Prey selection by Oldsquaws in a Beaufort Sea lagoon, Alaska

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1. Abstract

The feeding ecology of Oldsquaws (*Clangula hyemalis* L.) was investigated during July–September of 1977–78 in Simpson Lagoon on the Beaufort Sea coast of Alaska. Few species of prey were available. Volumetric analyses of the stomachs of actively feeding birds collected systematically throughout both summers indicated that the diet consisted 70% of two mysids (*Mysis relicta* and *M. litoralis*) and 15% of one amphipod (*Onisimus glacialis*). The remainder of the diet was mainly bivalves. Oldsquaws fed primarily in the portions of the lagoon that ranged from 2 to 3 m in depth, where prey densities were highest. Oldsquaws fed selectively on larger mysids and amphipods, and preyed most effectively (more food found in their stomachs) in areas where prey was most dense and biomass was greatest.

2. Résumé

De juillet à septembre 1977 et 1978, nous avons étudié l'écologie alimentaire des Canards kakawis (*Clangula hyemalis* L.) dans le lagon de Simpson, sur la côte de la mer de Beaufort, en Alaska. Nous avons trouvé peu d'espèces de proies. En effet, d'après l'analyse volumétrique des estomacs des oiseaux qui se nourrissaient activement et qui ont été recueillis systématiquement durant les deux étés, le régime de ces canards se composait essentiellement de 70 % de deux mysis (*Mysis relicta* et *M. litoralis*) et de 15 % d'un amphipode (*Onisimus glacialis*). À cela s'ajoutaient des bivalves. Les Canards kakawis se nourrissaient surtout dans les parties du lagon d'une profondeur de 2 à 3 m où la densité des proies était la plus forte. Ils choisissaient de préférence les mysis et les amphipodes les plus gros et pêchaient plus efficacement (jugé d'après une plus grande quantité de nourriture dans leur estomac) dans les zones où les proies étaient les plus denses et la biomasse, supérieure.

3. Introduction

Tens of thousands of male Oldsquaws and a small number of non-breeding females congregate in nearshore Beaufort Sea lagoons during July and August (Johnson and Richardson 1982). In contrast, breeding female Oldsquaws remain with their broods on freshwater tundra lakes and ponds, often until ice forces them to leave these for the coastal lagoons in mid to late September. This paper describes the feeding relationships between Oldsquaw ducks (*Clangula hyemalis*) and their invertebrate prey in Simpson Lagoon, one of a series of shallow lagoons on the north coast of Alaska (Fig. 1).

The main purpose of this study was to determine which prey organisms formed the important components of Oldsquaw diets in the study area, and to determine the relationship between prey availability and prey selection by feeding Oldsquaws. Investigations of the feeding ecology of marine birds provide a key link in the interpretation of the relationship between biological productivity and abundance of birds. The studies of Oldsquaws were part of a larger interdisciplinary study of ecological processes (LGL 1981).

4. Methods

4.1. Collection of birds and habitat samples

The procedures for collecting Oldsquaws and Oldsquaw feeding habitat samples during 1977 were the following:

1. A flock of Oldsquaws was located and watched for 3–5 min to determine whether some birds appeared to be feeding by diving. An estimate was made of the flock size.
2. Observers then sped into the flock by boat (4.9-m Zodiac with 35-hp outboard), dropped an anchored buoy into the water as the vessel slowed, and shot as many birds as possible (generally three to eight individuals).
3. Birds were retrieved and labelled. To mitigate post-mortem digestion, the esophagus, proventriculus, and gizzard were injected immediately with absolute isopropyl alcohol. The esophagus was then plugged with paper.
4. Habitat sampling occurred after the collecting party returned to the buoy.

a. For each set of birds collected, two zooplankton samples were obtained, one from the surface water and another from the mid-water column. This was accomplished by towing both a surface-supported 14-by-10-cm neuston net (mesh size 0.079 mm) and a submerged (1-m deep) 0.25-m diameter macroplankton net (mesh size 0.239; see Griffiths and Dillinger (1981) for more details of sampling equipment).

b. One sample from the lagoon epibenthos (bottom community) was collected. From a stationary boat in the area of the buoy the 0.25-m macroplankton net was towed manually across the bottom of the lagoon for a distance of approximately 10 m at a speed of approximately 0.5–1.0 m/s. The water depth at this location was measured with the buoy rope. Observations by SCUBA divers in this study indicated that the epibenthic community in Simpson Lagoon extended from the bottom surface upward to about 0.25–0.75 cm and included a suspension of detrital material several centimetres thick. The 0.25-m macroplankton net was a relatively crude device for sampling the epibenthos;

no doubt many fast-moving organisms (e.g. mysids) escaped from the net before it could be retrieved. The net often bounced along the bottom and scraped a thin layer of mud and accompanying infaunal organisms from the top 1 cm of bottom substrate.

c. Habitat samples were washed immediately from the sampling nets and preserved in 10% neutral Formalin.

During 1977, 31 collections of Oldsquaws ($\bar{x}$ = 2.8 birds/collection; total = 87) were made in Simpson Lagoon from 11 July through 14 September. During 1978, 45 collections ($\bar{x}$ = 2.4 birds/collection; total = 108) were made in Simpson Lagoon from 10 July to 27 September. The same general procedures for collecting Oldsquaws were followed in both 1977 and 1978. Prior to making collections in 1978, however, some flocks were watched more carefully and longer (10–30 min) to determine whether they appeared to be feeding. Of the 81 feeding birds that were collected in 1978, 65 (80%) had identifiable food in their stomachs, whereas of the 27 birds that were taken indiscriminately with no prior observations of behaviour, only 7 (26%) contained some identifiable food. During 1977, 54 (62%) of the Oldsquaws collected had identifiable food in their stomachs; that proportion was similar to the overall value for the 1978 collections (67%). Thus, optimum use and least wastage of Oldsquaw specimens depends on adequate observation to determine that the birds are actively feeding and will be useful in prey analyses.

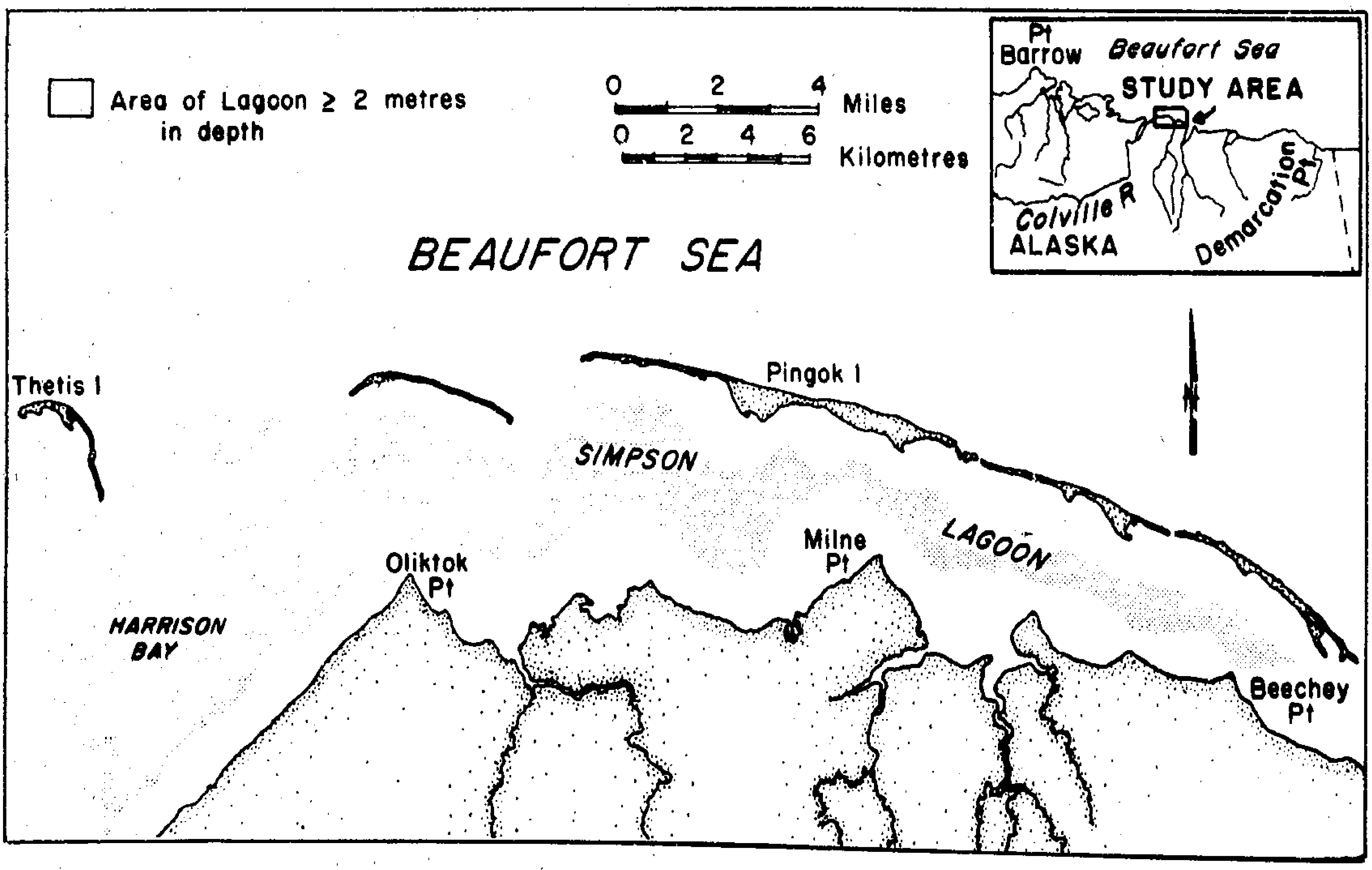
Studies during 1977 (Griffiths and Dillinger 1981, Johnson and Richardson 1981) indicated that Oldsquaws fed primarily on epibenthic invertebrates and bivalves found on or near the lagoon bottom. Therefore, during 1978, samples for analyses of food availability were collected only from this level of the lagoon. To minimize escapement of mobile epibenthic animals, the drop-net method (mesh 1.0 mm; Fig. 2) of Griffiths and Dillinger (1981) was substituted in 1978 for the 0.25-m macroplankton net tows. The drop net sampled from the bottom surface of the lagoon (including approximately 1 cm of substrate) and also from the bottom 95 cm of the water column. Three to five drop-net samples were collected immediately at each location where birds were collected.

4.2. Laboratory techniques

Within 24 h of collection all birds were dissected in a field laboratory and food items were preserved. The esophagus, proventriculus, and gizzard were removed as a single unit from each bird. During 1978 this unit was slit lengthwise, and an arbitrary measure of fullness (Hynes 1950, Griffiths *et al.* 1975; see below) was assigned to the total unit. A cursory and tentative description of the contents was also recorded. These contents were then washed with 10% neutral Formalin into a 227-mL bottle for later re-examination. During 1977 no measure of fullness was assigned in the field, but all other procedures were the same.

To assess and compare the importance of various invertebrate taxa in the diet of Oldsquaws in 1977 and 1978, the preserved stomach contents were sorted by trained invertebrate zoologists, and an estimate was made of the

Figure 1
Simpson Lagoon, Alaska



relative volume of each major taxon (e.g. amphipod, mysid, copepod, isopod, and so on) following the procedures developed by Hynes (1950) and modified by Griffiths *et al.* (1975). Twenty points were assigned to the fullest Oldsquaw stomach analysed. The fullness of each other stomach was subsequently gauged against the fullest stomach, and a corresponding number of points were assigned. After the sample had been sorted, and after each major taxon had been bottled, the total number of points thus assigned to each stomach was partitioned among the major invertebrate taxa present according to the relative volume of each. No distinction was made between whole organisms and fractions thereof. Pieces of unidentified organisms were classified as such.

During 1977 and 1978, each habitat sample was sorted and bottled by major taxon. Twenty points were assigned to the total volume of each sample, and then an estimate of the relative proportions (volumes) of the total 20 points was assigned to the various major taxa in the sample.

During 1977 the two most important taxa (mysids and amphipods) present in the stomachs and habitat samples were sorted further, identified to the species level, and weighed (Formalin wet weight). For a size comparison, 20 individuals each of mysids and amphipods were selected randomly from each Oldsquaw stomach and from its associated habitat samples; these individuals were measured to the nearest millimetre. During 1978 a much more detailed system of sorting and measuring was adopted: all individuals present in the stomachs and habitat samples were sorted to major taxa, identified to the species level, counted, weighed, and measured.

No studies were conducted to determine if the contents of the esophagus, proventriculus, and gizzard differed significantly. Therefore, as shown by Bartonek (1968), Bartonek and Hickey (1969), and Swanson and Bartonek (1970), some bias in prey analysis may have resulted because of differential digestion in these portions of Oldsquaw digestive tracts. Very few soft-bodied invertebrates were found in Oldsquaw digestive tracts or their feeding habitat (epibenthos), however, and our detailed laboratory analyses in 1978 confirmed that the broken shells of bivalves and the telsons and adjacent urosomes of mysids and amphipods remained identifiable and measurable in Oldsquaw gizzards. Reference collections were made of all Oldsquaw prey organisms, and regression equations were developed to relate the partial length of incompletely digested invertebrate organisms to total length, weight, and caloric value of whole organisms of the same species. Further details of the identifying, sorting, counting, weighing, and measuring procedures followed during 1977 and 1978 are described in Griffiths and Dillinger (1981).

All results presented are of the total seasonal diets of Oldsquaws. Cluster analyses (see Clifford and Stephenson 1975:134 for procedures) indicated no justification for further, more detailed categorizations of early, middle, and late season diets of Oldsquaws.

5. Results

5.1. Oldsquaw diet

Of the 87 Oldsquaws collected during 1977, 15 had empty stomachs and 18 contained only unidentifiable material. The average diet of the remaining 54 birds included, on a percent estimated volume basis, 58.7% mysids, 14.2% amphipods, 8.1% bivalves, 2.3% isopods, 2.3% small fishes, and 14.2% unidentifiable material (Table 1).

The Oldsquaw diet during 1978 was similar to that in 1977 (Morisita Similarity Index, $C = 0.74$; Horn 1966). Of the 108 Oldsquaws collected during 1978, 34 had empty stomachs and 2 contained only unidentifiable material. The average diet of the remaining 72 birds, on a percent estimated volume basis, was 68.5% mysids, 15.5% amphipods, and 12.1% bivalves (Table 1). Unidentifiable material comprised a much smaller portion of the stomach contents in 1978 (1.5%) than in 1977 (14.2%) because of the availability of completed reference collections and improved identification procedures in the second year of study.

Table 2 provides a comparison of the proportions of major taxa found in Oldsquaw stomachs as determined by precise measurements of wet weight, ash-free dry weight, energy content (kilocalories), and abundance (total individuals) as well as by the qualitative, modified Hynes Point method. The Hynes Point method proved to be a relatively accurate indicator of the proportion and importance of various major taxa of prey organisms consumed by Oldsquaws. Percentages computed from Hynes Point values were almost identical and were not significantly different ($P > 0.05$) from percentages computed from ash-free dry weight and energy content values (see Table 2).

The main prey species were the mysids *Mysis litoralis* and *M. relicta*, the amphipod *Onisimus glacialis*, and the bivalves *Portlandia arctica* and *Cyrtodaria kurriana* (Table 3).

5.2. Prey availability

Gear used for surface and mid-water collections in 1977 probably provided a reasonably accurate indicator of prey availability there, but epibenthic invertebrates of the

Table 1
Percentage volumetric comparison of Oldsquaw diet in relation to composition of epibenthic samples from Simpson Lagoon

	1977		1978	
Prey	Oldsquaw diet (N = 54; total points* = 443)	Epibenthic samples (N = 18; total points = 160)	Oldsquaw diet (N = 72; total points = 422)	Epibenthic samples (N = 39; total points = 166†)
Mysids	58.7	28.1 (42.5)†	68.5	48.9
Amphipods	14.2	27.5 (41.5)	15.5	36.6
Bivalves	8.1	1.9 (2.8)	12.1	7.1
Isopods	2.3	0	1.0	1.1
Fishes	2.3	0	0.2	0.3
Copepods	0.1	33.8	0.2	0.5
Polychaetes	0	1.9 (2.8)	0.7	2.4
Euphausiids	0	0	0.2	0
Priapulids	0	0	0.1	1.1
Tunicates	0	0	0.1	0.6
Cnidarians	0	2.5 (3.8)	0	0.8
Pteropods	0	3.1 (4.7)	0	0
Ostracods	0	0.6 (0.9)	0	0
Foraminiferans	0	0.6 (0.9)	0	0
Sponges	0	0	0	0.1
Chaetognaths	0	0	0	0.4
Cumaceans	0	0	0	0.1
Unidentifiable	14.2	0	1.5	0
Total	99.9	100.0	100.1	100.0

*See Griffiths *et al.* (1975) for a description of the points method for assessing the relative importance of food organisms

†Recomputed percentages after omitting copepods, whose appearance in epibenthic samples may have been an artifact of the sampling method

types important to Oldsquaws were especially difficult to sample quantitatively. Methods used to sample such animals in 1978 were much improved over those used in 1977. These problems must be recognized when interpreting the data concerning food availability.

Few mysids or amphipods were collected from the surface waters of the lagoon (Fig. 3). This evidence, plus our observations and published information (see Discussion) on the diving behaviour of Oldsquaws, indicated that Oldsquaws probably rarely feed in this layer. The predominant invertebrate taxa present in this layer during 1977 were, on an estimated percent of total volume basis, copepods (68.1%) and cnidarians (16.7%). Most of the remainder of the organisms collected in this habitat were amphipods (5.7%) and chaetognaths (3.3%).

Copepods represented almost two-thirds (64.4%) of the total volume of invertebrate organisms present in the mid-water habitat samples (Fig. 3); this proportion was similar to that found in the surface water samples. Mysids and amphipods comprised 11.7 and 9.4%, respectively, of the mid-water samples. Cnidarians, chaetognaths, and ctenophores represented a major proportion of the remainder of the mid-water samples during 1977.

Copepods, mysids, and amphipods comprised the major proportions (33.8, 28.1, and 27.5%, respectively) of the epibenthic samples collected during 1977 (Table 1). Observations by a SCUBA diver at several locations in Simpson Lagoon during 1977 and 1978, indicated that mysids and amphipods were the most conspicuous invertebrate organisms present in the epibenthos (Griffiths and Dillinger 1981). The relatively large volume of copepods in the "epibenthic" samples taken during 1977 was probably an artifact of the sampling equipment (0.25-m

Figure 2
Shallow water drop net used to sample invertebrates in Simpson Lagoon

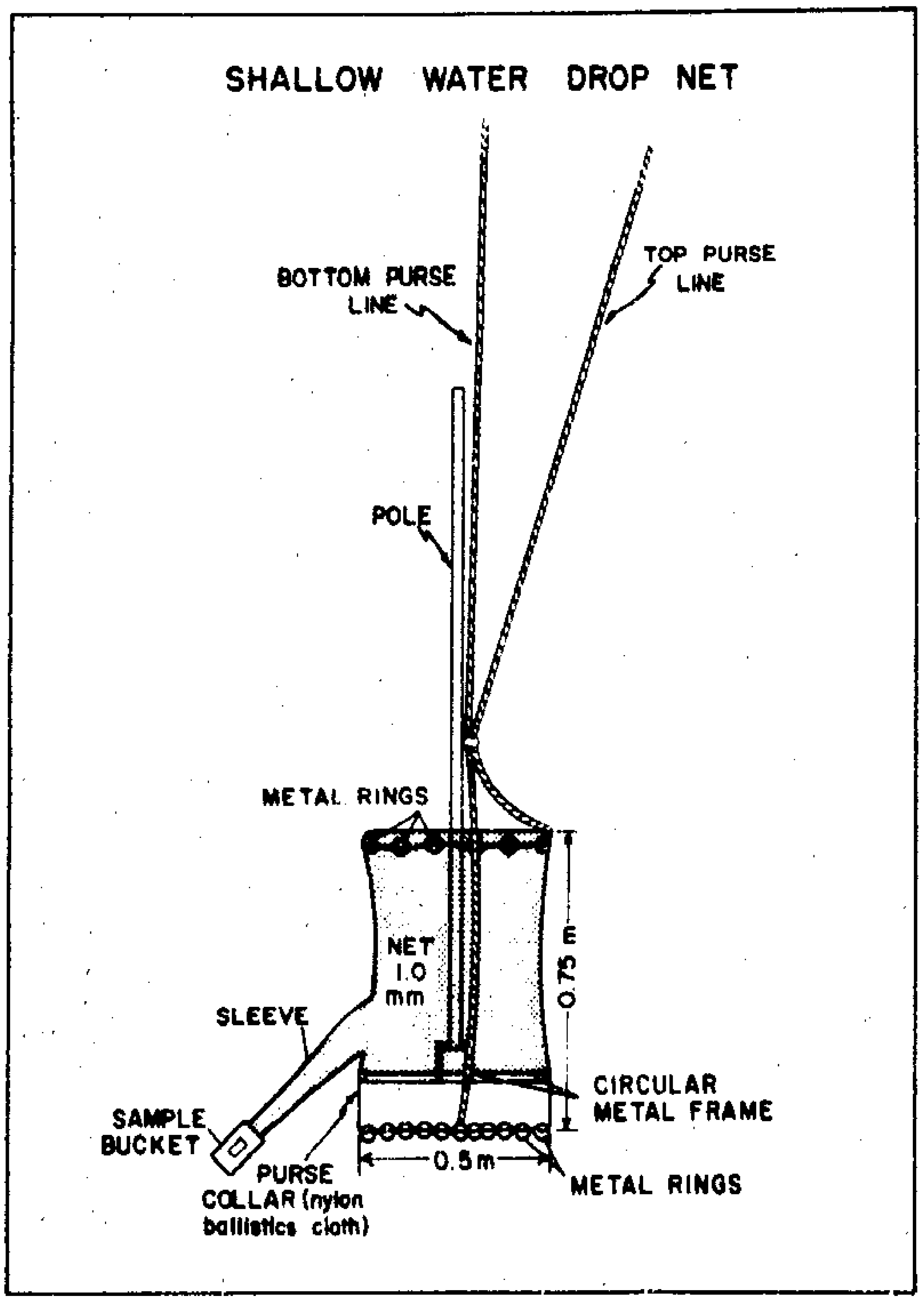


Table 3
Identifiable prey consumed by Oldsquaws in Simpson Lagoon*

Prey	1977 Oldsquaws (*N* = 54)	1978 Oldsquaws (*N* = 72)
Mysids		
Mysis litoralis and *M. relicta*	67.6	79.7
Amphipods		
Onisimus glacialis	8.0	10.4
Parathemisto spp.	4.9	0.3
Gammarus setosus	1.7	0.8
Gammaracanthus loricatus	1.2	0.7
Apherusa glacialis	<0.1	—
Pontoporeia affinis and *P. femorata*	—	<0.2
Bivalves		
Cyrtodaria kurriana	7.1	5.1
Portlandia arctica	2.4	1.1
Isopods	2.7	0.9
Fishes	2.7	0.4
Copepods	1.2	<0.1
Cumaceans	—	0.1
Euphausiids	—	0.1
Polychaetes	—	0.1
Others	—	0.3
Total	99.7	100.3

*Presented as percent composition (wet weight).

Table 2
Diet of Oldsquaws in Simpson Lagoon during 1978 as determined by various measures

	Volume		Abundance		Wet weight		Ash-free dry weight		Energy content	
Prey	**Points***	**%**	**No.**	**%**	**g**	**%**	**g**	**%**	**kcal**	**%**
Mysids	289	68.5	6464	75.0	155.1	77.4	17.9	69.7	97.5	69.8
Amphipods	65¼	15.5	1845	21.4	23.7	11.8	4.2	16.3	21.3	15.3
Bivalves	51¼	12.1	260	3.0	13.3	6.6	2.6	10.1	14.7	10.5
Other taxa	16½	3.9	48	0.6	8.3	4.1	1.0	3.9	6.1	4.4
Total	422	100.0	8617	100.0	200.4	99.9	25.7	100.0	139.6	100.0

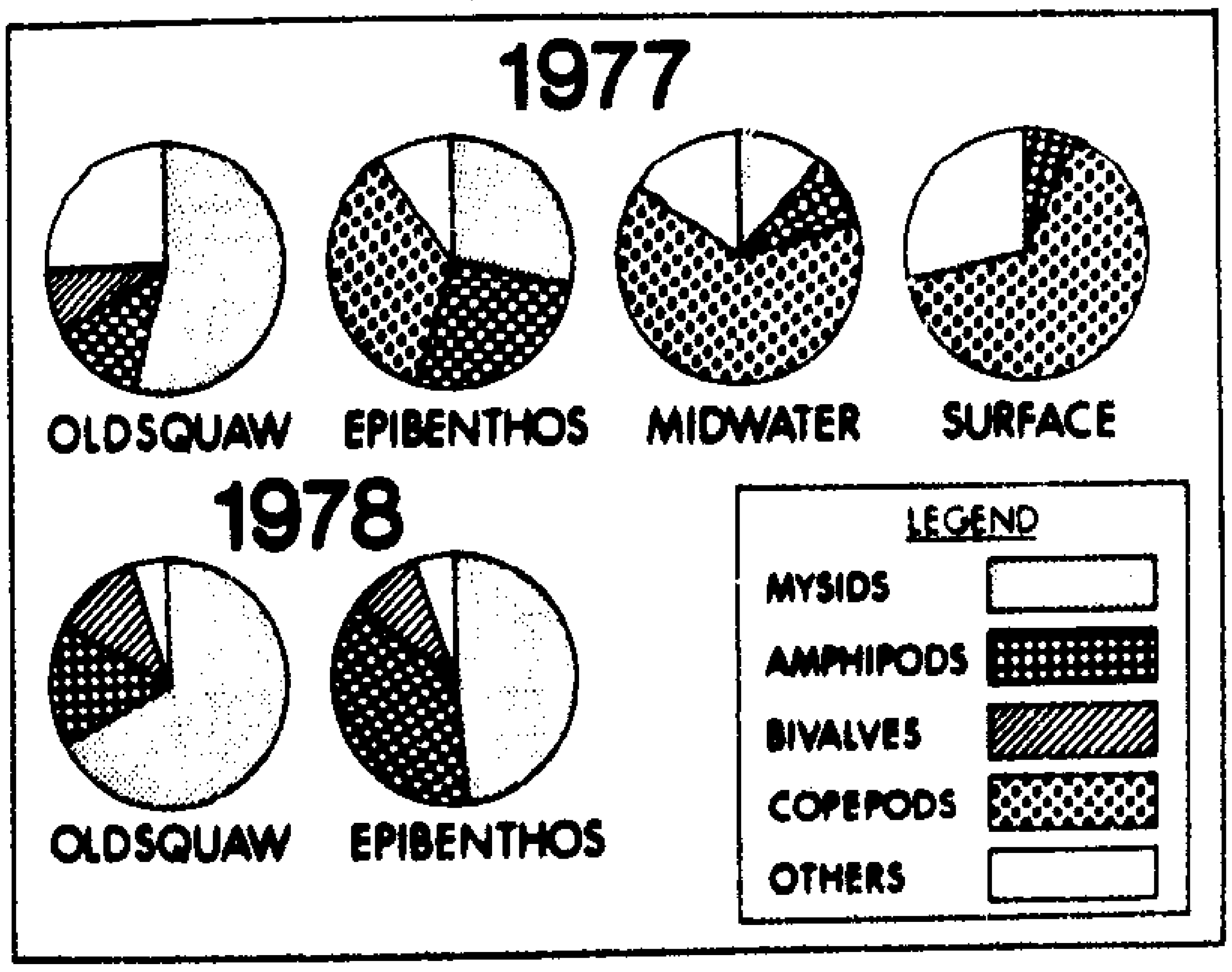
*See Griffiths *et al.* (1975) for a description of the points method for assessing the relative importance of food organisms. Points listed in this table are only those of identifiable taxa.

macroplankton net); they presumably were taken in the water column as the net sank and was retrieved.

Because both mysids and amphipods, the organisms that comprised the major proportions of the diet of Oldsquaws during 1977, were proportionately most abundant in the lagoon epibenthos, oldsquaws probably fed almost exclusively from this habitat rather than from either the surface or the mid-water layers where mysids and amphipods were relatively uncommon. The few copepods in the diet of Oldsquaws during 1977 may have been taken incidentally during the process of feeding on other epibenthic invertebrates (Table 1, Fig. 3).

Mysids and amphipods collectively represented 85.5% of the estimated volume of invertebrates in the 1978 epibenthos samples. Although the drop-net sampling technique was not designed as an infaunal sampler, a notably larger proportion of the estimated volume of epibenthic samples consisted of bivalves in 1978 (7.1%) than in 1977 (1.9%). Differences in wet weights of bivalves in 1977 (9.5%) and 1978 (6.2%) were not as marked, however (Table 3). Perhaps because more effective sampling gear was used during 1978, the relative importance of copepods in the epibenthos was markedly lower in 1978 (0.5% of estimated volume) than in 1977 (33.8%).

Figure 3
Volumetric composition of Oldsquaw diets and feeding habitat samples in Simpson Lagoon



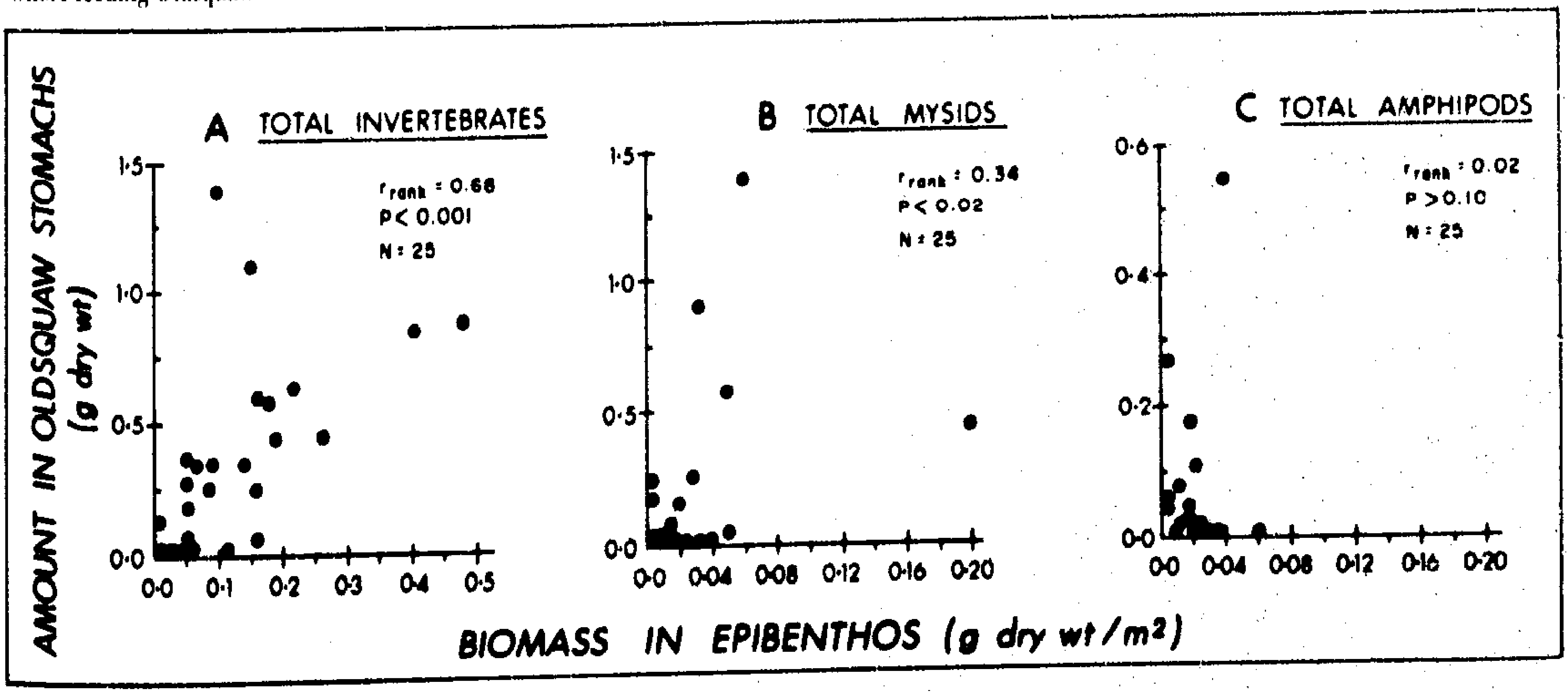
5.3. Selectivity in diet

The results from 1978, when more effective epibenthic sampling gear was used, show a generally close relationship between the relative volumes of major invertebrate taxa in Oldsquaw stomachs and in the epibenthic habitats (Table 1, Fig. 3). Furthermore, the weights of invertebrates as a group, and of mysids in particular, in the stomach contents of individual Oldsquaws were positively and significantly correlated with the availability of these animals in the epibenthos at the place and time of collection (Fig. 4). However, diet was not totally parallel to food availability. In both 1977 and 1978 the relative proportions of mysids found in Oldsquaw stomachs were substantially greater than those found in feeding habitats (Table 1). The differences in 1977 between mysids in the diet and in the epibenthos remain large even if copepods are not considered in the epibenthos percentage computations.

In contrast to the mysids, the weights of amphipods in the stomachs in 1978 showed no positive or significant correlation with the availability of these animals in the epibenthos (Fig. 3). During both 1977 and 1978, the proportions of amphipods in Oldsquaw stomachs were about half those found in feeding habitats (Table 1).

Data from both 1977 and 1978 indicate that, on the basis of the total season diet, the average sizes of mysids and amphipods consumed by Oldsquaws were significantly larger than the average sizes of the same species found in the epibenthos (Table 4; Fig. 5). Hence, in Simpson Lagoon,

Figure 4
Relationship in Simpson Lagoon in 1978 between amount of prey in stomachs of feeding Oldsquaws and the biomass of prey in the epibenthos where feeding Oldsquaws were collected



feeding Oldsquaws apparently tended to select larger individuals of at least the most common prey species, especially mysids, found in epibenthic feeding habitats. In 1978, this selection by Oldsquaws of the large size classes of invertebrates is most apparent during mid July for all major prey consumed, and is less apparent later in the season, especially for *Mysis litoralis* (Table 5).

6. Discussion

Oldsquaws in Simpson Lagoon, as at other locations, are largely opportunistic feeders — they prey on organisms in accordance with their availability. In coastal wintering areas in North America (Stott and Olson 1973; Vermeer and Levings 1977, Sanger and Jones 1981), as in Europe (Madsen 1954, Nilsson 1972, Bagge *et al.* 1973), Oldsquaws feed extensively on those organisms that are most abundant, primarily epibenthic crustaceans and molluscs. Gjosaeter and Saetre (1974) reported Oldsquaws and eiders feeding extensively on the eggs of capelin (*Mallotus villosus*) during the spawning season of this fish in the Barents Sea.

In freshwater habitats also, Cottam (1939), Bengtson (1971), and Pehrsson (1974) showed that abundant crustaceans comprise a major proportion of the diet of Oldsquaws. Lagler and Wienert (1948) reported crustaceans and molluscs to be important prey of Oldsquaws at locations in Lake Michigan where Eggleton (1936) had earlier found the greatest abundance of these invertebrates. An analysis of stomachs of Oldsquaws taken from gill nets in Lake Michigan showed them to be opportunistic in their feeding behaviour. There was a close relationship between the prey items in groups of ducks taken in the same haul of nets; therefore it was concluded that the Oldsquaws were simply utilizing, on a non-selective basis, whatever food resources were available in the area in which they were taken (R.S.

Table 4
Comparison of the sizes of the most important marine invertebrates taken from Oldsquaw stomachs and from the epibenthos in Simpson Lagoon

Prey species	Prey length in Oldsquaw stomach, mm	Prey length in epibenthic sample,* mm	N	Z†	$P<$
1977					
Mysis litoralis	13.3 ± 2.6‡	10.7 ± 3.4	20	1.97	0.06
Mysis relicta	12.7 ± 1.4	10.6 ± 1.5	20	2.91	0.01
Onisimus glacialis	5.6 ± 1.2	4.4 ± 1.7	20	2.35	0.03
1978					
Mysis litoralis	12.4 ± 2.2	8.9 ± 3.5	20	2.89	0.01
Mysis relicta	12.1 ± 1.9	8.8 ± 2.1	20	2.61	0.02
Onisimus glacialis	5.8 ± 1.0	4.2 ± 0.8	20	2.94	0.01

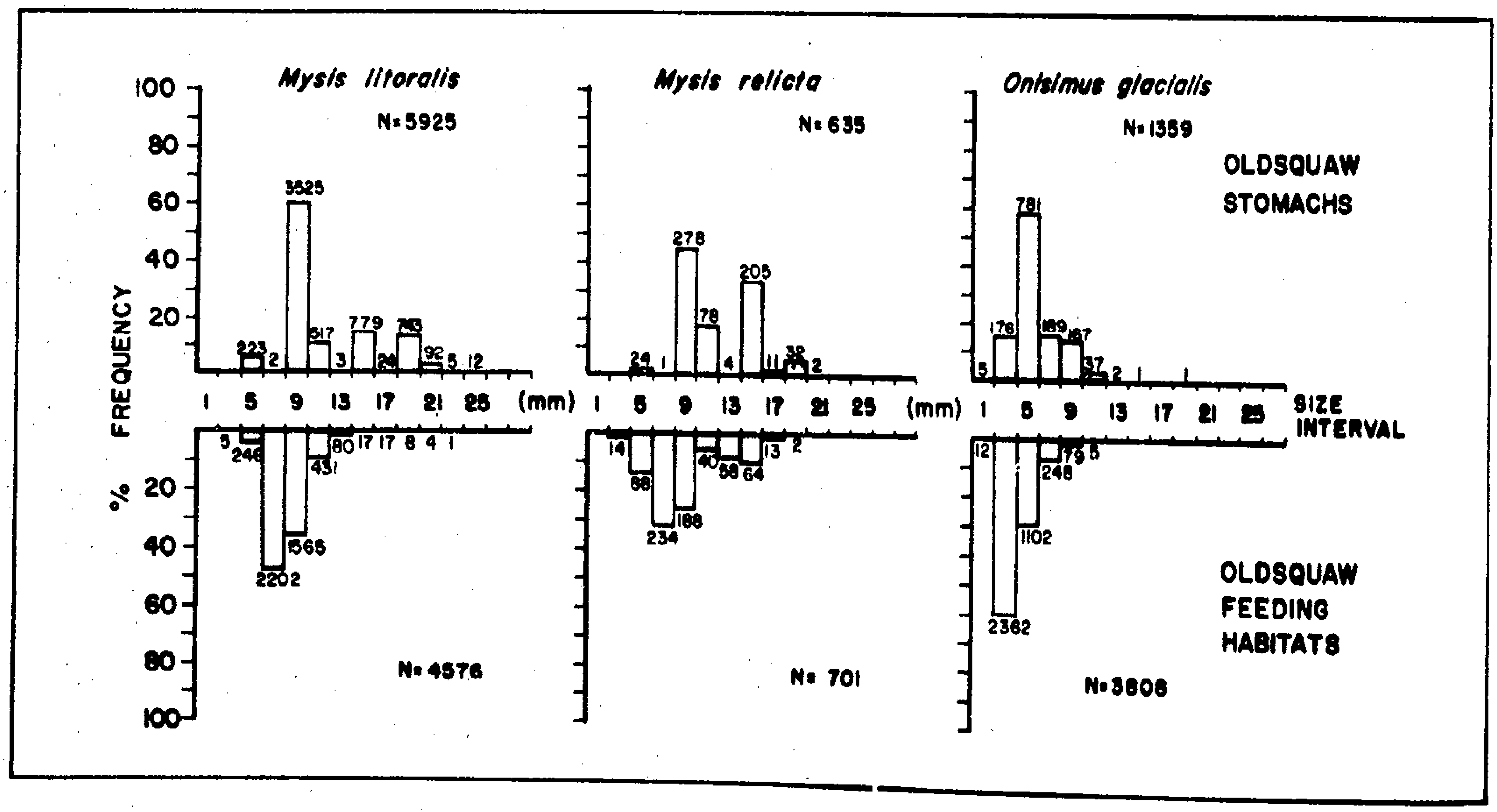
*Epibenthic samples were collected at the locations where birds were collected.
†Wilcoxon's matched-pairs tests
‡Mean ± standard deviation.

Table 5
Comparisons of sizes of prey available and eaten by Oldsquaws in Simpson Lagoon during 1978

Prey species	Overlap index* for various sampling periods			
	Mid July (N = 8–14)†	Early-August (N = 5–12)	Mid August (N = 5–13)	Late August (N = 10–13)
Mysis litoralis	0.12	0.09	0.82	0.83
Mysis relicta	0.21	0.64	0.85	0.71
Onisimus glacialis	0.37	0.65	0.75	0.82

*Morisita Overlap Index (Horn 1966).
†N = range in number of stomachs compared.

Figure 5
Distribution of sizes of prey in the stomachs of feeding Oldsquaws and in the epibenthos where feeding Oldsquaws were collected



Ellarson, pers. comm. 1982). In northern Sweden, Pehrsson (1973) found that both female Oldsquaws with broods and other post-breeding Oldsquaws selected and were concentrated on lakes that supported high densities of euphyllopod crustaceans. Hull (1914) and Ellarson (1956:215) recorded Oldsquaws feeding on locally abundant minnows in Lake Michigan.

The relationship between Oldsquaws and their benthic prey in Simpson Lagoon is remarkably similar to that in portions of Lake Michigan. In Simpson Lagoon the principal prey of Oldsquaws consisted of two species of mysids, two amphipods, and two bivalves. The two mysids and *Onisimus glacialis* are epibenthic-dwelling crustaceans. In Simpson Lagoon and many other lagoons along the Beaufort Sea coast these crustaceans are associated with a detrital suspension several centimetres thick on the lagoon bottom (Griffiths and Dillinger 1981).

In Lake Michigan, Peterson and Ellarson (1977) found the primary prey to be a single species of epibenthic amphipod (*Pontoporeia affinis*; 82% of winter diet). Furthermore, they found that Oldsquaws concentrated to feed in the same areas where *Pontoporeia affinis* reached maximum density. Field experiments in Lake Michigan by Marzolf (1962, in Peterson and Ellarson 1977) indicated that a thin detrital film (less than 5 mm) was generally present on the bottom of the lake. His laboratory experiments also suggested that *Pontoporeia* densities were positively correlated with the density of bacteria in this organic matter. Although Schell (1980) found no such relationship between the common invertebrates (e.g. mysids and *Onisimus*) living in Simpson Lagoon and peat-associated bacteria, further study of other types of detritus and bacteria may show a relationship in Simpson Lagoon similar to that described by Marzolf (1962) in Lake Michigan.

The standing stock of benthic infauna (bivalves, polychaetes, cumaceans, tunicates, and other organisms) in Simpson Lagoon substrates is at least as high as that of the mobile epibenthos (2.2 g *vs.* 0.1–2.5 g ash-free dry wt/m^2; Griffiths and Dillinger 1981). Nevertheless, only 10% or less of the diet of Oldsquaws in Simpson Lagoon was found to be composed of bivalves (primarily *Cyrtodaria kurriana* and, to a lesser extent, *Portlandia arctica*), cumaceans, and polychaetes (Table 3). Some of these organisms may have been available in the epibenthos (H. Feder, Univ. of Alaska, pers. comm. 1981), so the percentages of the diet represented by infaunal organisms may have been even lower.

In Milwaukee Harbor in Lake Michigan, infaunal oligochaetes (Tubificidae) were very abundant in winter (up to 335 000/m^2; Rofritz 1972:56) and were almost the exclusive diet of most Oldsquaws, even though molluscs and crustaceans were also present in the benthos where the birds were feeding (Rofritz 1977). It was suggested that Oldsquaws in Milwaukee harbour may have selected oligochaetes as food during winter because of their significantly higher caloric value per gram of body weight than the other benthic fauna present. Oligochaetes were absent, however, from the diet of some Oldsquaws. These worms may have been in burrows in the sand and silt substrate during some periods and at some locations, and therefore may have been largely inaccessible to some Oldsquaws.

My results suggest that Oldsquaws select the larger mysids and amphipods, and prey most effectively in areas where the density and biomass of food are high (Figs. 4 and 5). Griffiths and Dillinger (1981), in systematic samples at shallow and deep stations in Simpson Lagoon that were established independently of the presence or absence of Oldsquaws, showed that the density of invertebrates was not homogeneous. They found that densities of both mysids and amphipods were significantly greater at their deep ($\bar{x}$ = 2.5 m) lagoon sampling stations in the central trough near the middle of Simpson Lagoon than elsewhere. Average depths where Oldsquaws were feeding and were collected in Simpson Lagoon during both 1977 and 1978 ranged from 2 to 3 m, namely, in the area where densities of lagoon invertebrates were highest.

We have not investigated rates of predation by Oldsquaws. This aspect of the functional feeding response is an important one because it no doubt would be affected by changes in the density of invertebrates. If dramatic reductions in invertebrate density should occur because of oil pollution (see Cabioch 1980, Berne *et al.* 1980), Oldsquaws and other organisms dependent on invertebrates for food may be forced to: (1) move to a more suitable area, or (2) increase their searching time, thus becoming less efficient. We know little of the local movements of flocks of Oldsquaws. Turnover rates of individuals within flocks or of flocks within a lagoon system are not well understood.

Nilsson (1970) indicated that Oldsquaws he observed wintering along the coast of south Sweden during 1964–67 spent approximately 79% of daylight hours diving and that the rate of feeding increased as the ambient temperatures along the coast decreased. Thus, Oldsquaws are capable of functional changes in their feeding behaviour in response to some types of natural perturbations. It remains to be seen, however, whether these seaducks can adapt to the increased disturbance and development-related alterations of their lagoon habitats along the Beaufort Sea coast of Alaska.

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8. Literature cited

Bagge, P.; Lemmetyinen, R.; Raitis, T. 1973. Spring food of some diving waterfowl in the southwestern Finnish Archipelago. Oikos Suppl. 15: 146–150.

Bartonek, J.C. 1968. Summer foods and feeding habits of diving ducks in Manitoba. Ph.D. Thesis. Univ. Wisconsin. Madison. 113 pp.

Bartonek, J.C.; Hickey, J.J. 1969. Food habits of Canvasbacks, Redheads and Lesser Scaup in Manitoba. Condor 71:280–290.

Bengtson, S.-A. 1971. Food and feeding of diving ducks breeding at Lake Myvatn, Iceland. Ornis Fenn. 48:77–92.

Berne, S.; Marchand, M.; d'Ozouville, L. 1980. Pollution of sea water and marine sediments in coastal areas. Ambio 9:287–293.

Cabioch, L. 1980. Pollution of subtidal sediments and disturbance of benthic animal communities. Ambio 9:294–296.

Clifford, H.T.; Stephenson, W. 1975. An introduction to numerical classification. Acad. Press. New York. 309 pp.

Cottam, C. 1939. Food habits of North American diving ducks. U.S. Dep. Agric. Tech. Bull. 643. 140 pp.

Craig, P.C.; Haldorson, L. 1981. Beaufort Sea barrier island – lagoon ecological process studies: final report, Simpson Lagoon. Part 4. Fishes. Pages 384–655 *in* Environ. Assess. Alaskan Cont. Shelf. Final Rep. Princ. Invest. Vol. 7. NOAA/BLM, OCSEAP. Boulder, Colo.

Eggleton, F.E. 1936. Productivity of the profundal benthic zone in Lake Michigan. Papers Mich. Acad. Sci. Arts and Letters 22:593–611.

Ellarson, R.S. 1956. A study of the Oldsquaw duck in Lake Michigan. Ph.D. Thesis. Univ. Wisconsin. Madison. 321 pp.

Gjosaeter, J.; Saetre, R. 1974. Predation of eggs of capelin (*Mallotus villosus*) by diving ducks. Astarte 7:1–219.

Griffiths, W.B.; Dillinger, R.E. 1981. Beaufort Sea barrier island – lagoon ecological process studies: final report, Simpson Lagoon. Part 5. Invertebrates. Pages 1–198 *in* Environ. Assess. Alaskan Cont. Shelf. Final Rep. Princ. Invest. Vol. 8. NOAA/BLM, OCSEAP. Boulder, Colo.

Griffiths, W.B.; Craig, P.C.; Walder, G.; Mann, G. 1975. Fisheries investigations in a coastal region of the Beaufort Sea (Nunaluk Lagoon, Y.T.) Arct. Gas Biol. Rep. Ser. 34:1–219.

Horn, H.S. 1966. Measurement of "overlap" in comparative ecological studies. Am. Nat. 100:419–429.

Hull, E.D. 1914. Habits of the Oldsquaw (*Harelda hyemalis*) in Jackson Park, Chicago. Wilson Bull. 26:116–123.

Hynes, H.B.N. 1950. The food of the freshwater sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*), with a review of methods used in studies of the food of fishes. J. Anim. Ecol. 19:36–58.

Johnson, S.R.; Richardson, W.J. 1981. Beaufort Sea barrier island – lagoon ecological process studies: final report, Simpson Lagoon. Part 3. Birds. Pages 109–383 *in* Environ. Assess. Alaskan Cont. Shelf. Final Rep. Princ. Invest. Vol. 7. BLM/NOAA, OCSEAP. Boulder, Colo.

Johnson, S.R.; Richardson, W.J. 1982. Waterbird migration near the Yukon and Alaskan coast of the Beaufort Sea. II. Moult migration of seaducks. Arctic 35:291–301.

LGL Ecological Research Associates, Inc. 1981. Beaufort Sea barrier island – lagoon ecological process studies: final report, Simpson Lagoon. Environ. Assess. Alaskan Cont. Shelf. Final Rep. Princ. Invest. Vols. 7 and 8. NOAA/BLM, OCSEAP. Boulder, Colo.

Lagler, K.F.; Wienert, C.C. 1948. Food of the Oldsquaw in Lake Michigan. Wilson Bull. 60:118.

Madsen, F.J. 1954. On the food habits of diving ducks in Denmark. Dan. Rev. Game Biol. 2:157–256.

Marzolf, G.R. 1962. Substrate relations of the burrowing amphipod, *Pontoporeia affinis* Lindstrom. Ph.D. Thesis. Univ. Mich. Ann Arbor. (Original not seen.)

Nilsson, L. 1970. Food-seeking activity of south Swedish diving ducks in the non-breeding season. Oikos 21:145–154.

Nilsson, L. 1972. Habitat selection, food choices and feeding habits of diving ducks in coastal waters of south Sweden during the non-breeding season. Ornis Scand. 3:55–78.

Pehrsson, O. 1973. Chief prey as a factor regulating populations of eider (*Somateria mollissima*) and long-tailed ducks (*Clangula hyemalis*). Zool. Revy 35:89–92.

Pehrsson, O. 1974. Nutrition of small ducklings regulating breeding area and reproductive output in the long-tailed duck (*Clangula hyemalis*). XI Congr. Int. Union Game Biol. Stockholm (1973):259–264.

Peterson, S.R. 1976. The Oldsquaw: body measurements, food habits, and environmental contaminants. Ph.D. Thesis. Univ. Wisconsin. Madison. 132 pp.

Peterson, S.R.; Ellarson, R.S. 1977. Food habits of Oldsquaws wintering on Lake Michigan. Wilson Bull. 89:81–91.

Rofritz, D.J. 1972. Ecological investigations of waterfowl wintering in the Milwaukee Embayment. M.Sc. Thesis. Univ. Wisconsin. Milwaukee. 88 pp.

Rofritz, D.J. 1977. Oligochaeta as a winter food source for the Oldsquaw. J. Wildl. Manage. 41:590–591.

Sanger, G.A.; Jones, R.D. 1981. The winter feeding ecology and trophic relationships of marine birds in Kachemak Bay, Alaska. Pages 161–294 *in* Environ. Assess. Alaskan Cont. Shelf. Final Rep. Princ. Invest. Vol. 16. NOAA/BLM, OCSEAP. Boulder, Colo.

Schell, D.M. 1980. Food web and nutrient dynamics studies in nearshore Alaskan Beaufort Sea waters. Pages 467–515 *in* Environ. Assess. Alaskan Cont. Shelf. Annu. Rep. Princ. Invest. for the year ending March 1980. Vol. 2. NOAA/BLM, OCSEAP. Boulder, Colo.

Stott, R.S.; Olson, D.P. 1973. Food-habitat relationships of sea ducks on the New Hampshire coastline. Ecology 54:996–1007.

Swanson, G.A.; Bartonek, J.C. 1970. Bias associated with food analysis in gizzards of Blue-winged Teal. J. Wildl. Manage. 34:739–746.

Vermeer, K.; Levings, C.D. 1977. Populations, biomass and food habits of ducks on the Fraser Delta intertidal area, British Columbia. Wildfowl 28:49–60.