27	21	48	74	3	56	16
Red-legged Kittiwake (stomachs)							
April						8	
May			1	10		1	12
June	1		1	5	1	28	8
July	1	7	22	26		3	1
August		2	12				1
September		21	3				
Stomachs with food	2	30	39	41	1	40	22
Stomachs examined	2	34	40	45	1	58	56
Common Murre (stomachs)							
April	1						
May				3			
June	5		5	2			3
July	9	14	1	25			
August	1	4	6	1	1		
September	6	1		1			
Stomachs with food	22	19	12	32	1		3
Stomachs examined	31	22	43	36	2		7
Thick-billed Murre (stomachs)							
May				1			
June	2	1	8			12	19
July	13	5	3	15	1	6	13
August		3	13	1		12	14
September	1						
Stomachs with food	16	9	24	17	1	30	46
Stomachs examined	22	15	35	25	1	36	71

Figure 2
Zones used to analyse seabird abundance around the Pribilof Islands. The concentric rings are 20, 60, and 110 km from the nearest island.
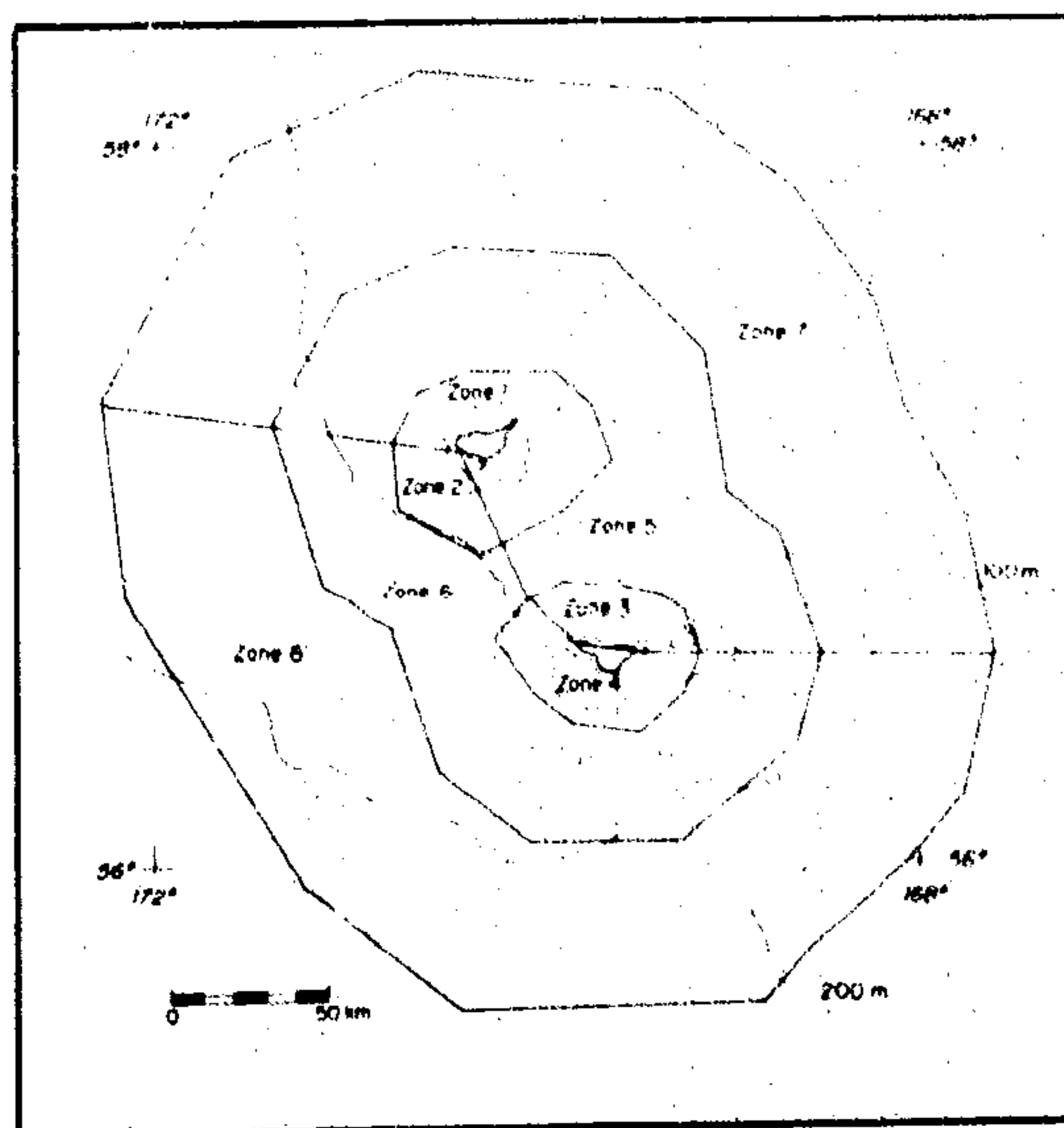
The ratios of these species between St. George and St. Paul were 2 to 1, 2 to 1, and 5 to 1 respectively (Sowls *et al.* 1978).

6.2. Distribution and diet

Foraging by Red-faced Cormorants was confined to within 20 km of the islands (Table 2). The highest densities of birds on the water (presumed to have recently fed) were observed northeast of St. Paul, an area of relatively shallow water. This species took a wide variety of prey: over 56 prey groups were identified in 127 samples. Benthic groups (shrimp, crabs, cottids, and other scorpaeniform fish) were the most important prey (Fig. 3). St. Paul birds took a greater proportion of shrimp than St. George birds (Fig. 4). Differences in the taking of shrimp were due to differences in the proportion of birds taking prey (Fig. 5). If analysis was restricted to those cormorants in which a given prey species was present, there were no significant differences at $P = 0.01$ between the two colonies in the average number or average volume of that prey species per bird. Differences in diet between populations on the two islands were due to the number of birds taking prey (Fig. 5), rather than how much a bird took.

Foraging by Common Murres occurred mostly within 60 km of the islands (Table 2). Density values are low because not all murres could be identified to species. Like the cormorant, Common Murres showed a consistent preference for the shallow waters in the northeast of the study area (Table 2). Diets differed significantly with respect to only one prey species: St. George birds contained a greater volume and number of euphausiids than St. Paul birds (Figs. 6 and 7). These differences were due to the proportion of birds taking a prey (Fig. 8). There were no significant

differences in the volume of a prey taxon taken by successful birds between islands ($P = 0.01$). However, the small number of birds collected on St. George ($N = 4$) may not

Figure 4
Number of prey in food samples of Red-faced Cormorants. Number is expressed as a percentage of the total number of items recorded in samples from one island. Solid bars indicate significant differences ($P = 0.01$) between islands
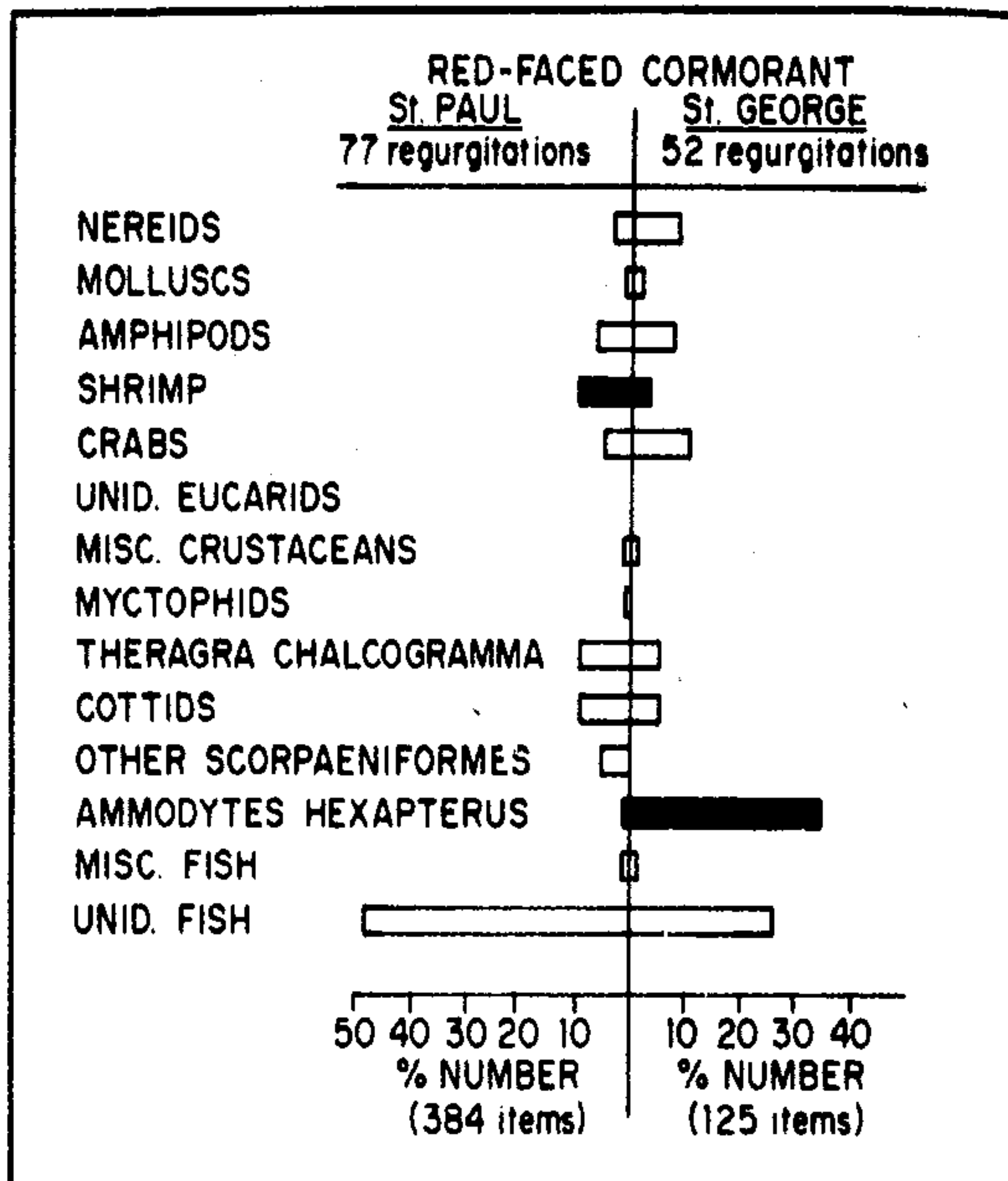

Figure 3
Volume of prey in food samples of Red-faced Cormorants. Volume is expressed as a percentage of the total volume found in samples from one island. Solid bars indicate significant differences ($P = 0.01$) between islands
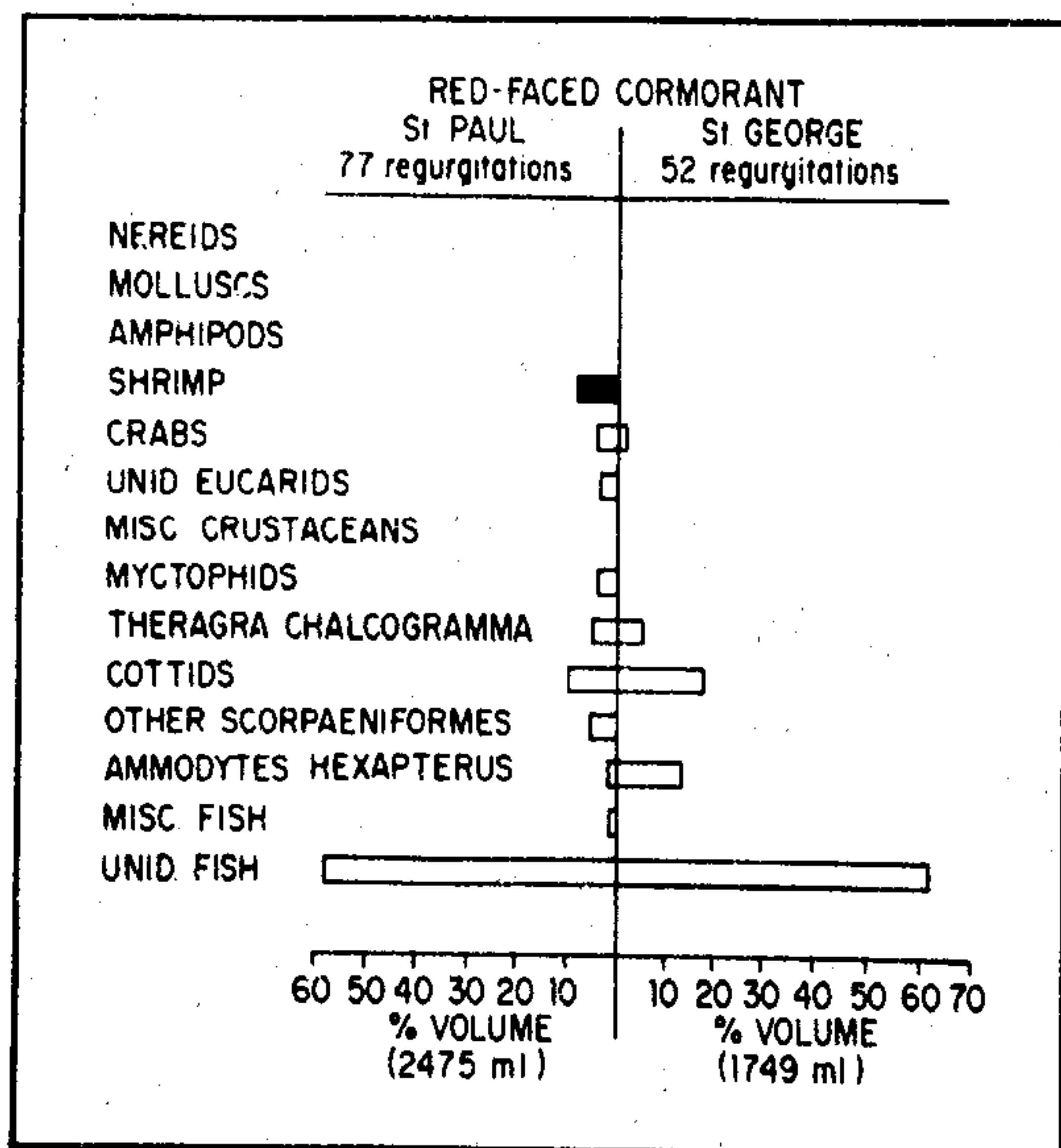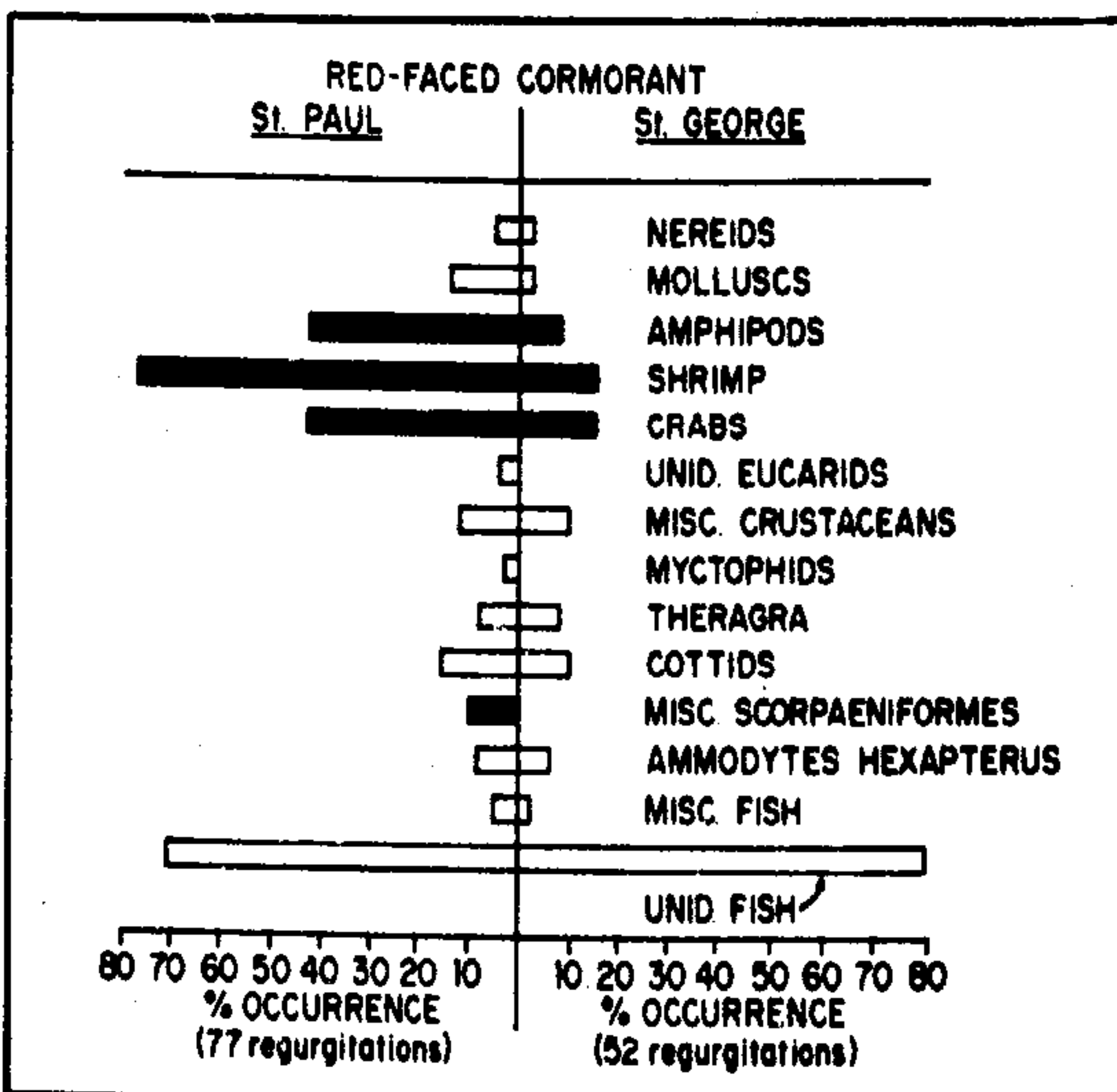

Figure 5
Occurrence of prey in food samples of Red-faced Cormorants. Occurrence is the percentage of samples with a prey, within each island. Solid bars indicate significant differences ($P = 0.01$) between islands

have been representative, although they were collected in different years (1976 and 1977) and months (June and July).

Black-legged Kittiwakes foraged at greater distances from the islands than Red-faced Cormorants or Common Murres, but like these species, Black-legged Kittiwakes showed a strong preference for shallow waters to the northeast of St. Paul (Zones 1, 5 and 7; Table 2). Walleye pollock (*Theragra chalcogramma*) was the most important prey species for Black-legged Kittiwakes and more were taken on St. Paul than St. George (Figs. 9 and 10). Observed differences between the two populations of Black-legged Kittiwakes were due to changes in the proportion of birds taking a prey (Fig. 11), rather than due to differences in number or volume taken by successful birds.

Thick-billed Murres foraged in considerable numbers in the most distant zones from the islands (Table 2),

which agrees with the morphological analysis of Spring (1971) who demonstrated adaptations for long distance flight in *U. lomvia*. This species showed a preference for deeper water, based on relatively low densities of birds northeast of St. Paul Island (Zone 1; Table 2). Invertebrates formed a major part of the diet (Figs. 12 and 13). Differences between the islands were small (Figs. 12 and 13), although a significantly greater proportion of St. George birds took euphausiids (Fig. 14), and the proportion of all invertebrates to all fish was higher on St. George than on St. Paul. There were no differences in number or volume of a prey taxon taken by successful birds on the two islands ($P = 0.01$).

The Red-legged Kittiwake showed a strong preference for waters at or beyond the shelf break (Table 2).

Figure 6
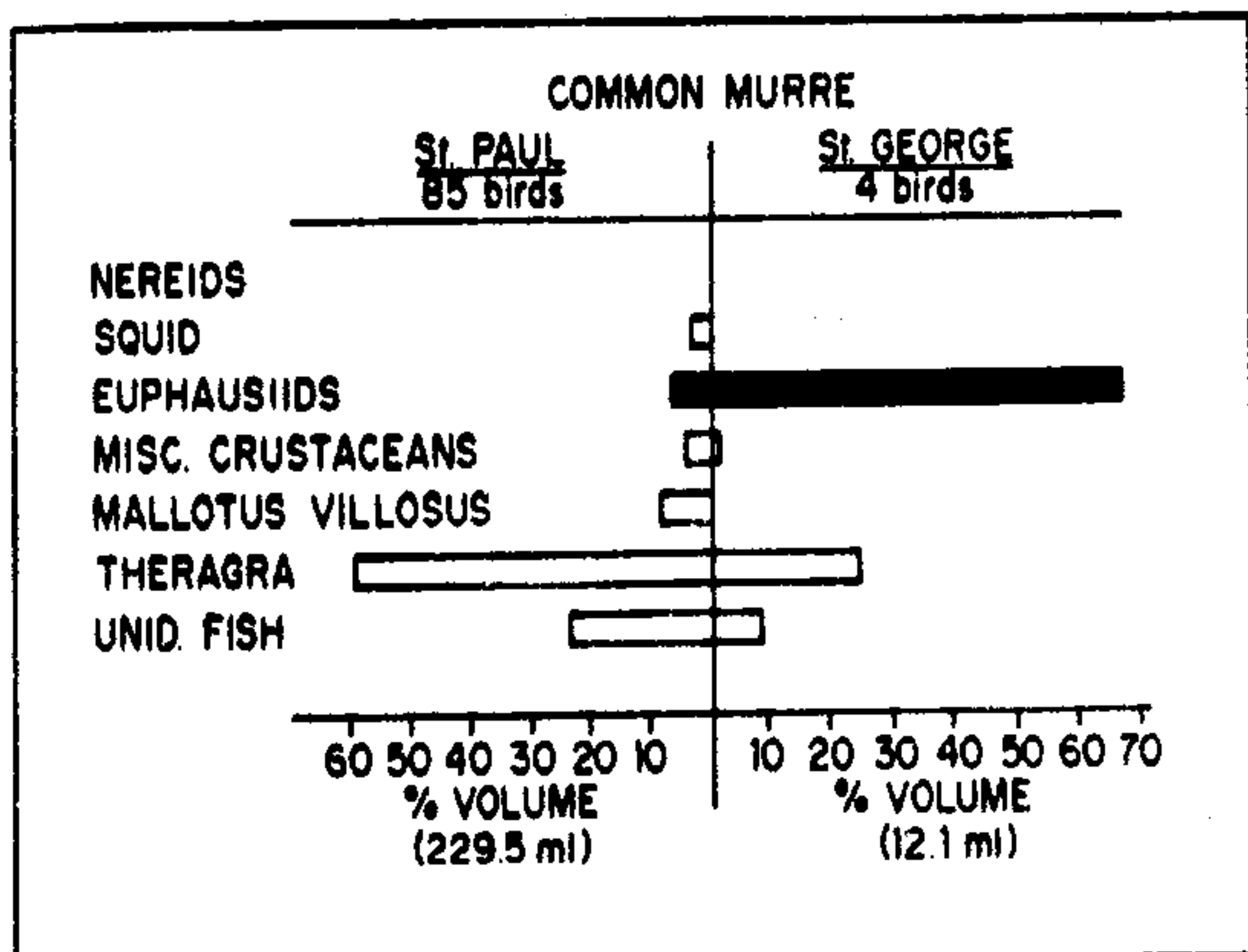Volume of prey in stomach samples of Common Murres. Solid bars: $P = 0.01$

Figure 7
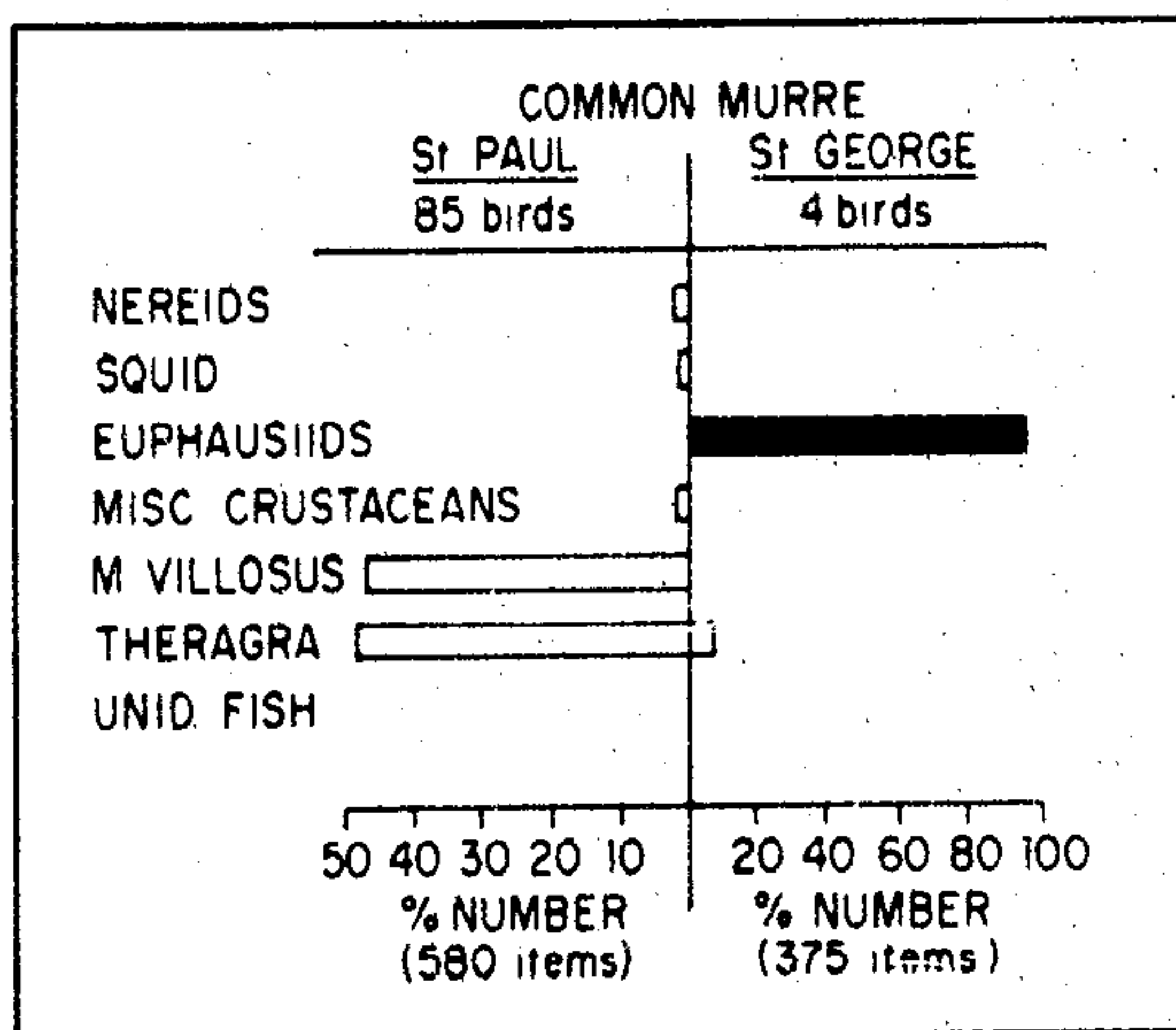Number of prey in stomach samples of Common Murres. Solid bars: $P = 0.01$

Table 2
Density of birds on the water (birds/km²) in eight zones around the Pribilof Islands. See Figure 2 for locations of zones

Distance			Red-faced Cormorant		Black-legged Kittiwake		Red-legged Kittiwake		Common Murre		Thick-billed Murre	
			NE	SW	NE	SW	NE	SW	NE	SW	NE	SW
20 km	St. Paul	Zone	1	2	1	2	1	2	1	2	1	2
		X*	0.94	0.51	0.36	0.08	0.009	0.0	0.22	0.05	0.15	0.32
		SD†	4.92	1.78	1.83	0.34	0.14	0.0	1.05	0.25	0.58	0.88
		N‡	217	74	217	74	917	74	217	74	217	74
	St. George	Zone	3	4	3	4	3	4	3	4	3	4
		X	0.45	0.18	0.12	0.21	0.02	0.03	0.21	0.02	0.70	0.64
		SD	1.79	0.90	0.46	1.28	0.18	0.21	1.06	0.12	2.81	2.83
		N	119	172	120	172	120	172	120	172	120	172
60 km		Zone	5	6	5	6	5	6	5	6	5	6
		X	0.005	0.008	0.32	0.16	0.06	0.30	0.18	0.15	0.53	0.27
		SD	0.09	0.13	1.66	1.09	0.45	3.06	0.69	0.86	1.68	0.97
		N	357	297	357	297	357	297	357	297	357	297
110 km		Zone	7	8	7	8	7	8	7	8	7	8
		X	0.003	0.0	0.22	0.13	0.0	0.30	0.06	0.009	0.22	0.35
		SD	0.06	0.0	1.62	0.99	0.0	3.99	0.34	0.12	0.90	2.52
		N	298	437	298	437	298	437	298	437	298	437

*X = average number of birds/km².
†SD = standard deviation.
‡N = number of transects.

Myctophids, a deep-water fish, were the principal prey (Figs. 15 and 16). There were no significant differences between colonies in the proportions of birds taking this prey (Fig. 17) but there were significant differences in the average number of myctophids per bird (Fig. 16). The number of myctophids per successful bird also differed significantly between St. Paul birds (6.5 fish per successful bird) and St. George birds (4.25 fish per successful bird). Volume of myctophids per bird (Fig. 15) did not differ significantly between the two islands, nor did volume per successful bird ($F = 0.01$).

7. Discussion

This comparative analysis of two seabird colonies demonstrated that (1) the distribution of birds foraging around breeding colonies can vary with local oceanographic differences; and (2) diets can differ significantly between populations of the same species on nearby colonies located in different oceanographic environments.

Figure 8
Occurrence of prey in stomach samples of Common Murres. Solid bars: $P = 0.01$

COMMON MURRE

Figure 9
Volume of prey in stomach samples of Black-legged Kittiwakes. Solid bars: $P = 0.01$

BLACK-LEGGED KITTIWAKE

Figure 10
Number of prey in stomach samples of Black-legged Kittiwakes. Solid bars: $P = 0.01$

BLACK-LEGGED KITTIWAKE
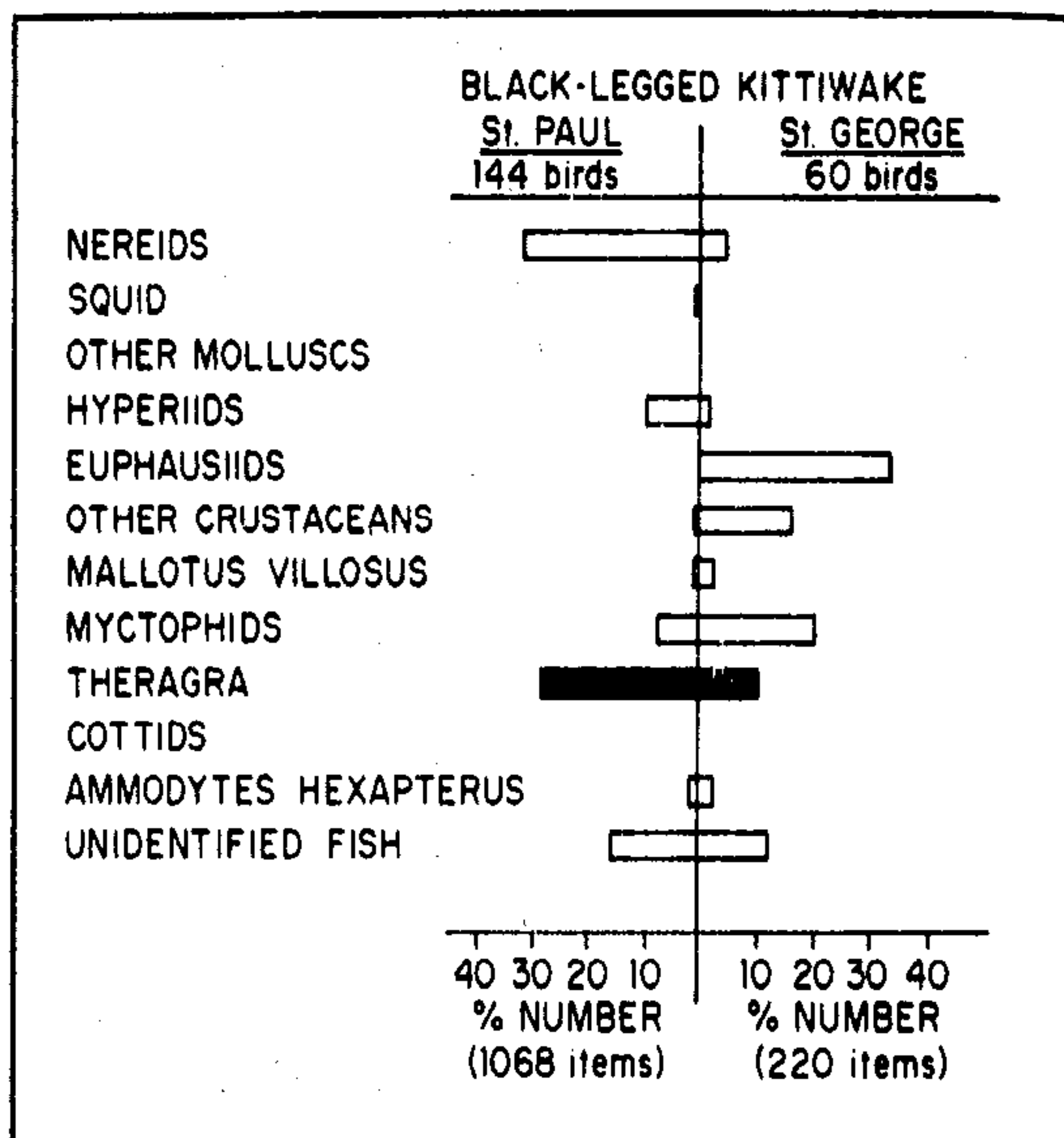
Figure 11
Occurrence of prey in stomach samples of Black-legged Kittiwakes. Solid bars: $P = 0.01$

BLACK-LEGGED KITTIWAKE
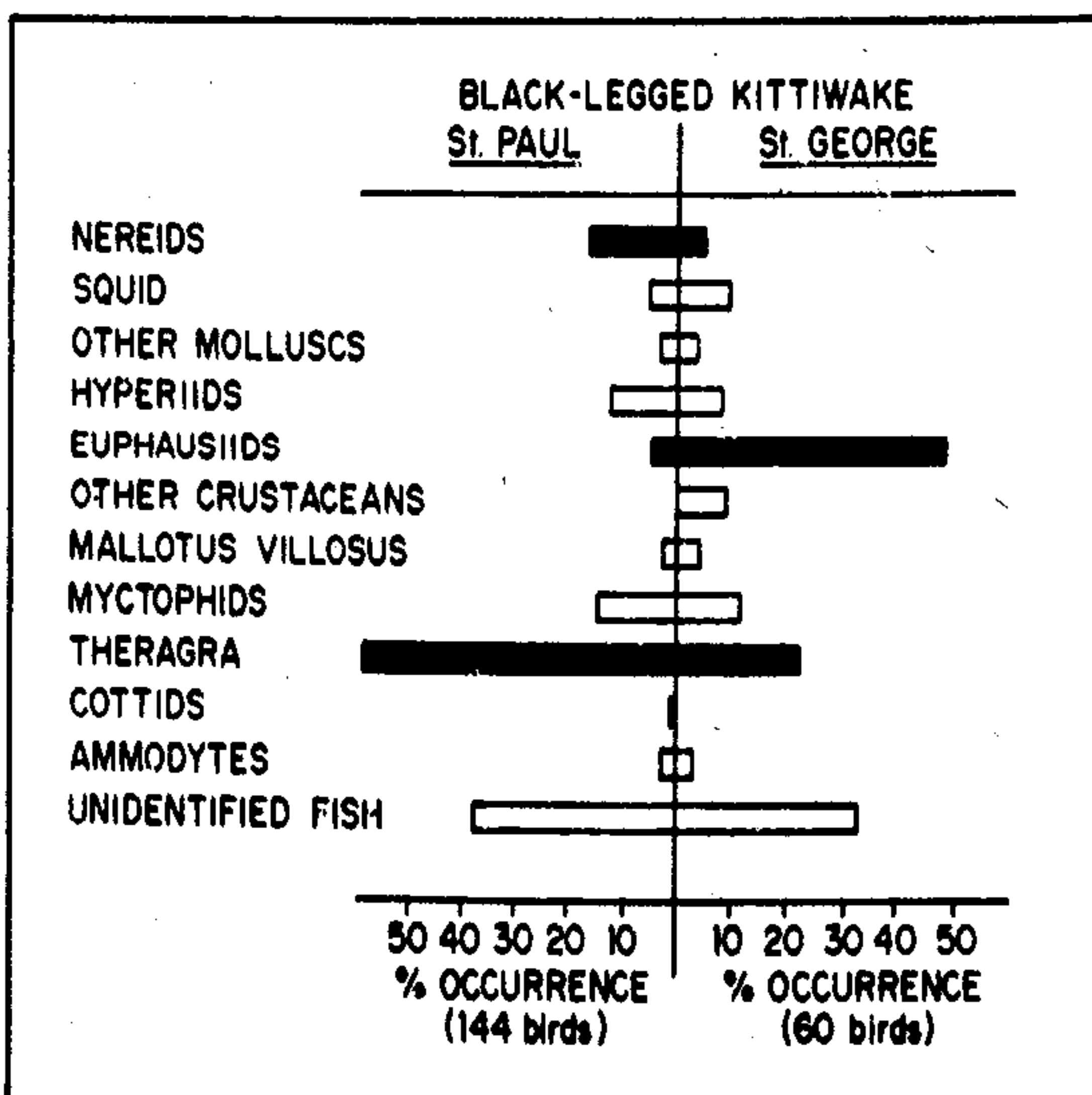
Previous ideas on foraging distribution around breeding colonies have been from inference only (Pearson 1968, Ashmole and Ashmole 1967, Croxall and Prince 1980) and from scattered observations at sea (Cody 1974, Ashmole and Ashmole 1967). Foraging distribution as a function of distance from the colony was modelled by Cody (1974) who predicted species replacement along radii extending outward from a colony. Cody's own data failed to support the model (Bédard 1976) and radial replacement of predators could result from radial replacement of prey, rather than optimal return rates as a function of predator size and flight range as predicted by Cody. The asymmetrical distribution of birds around the Pribilof Islands in-

dicates that foraging distribution is not related entirely to distance. Prey type and availability is likely to be related to both distance and direction, and prey distribution will need to be included in any realistic model of seabird foraging.

Analyses of diet relative to oceanographic conditions include those of Bradstreet (1980) and Hartley and Fisher (1936) (see also Briggs *et al.*, this volume), who collected foraging birds from different habitats. Bradstreet found that alcids feeding at onshore ice-edges took different proportions of prey from birds feeding at offshore ice-edges. Hartley and Fisher found that euphausiids were taken by most birds feeding in waters at the foot of a glacier, whereas amphipods appeared in the diets of birds feeding in waters affected by stream runoff. Local variation in diets of breeding seabirds has been reported by Uspenski (1958) and Belopolskii (1957), but no attempt was made to relate these differences to local oceanographic conditions.

Figure 12
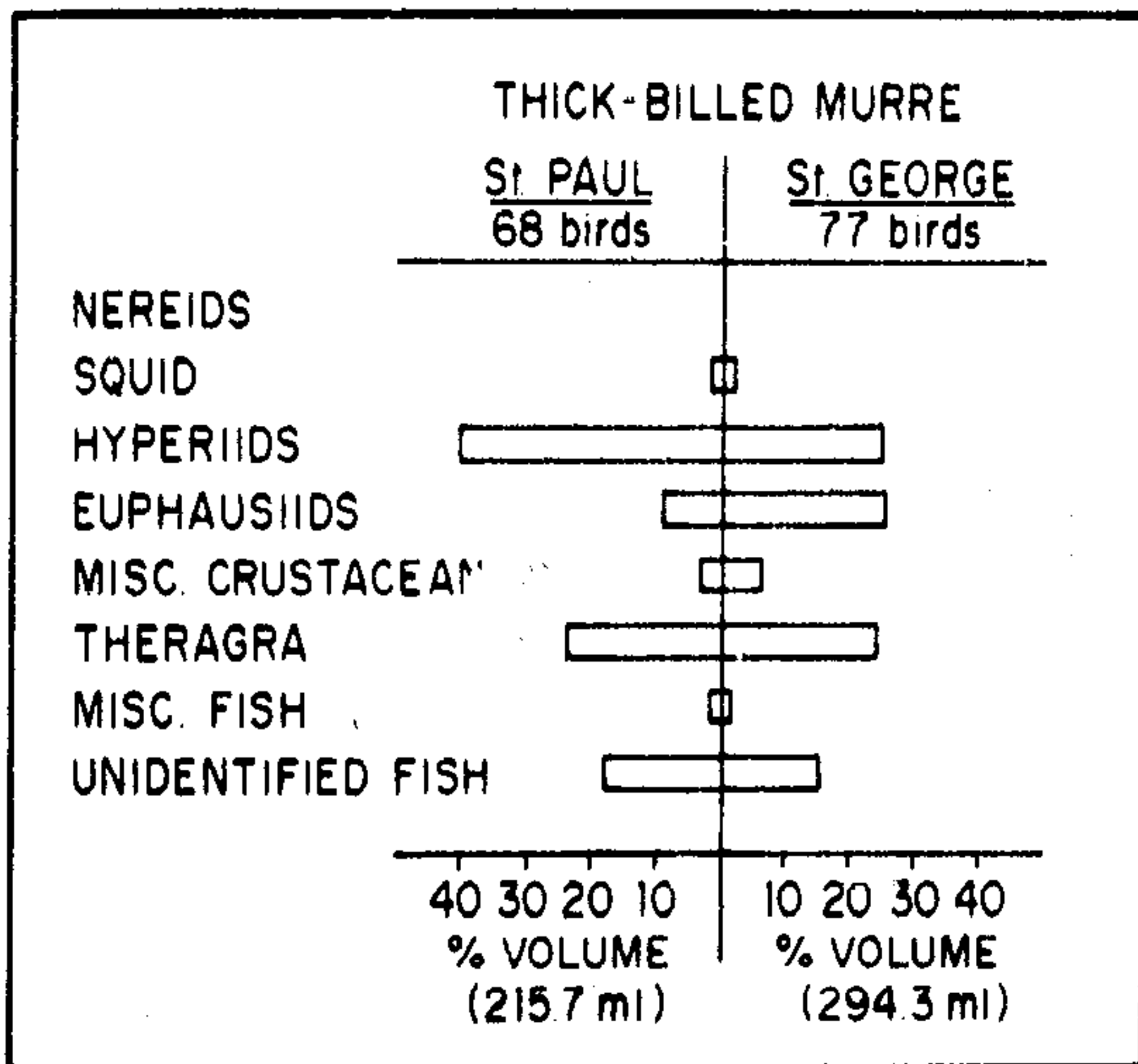Volume of prey in stomach samples of Thick-billed Murres

Figure 13
Number of prey in stomach samples of Thick-billed Murres

Figure 14
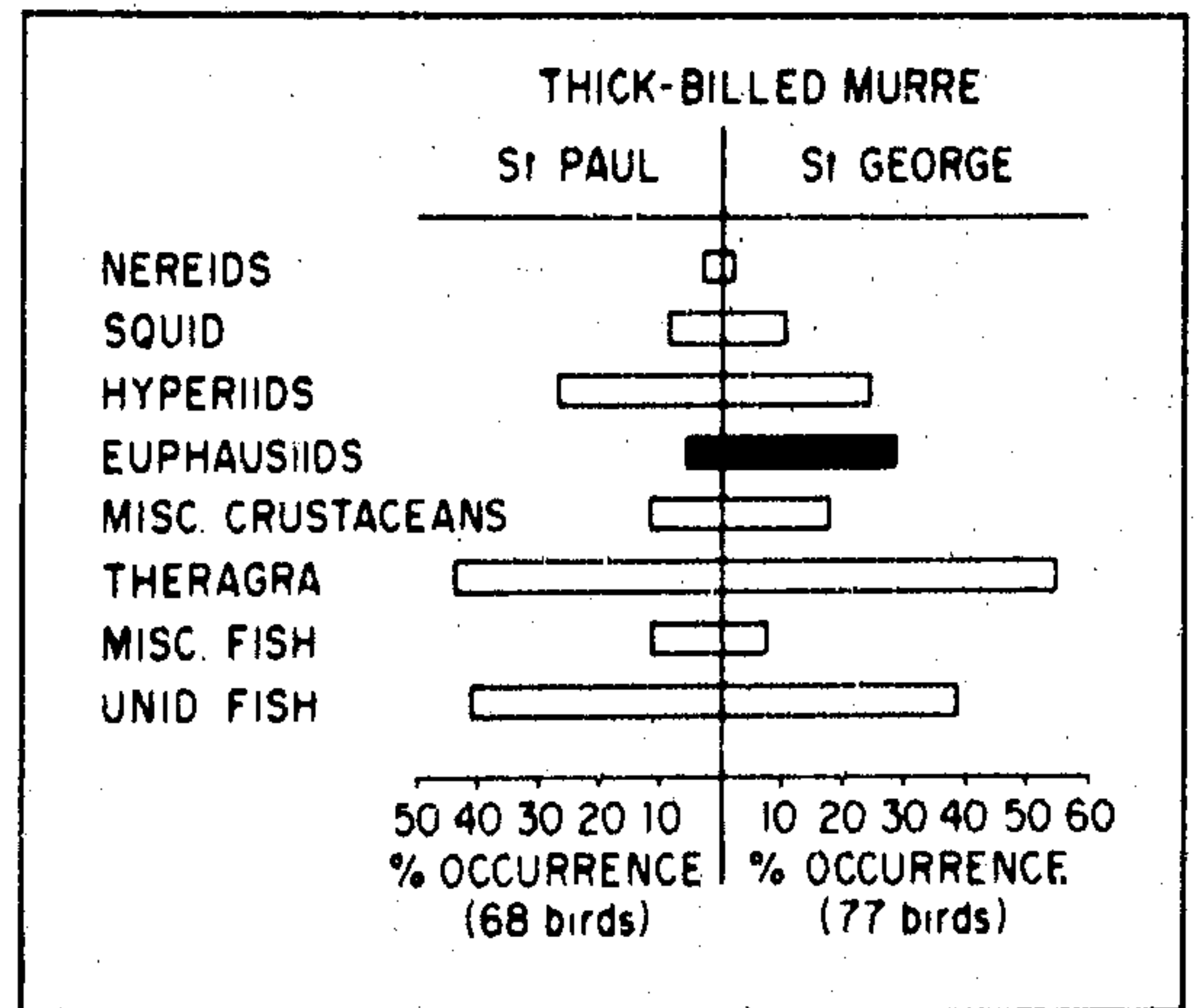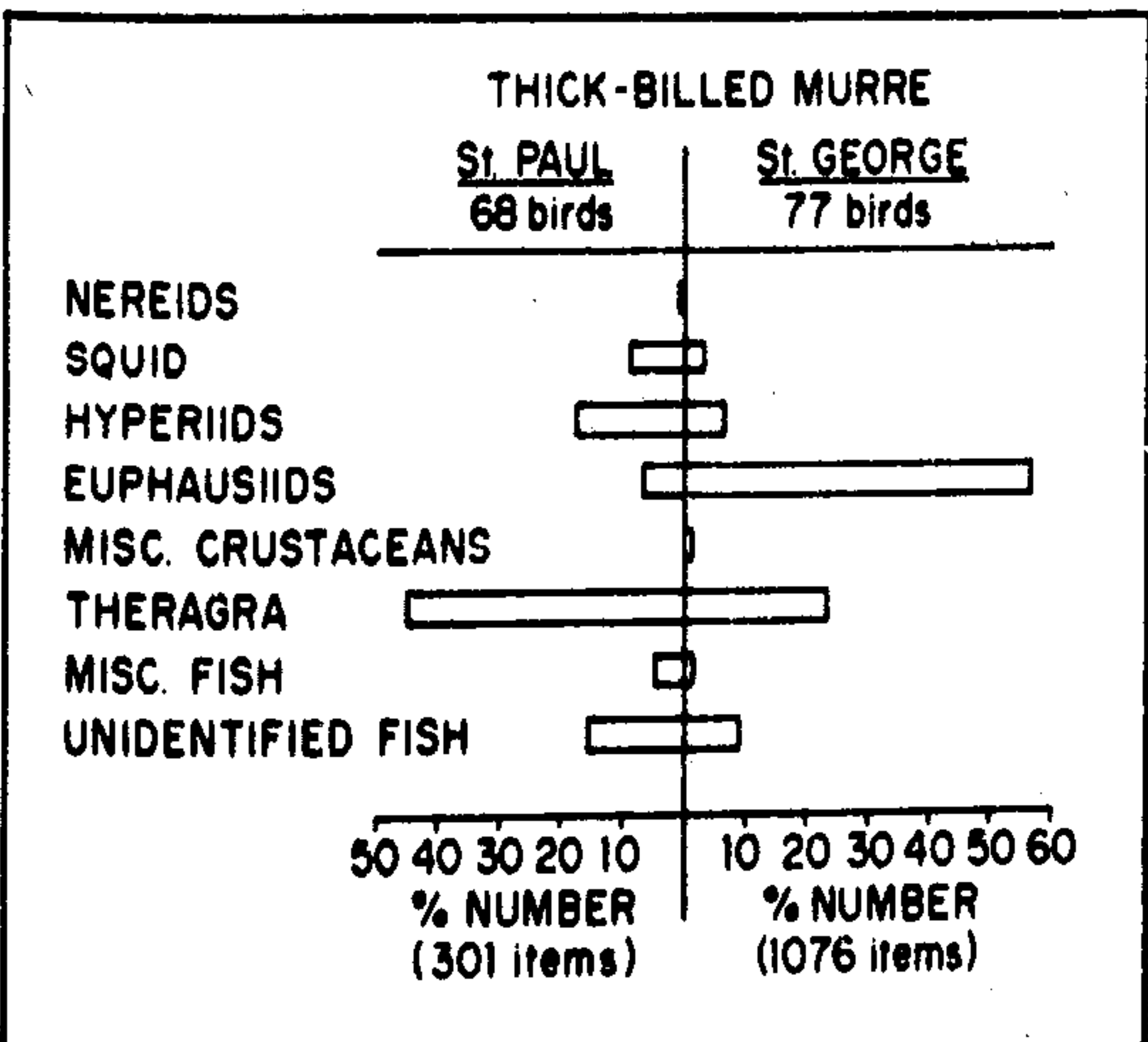Occurrence of prey in stomach samples of Thick-billed Murres. Solid bars: $P = 0.01$

Figure 15
Volume of prey in stomach samples of Red-legged Kittiwakes. Solid bars. $P = 0.01$

RED-LEGGED KITTIWAKE
St. PAUL (112 birds)   St. GEORGE (63 birds)

NEREIDS
SQUID
HYPERIIDS
EUPHAUSIIDS
MISC. CRUSTACEANS
MALLOTUS VILLOSUS
MYCTOPHIDS
THERAGRA
UNIDENTIFIED FISH

60 50 40 30 20 10 | 10 20 30 40 50 60
% NUMBER (728 items)   % NUMBER (188 items)

RED-LEGGED KITTIWAKE
St. PAUL   St. GEORGE

NEREIDS
SQUID
HYPERIIDS
EUPHAUSIIDS
MISC. CRUSTACEANS
MALLOTUS VILLOSUS
MYCTOPHIDS
THERAGRA
UNIDENTIFIED FISH

60 40 20 | 20 40 60
% OCCURRENCE (112 birds)   % OCCURRENCE (63 birds)

Comparison of the two Pribilof colonies suggests that habitat selection occurred relative to oceanographic features that influence productivity and transfer of energy through the food web. Two of the three coastal species (Common Murre and Red-faced Cormorant) were found predominantly on shallow waters to the northeast of the Pribilofs (Table 2), waters with the same mixing regimes found in the coastal and middle shelf domains in the southeastern Bering Sea (Kinder et al., in press). The third species common in coastal colonies, the Black-legged Kittiwake, was found at greater distances from the island than Common Murres and Red-faced Cormorants, but like these two, Black-legged Kittiwakes were most often found on the relatively shallow waters extending to the northeast of the islands, except in the immediate vicinity of St. George Island (Table 2). Thus, elements of these three populations on the Pribilofs used the islands as if they were a coastal site. In contrast, Red-legged Kittiwakes concentrated their foraging in deep waters well offshore (Table 2). This pattern of habitat selection gives this predator access to a prey group (myctophids) that were taken throughout the breeding season, unlike pollock. Myctophids were abundant dietary items from May to September, whereas pollock were taken primarily in July (Hunt et al. 1980).

Wiens et al. (1978) estimated that energy flux near the St. George breeding colony was 18 times greater than energy flux near the St. Paul colony. Much of this difference was due to the large populations of Thick-billed Murres and Northern Fulmars on St. George. The ability of these two species to obtain significant proportions of their diet near the shelf break may be critical for supporting the large populations on St. George Island. Large-bodied zooplankton (Neocalanus cristatus, N. plumchrus, and Eucalanus bungii) appear to be a key link in the food chain. High standing stocks of these species (7–180 g wet weight/m²) occurred along the outer part of the continental shelf in three successive years relative to those in the coastal and middle domain waters (Cooney 1981). These species overwinter at depth as adults, and rise to the surface in the spring to take advantage of the spring phytoplankton bloom. Large copepods are the major prey of juvenile pollock (Clarke 1978) when these fish reach the size range taken by seabirds (Hunt et al. 1981a). Spawning pollock concentrate along the outer shelf and juveniles appear to concentrate in the region of
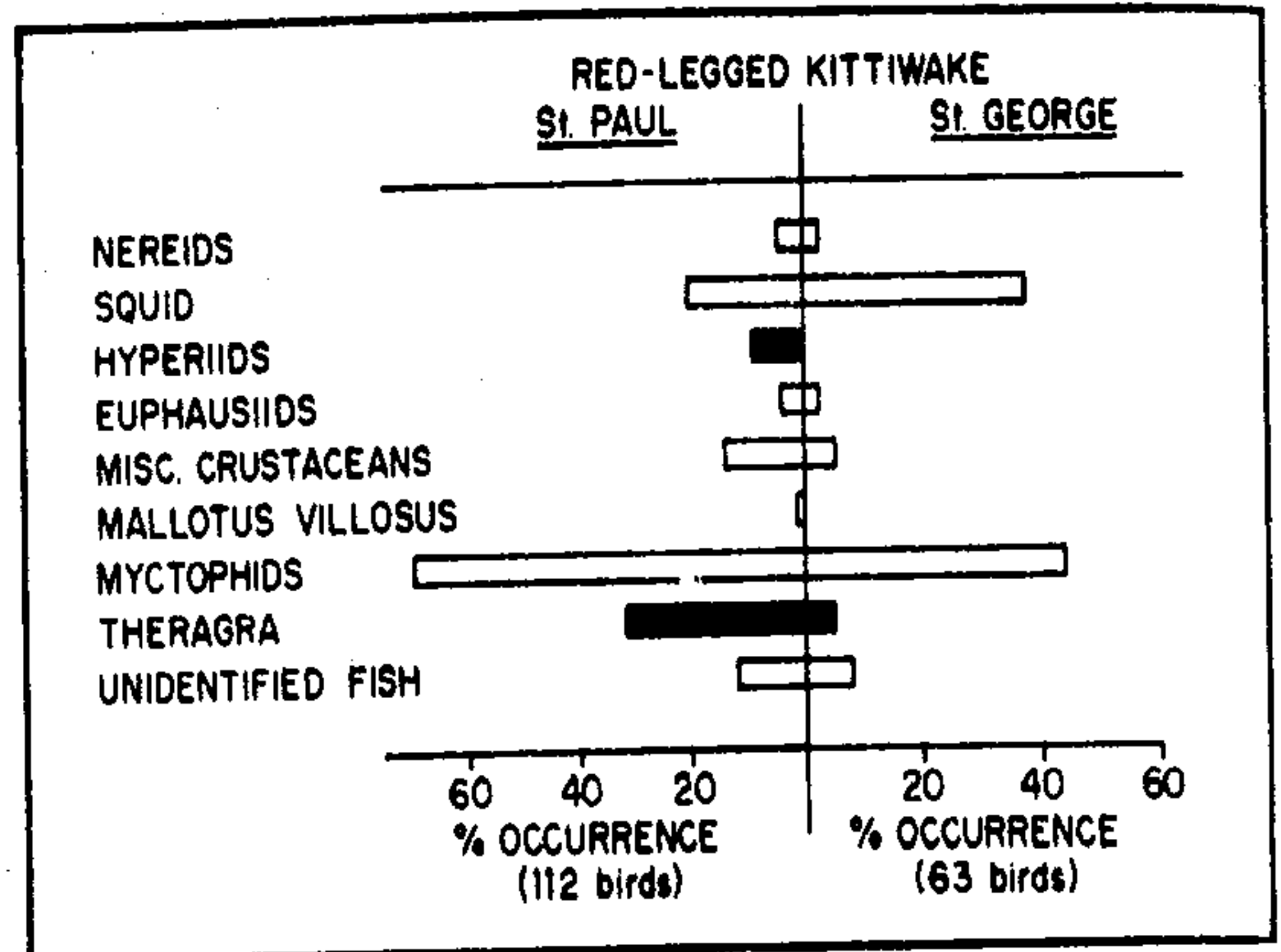
the Pribilof Islands before dispersing outwards across the shelf (Smith 1981).

One feature of the diets of seabirds on the Pribilof Islands is the paucity of surface schooling fish, such as Ammodytes or osmerids. The near absence of these fish in the diets of seabirds at the Pribilofs suggest that these shallow water fish are not abundant around the Pribilof Islands. The two major prey groups at the Pribilofs are a demersal fish (walleye pollock), and species that migrate vertically (myctophid fish and euphausiids). Pollock are important prey on both islands, while the vertical migrants are more important on St. George. Vertical migration may be an important mechanism bringing food to the surface in deep waters south of the islands, while shallow waters may be important in making food accessible to diving birds around the islands and to the north of St. Paul. Ashmole and Ashmole (1967) noted the importance of vertically migrating prey in the ecology of seabirds breeding on oceanic islands in the tropics. Factors that govern vertical migration of nekton may prove to be a major factor in the lives of oceanic, as opposed to coastal breeding seabirds.

Our knowledge of the hydrography of the southeastern Bering Sea has advanced rapidly in the last decade, largely as a result of work sponsored by the Outer Continental Shelf Environmental Assessment Program (National Oceanographic and Atmospheric Administration) and PROBES (Processes and Resources of the Bering Shelf Ecosystem). The concept of a current flowing northward across the shelf, fed by a net influx of North Pacific water through the Aleutian passes, has been replaced by the concept of well differentiated water masses that undergo little net advection, though they oscillate with the tide (Coachman and Charnell 1979, Kinder and Schumacher 1981). The lack of net advection across the shelf in the southeastern Bering Sea has a number of important biological consequences. First, the physical characteristics of the water inhabited by marine life is conditioned by local forces, including heating by the sun, stirring and mixing by the wind and tidal action. Second, critical nutrients such as silicate, nitrates, and phosphates are not replenished by water from elsewhere. Third, there is little opportunity for lateral transport of biological populations.

Understanding of the biological oceanography of the region is still in a state of flux, but at present it is clear that there is an abrupt change in species composition across the shelf, and that this change coincides with the middle front, which is associated with the 100-m isobath. There are differences in population density on either side of the 100-m isobath for several species of zooplankton (Cooney 1981), fish (Bakkala et al. 1979), benthos (Haflinger 1981), and birds (Hunt et al. 1981c). Differences in biomass have been reported in several ecological assemblages, most notably chain-forming diatoms (Goering and Iverson 1981), deposit-feeding infauna (Haflinger 1981) large-bodied copepods (Cooney 1981), and surface-feeding birds (Schneider and Hunt 1982).

Differences in species composition on either side of fronts between water masses are well documented for marine ecosystems. Differences in population density of various organisms on either side of fronts have been reported for the southeastern Bering Sea (Iverson et al. 1979), the North Sea (Joiris 1978), and the Sargasso Sea (Backus et al. 1969). The association between marine birds and water masses is well documented, beginning with the work of Murphy (1936) and extending to the finer scale analyses of Brown et al. (1975) and Pocklington (1979). The asymmetrical distribution of birds around the Pribilof Islands extends this result to the distribution of birds around breeding colonies.

Although the association between marine populations and water masses is well known, the underlying mechanisms are not. In the North Sea, Joiris (1978) emphasized differences in algal mortality and bacterial activity in adjacent water masses. In the Bering Sea, Cooney (1981), Goering and Iverson (1981), Iverson et al. (1979), and Schneider and Hunt (1982) emphasized differential grazing pressure due to the ontogenetic migration of large-bodied zooplankton into surface waters of the outer shelf during the spring bloom. These zooplankton may supply food to surface-feeding birds either directly (storm-petrels) or indirectly through squid and fish (Fulmars and Red-legged Kittiwakes). Lower grazing pressure over the middle shelf allows more phytoplankton to sink to the bottom to feed benthic detritivores and their predators (Haflinger 1981). An important but untested aspect of this hypothesis is that the lateral (especially shoreward) movement of large-bodied zooplankton is limited by the fronts, despite the mobility of these animals. The hypothesis does not account for distribution of diving birds, most notably the large biomass of murres in the outer domain near the Pribilof Islands.

Recent work suggests that some of the mechanisms responsible for the association between marine populations and water masses may be acting at small spatial scales. Cooney (1981) showed that the biomass of large-bodied copepods is high near the shelf-break front, and decreases across the outer shelf domain toward land. Seabirds aggregate at both the shelf break and the inner fronts in Bristol Bay (Schneider 1982), and significant aggregations of murres associate with fronts around the Pribilof Islands (Kinder et al. 1983). Seabirds need to be examined relative to large- and small-scale physical and biological phenomena to understand the trophic processes that link them to marine ecosystems.

In summary, the two Pribilof colonies differed in colony composition, diet of individual species, and distribution of birds around the colony. An understanding of the physical factors that influence marine food webs suggests that these differences between the two colonies are a function of the heterogeneous ocean that surrounds the colonies.

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