The Diets and Feeding Habits of Some Deep-Water Benthic Skates (*Rajidae*) in the Pacific Waters Off the Northern Kuril Islands and Southeastern Kamchatka

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The Diets and Feeding Habits of Some Deep-Water Benthic Skates (*Rajidae*) in the Pacific Waters Off the Northern Kuril Islands and Southeastern Kamchatka

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ABSTRACT: On the basis of shipboard analysis, the diets of 7 species of deep-benthic skates were examined: Aleutian skate *Bathyraja aleutica*, sandpaper skate *B. interrupta*, Alaska skate *B. parmifera*, *B. matsubarai*, whiteblotched skate *B. maculata*, whitebrow skate *B. minispinosa*, and Okhotsk skate *B. violacea*. The diet of predatory skates (Alaska skate, Aleutian skate, whiteblotched skate, and *B. matsubarai*) consisted of large crustaceans, cephalopods and fishes. Benthophagic skates (sandpaper skate, Okhotsk skate, and probably whitebrow skate) consumed mainly amphipods and worms. The consumption of worms and crustaceans (especially small crustaceans) in diets of predatory skates declined with increasing skate size, whereas cephalopod and fish frequency of occurrence increased. For benthophage skates occurrence of amphipods in stomachs declined with increasing skate size and consumption of shrimps and other large crustaceans, as well as squids, increased.

INTRODUCTION

The skate family Rajidae plays an important role in ecosystems of the North Pacific basin. Rajids are a significant element of food webs in benthic communities. On the one hand, skates consume commercially important species, such as walleye pollock *Theragra chalcogramma*, flathead sole *Hippoglossoides elassodon*, yellowfin sole *Pleuronectes asper*, rock sole *Pleuronectes bilineatus*, Pacific cod *Gadus macrocephalus*, Pacific herring *Clupea pallasi*, Tanner crabs *Chionoecetes* (Livingston and deReynier 1996). On the other hand, skates themselves have some commercial importance. For example, they are processed into fish-meat jelly and dried skate wing (Ishihara 1990). Nevertheless, skates remain the least investigated group among the elasmobranchs.

A review of recent publications indicate that study of skates in the North Pacific is scant. Most of the literature deals with skate taxonomy and descriptions of new species; taxonomy of skates is still poorly developed, and their biology is even less known. Only Ishiyama (1958) has considered age and growth of some species of the family Rajidae. Some peculiarities of the bathymetric distribution of skates in the genus *Bathyraja* are given in papers of McEachran and Miyake (1990) and Nakaya and Shirai (1992). Feeding habits of *Bathyraja* in the North Pacific are practically unknown. The diet of Alaska skate *Bathyraja parmifera* is briefly described in the papers of Mito (1974) and Brodeur and Livingston (1988). The purpose of this paper is to describe the diets of 7 species of deep-benthic skates of the genus *Bathyraja* that inhabit the Pacific waters off the North Kuril Islands and Southeast Kamchatka.

METHODS

In this study, stomach contents of skates brought aboard Japanese trawler *Tora Maru No. 58* from May to July 1996 were analyzed. The stomach samples were selected without known bias from bottom trawl hauls carried out around the clock in the Pacific waters off the North Kuril Islands and southeastern coast of Kamchatka between 48° and 51°30' N at depths of 108–646 m (Figure 1). Skates species were identified using identification keys and descriptions published by Ishiyama (1958), Dolganov (1983), Masuda et al. (1984), and Ishihara and Ishiyama (1985) and considered according to the last classification of nominal spe-

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Table 1. Frequency of occurrence (FO) of basic prey catagories of deep-water benthic skates based on shipboard analysis of stomachs collected from Pacific waters off the northern Kurils and southeastern Kamchatka in 1996 (Alu = Aleutian skate, Ala = Alaska skate, Wbd = whiteblotched skate, Bmt = *Bathyraja matsubarai*, Sdp = sandpaper skate, Wbr = whitebrow skate, Okh = Okhotsk skate).

	Predators FO (%)				Benthophages FO (%)		
Prey Category	Alu	Ala	Wbd	Bmt	Sdp	Wbr	Okh
Total number of stomachs (n_T)	167	19	612	308	267	18	91
Empty stomachs (n_E)	26	1	70	69	14	4	8
Nematod & annelid worms	4.2	-	6.1	2.3	25.1	-	13.2
Mysids, isopods & amphipods	9.0	21.1	30.9	0.7	87.6	33.3	67.0
Shrimps & crabs	44.9	21.1	23.9	43.2	9.4	50.0	57.1
Clams & snails	-	-	0.2	0.3	-	-	-
Squids & octopuses	25.7	31.6	35.6	19.2	4.1	-	5.5
Benthic fish	35.3	42.2	8.8	8.4	-	5.6	-
Pelagic fish	1.8	5.3	2.8	3.9	-	5.6	-
Miscellaneous fish	13.2	10.5	12.3	12.7	-	-	2.2
Miscellaneous prey	3.6	-	4.9	7.5	3.4	-	1.1

cies (McEachran and Miyake 1990). Standard lengths of skate bodies (snout to the end of caudal peduncle) were measured, and stomach fullness index was defined according to a 5-number scale: 0 = empty stomach to 4 = full stomach.

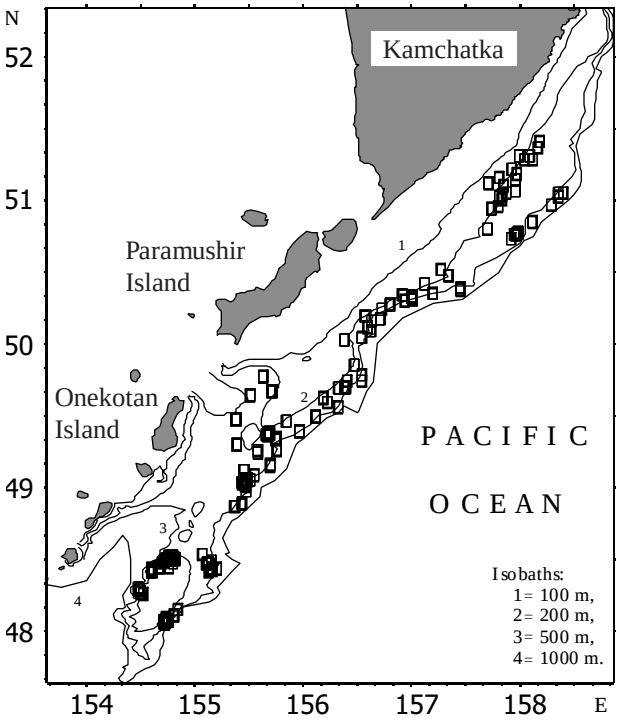

Figure 1. Map of the study area, showing demersal trawl stations (hollow rectangles) at which skates (*Bathyraja* spp.) were caught.

The frequency of occurrence (FO) was estimated as a number of stomachs that contained that food item divided by the total number of stomachs examined. The normalized frequency of occurrence was also calculated (i.e., number of food items of that type divided by the total number of food items). Quantitative stomach content analyses, which measures stomach content weight and the weight of prey items, were not performed.

RESULTS

Stomachs examined and those with food were as follows: 167/141 Aleutian skates *Bathyraja aleutica*, 267/253 sandpaper skates *B. interrupta*, 612/542 whiteblotched skates *B. maculata*, 308/239 skates *Bathyraja matsubarai*, 18/14 whitebrow skates *B. minispinosa*, 19/18 Alaska skates, and 91/83 Okhotsk skates *B. violacea.* Among the skate stomachs analyzed, 4 prey groups represented the majority of forage organisms: worms, crustaceans, cephalopods, and fishes (Table 1).

General Description of Diets

Aleutian skate fed most frequently on crustaceans, shrimps being the most frequent component (Table 2). Fish were the second most frequently occurring prey, Atka mackerel *Pleurogrammus monopterygius*, darkfin sculpin *Malacocottus zonurus*, and walleye pollock *Theragra chalcogramma* being the most common. Cephalopods in the diet of Aleutian skates were the third in rank, red (magistrate armhook) squid *Berryteuthis magister* being the most common.

Table 2. Frequency of occurrence (FO) of stomach contents of Aleutian skates (167 stomachs examined, 26 empty) from Pacific waters off the northern Kuril Islands and southeastern Kamchatka in 1996.

Taxa	Stomachs Occurring In	
	Nr Stomachs	FO (%)
Pandalidae (pandalid shrimps)	53	31.7
Berryteuthis magister (red squid)	31	18.6
Teleostei (unidentified fish)	22	13.2
Chionoecetes opilio (snow crab)	20	12.0
Amphipoda (amphipods)	15	9.0
Octopoda (octopuses)	11	6.6
Malacocottus zonurus (darkfin sculpin)	11	6.6
Pleurogrammus monopterygius (Atka mackerel)	10	6.0
Theragra chalcogramma (walleye pollock)	7	4.2
Unidentified organic material	6	3.6
Oligochaeta (oligochaet worms)	5	3.0
Icelus spp. (unidentified sculpins)	4	2.4
Hemilepidotus gilberti (sculpin)	3	1.8
Agonidae (unidentified poacher)	3	1.8
Bathyagonus nigripinnis (blackfin poacher)	3	1.8
Liparidae (unidentified snailfish)	3	1.8
Icelus canaliculatus (porehead sculpin)	2	1.2
Nematoda (roundworms)	1	0.6
Polychaeta (polychaet worms)	1	0.6
Crangonidae (crangonid shrimps)	1	0.6
Paguridae (hermit crabs)	1	0.6
Teuthida (unidentified squid)	1	0.6
Bathyraja interrupta (Bering skate)	1	0.6
Scopelosaurus harryi (scaly wearyfish)	1	0.6
Gasterosteus aculeatus (threespine stickleback)	1	0.6
Lycodes sp. (unidentified eelpout)	1	0.6
Lycenchelys sp. (unidentified eelpout)	1	0.6
Triglops forficata (scissortail sculpin)	1	0.6
Sarritor frenatus (sawback poacher)	1	0.6
Elassodiscus tremebundus (snailfish)	1	0.6

Sandpaper skates fed mainly on crustaceans, amphipods at 85.4% being by far the most frequently consumed item in the diet (Table 3). Worms were more frequently consumed by sandpaper skates than by any other skates, which tended to minimize the occurrence of other forage organisms more commonly consumed by other skates.

Diet of whiteblotched skate consisted mainly of crustaceans, amphipods, and shrimps being the most frequent, followed by mollusks (mainly red squid; Table 4). Fishes in their diet were the third most frequent prey group, Atka mackerel, sculpins, and walleye pollock being the most common prey.

Bathyraja matsubarai consumed crustaceans most frequently and in contrast to the other skates, most were *Chionoecetes opilio* snow crabs (Table 5). Fishes followed crustaceans with liparids, darkfin sculpin, and myctophids being the most frequent. Cephalopods, mostly red squid, were the third most frequent.

Data on diet composition of whitebrow skate were limited to 14 stomachs with food. Crustaceans, i.e., amphipods, snow crabs and shrimps, were the most frequent (Table 6). The only other food present was liparid and myctophid fishes.

Data on diet of Alaska skates were limited to the contents of 18 stomachs. Fishes occurred most fre-

Table 3. Frequency of occurrence (FO) of stomach contents of sandpaper skates (267 stomachs examined, 14 empty) from Pacific waters off the northern Kuril Islands and southeastern Kamchatka in 1996.

	Stomachs Occurring In	
Taxa	Nr Stomachs	FO (%)
Amphipoda (amphipods)	228	85.4
Oligochaeta (oligochaet worms)	52	19.5
Pandalidae (pandalid shrimps)	17	6.4
Berryteuthis magister (red squid)	10	3.7
Nematoda (roundworms)	8	3.0
Crangonidae (crangonid shrimps)	7	2.6
Polychaeta (polychaet worms)	6	2.2
Isopoda (isopods)	6	2.2
Unidentified organic material	6	2.2
Ophiuroidea (brittlestar)	2	0.7
Echiurida (echiurid worms)	1	0.4
Paguridae (hermit crabs)	1	0.4
Squid (unidentified)	1	0.4
Fish eggs (unidentified)	1	0.4

quently, Atka mackerel and sculpins being the most common (Table 7). Crustaceans were the second most frequently occurring prey, predominately amphipods and snow crabs. Cephalopods were the third most common, squids and octopuses sharing similar frequencies.

Okhotsk skates consumed mainly crustaceans, amphipods and snow crabs being the most frequent (Table 8). Worms were also often found in stomachs of this species. Eight other forage organisms were consumed far less frequently.

Food Habits vs Skate Size

Size differences

Worms, crustaceans (mainly amphipods and shrimps), and sculpins (mostly juvenile darkfin sculpin) were the most frequent food items in the diet of small Aleutian skates (<60 cm). Individuals >70 cm fed more frequently on large crustaceans (snow crabs), cephalopods and fishes (Figure 2A). Consumption of amphipods declined with size. The diet of Aleutian skates >100 cm consisted almost solely of fishes and cephalopods, and crustaceans were almost completely absent. Among the fishes consumed, large fish species, such as Atka mackerel, were common.

Small sandpaper skates (<40 cm) consumed mainly amphipods (Figure 2B). The FO of roundworms in the diet of this species was high. With increasing body length, the occurrence of amphipods and roundworms in the diet decreased. Sandpaper skates >50 cm fed mainly on annelid worms, squids, shrimps and other large crustaceans. Feeding of the largest sandpaper skates (>70 cm) was characterized by a decreased occurrence of amphipods; their diet consisted mainly of squids, large crustaceans, and annelid worms.

Small whiteblotched skate <40 cm ate mainly amphipods (Figure 2C). For those >50 cm, the prey consisted mainly of worms, shrimps, snow crabs, octopuses and small fishes species (sculpins, deepsea smelts, and myctophids). Those >70 cm consumed mainly octopuses and large fishes (Atka mackerel, walleye pollock), as well as hermit crabs. The FO of worms and shrimps among of the largest individuals, >100 cm, was low; their diet instead consisted mainly of cephalopods and fishes.

Small individuals of *B.matsubarai* (<70 cm) consumed mainly snow crabs (Figure 2D). Annelid worms were frequently consumed by skates of this size group. With increasing body length, the occurrence of snow crabs and annelid worms in the diet decreased. Skates >80 cm fed mainly on fish and cephalopods. Feeding of largest individuals (>90 cm) was characterized by an increased incidence of fish (mainly liparids and Atka mackerel) and cephalopods (mainly red squid).

For the 14 whitebrow skate stomachs examined, the FO of amphipods decreased as skate body length increased and snow crabs FO increased (Figure 2E). The largest individuals consumed predominantly fishes.

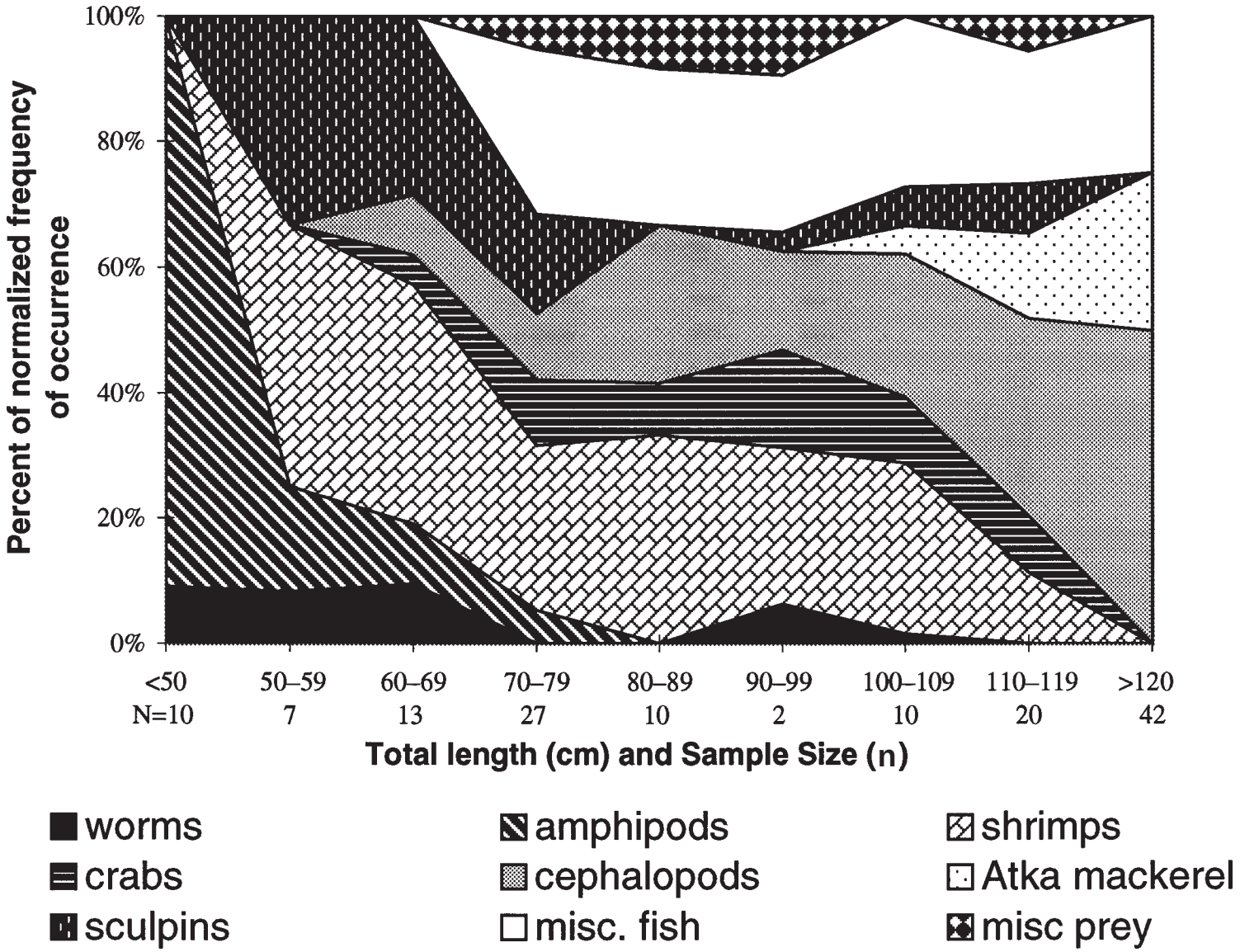

Figure 2A. Diet of Aleutian skates in terms of normalized frequency of occurrence by body length categories.

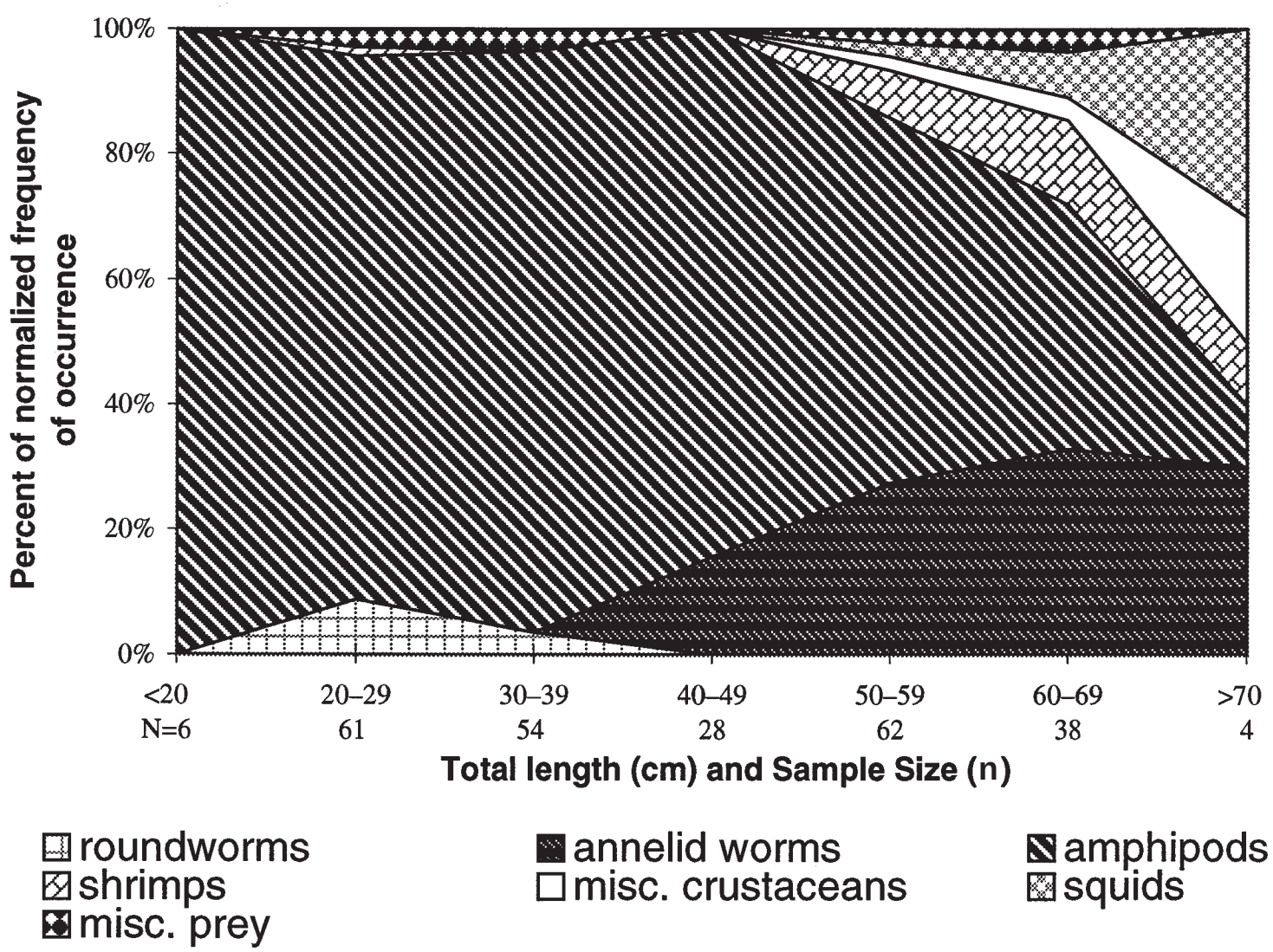

Figure 2B. Diet of sandpaper skates in terms of normalized frequency of occurrence by body length categories.

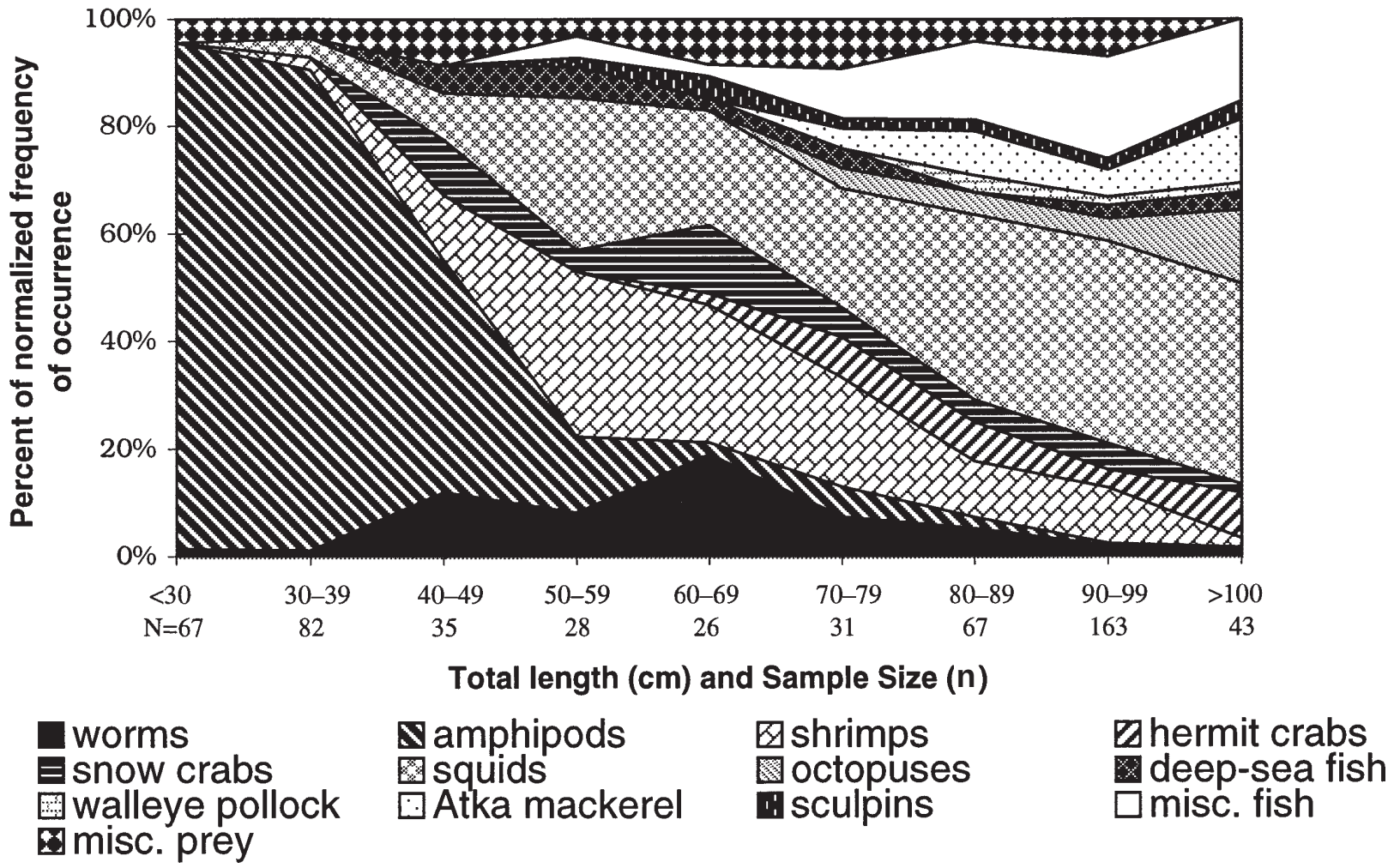

Figure 2C. Diet of whiteblotched skates in terms of normalized frequency of occurrence by body length categories.

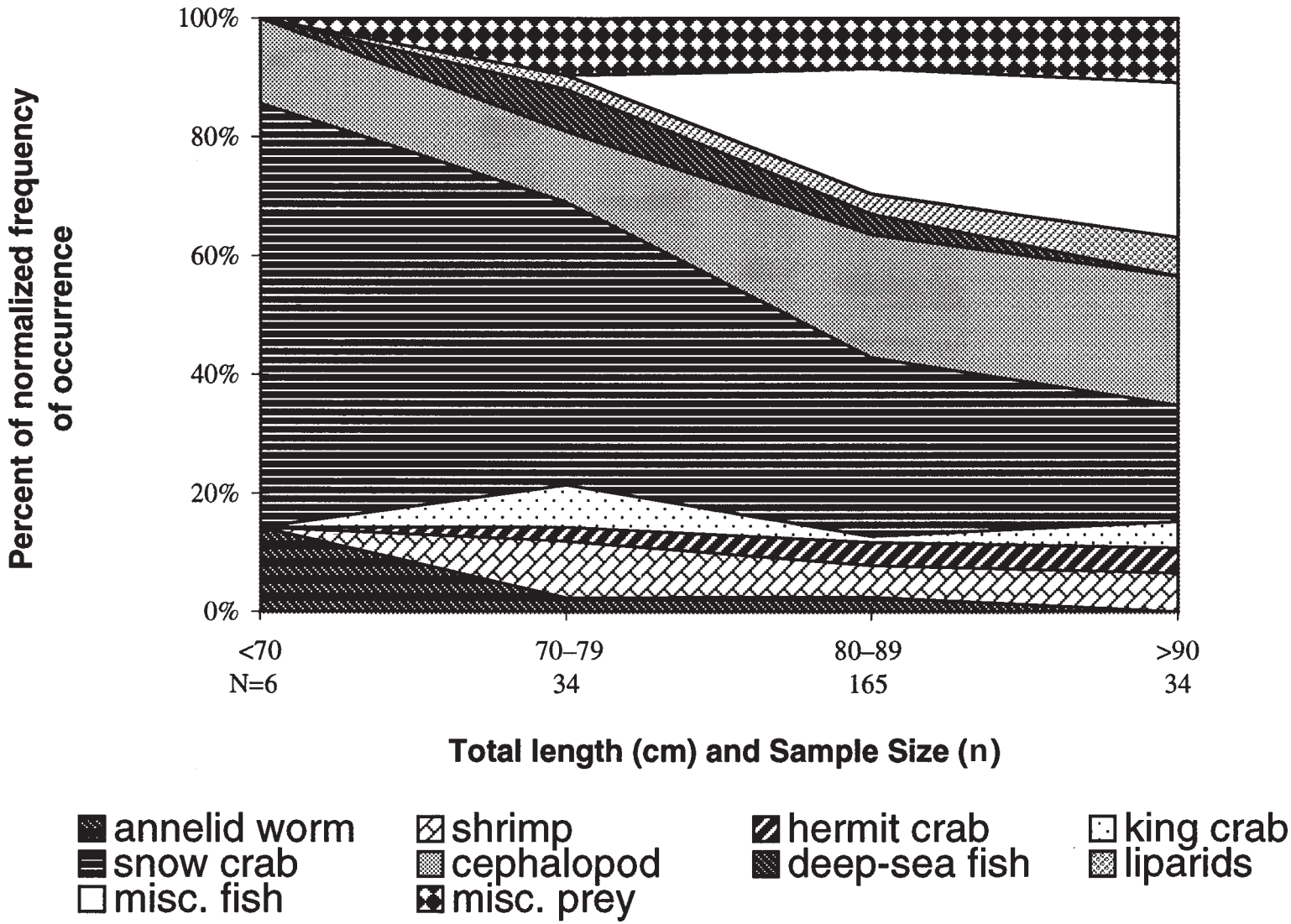

Figure 2D. Diet of skates *Bathyraja matsubarai* in terms of normalized frequency of occurrence by body length categories.

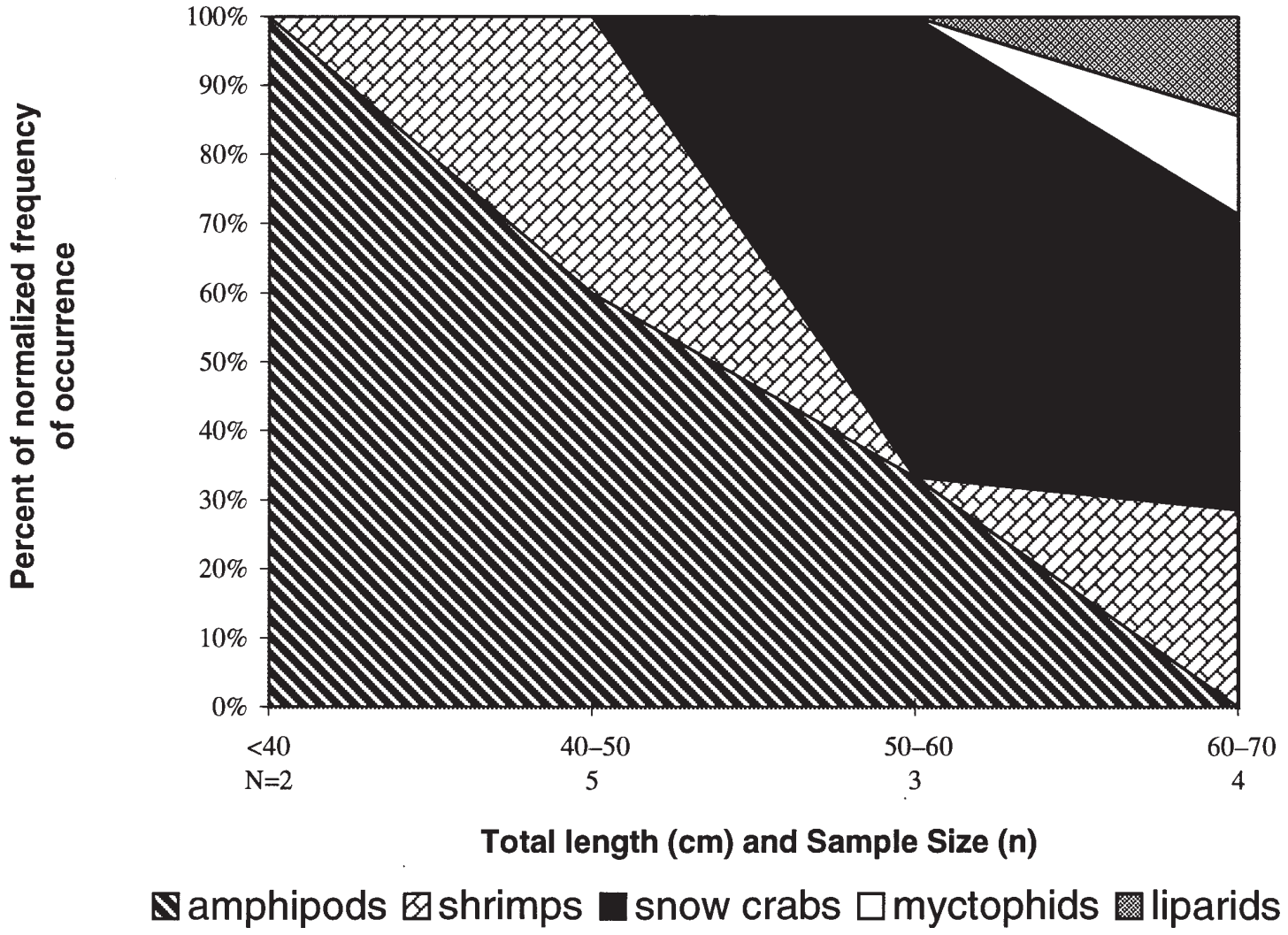

Figure 2E. Diet of whitebrow skates in terms of normalized frequency of occurrence by body length categories.

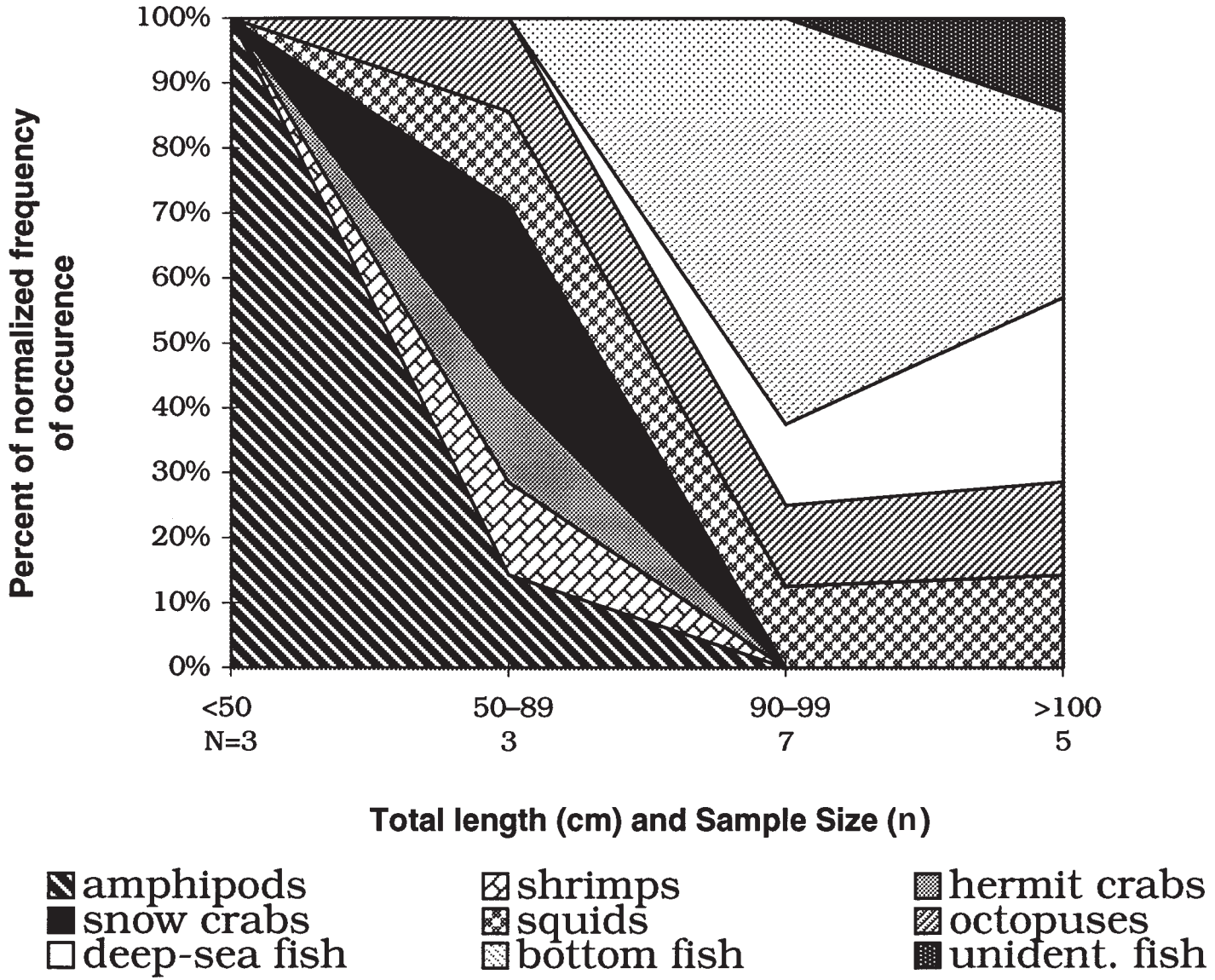

Figure 2F. Diet of Alaska skates in terms of normalized frequency of occurrence by body length categories.

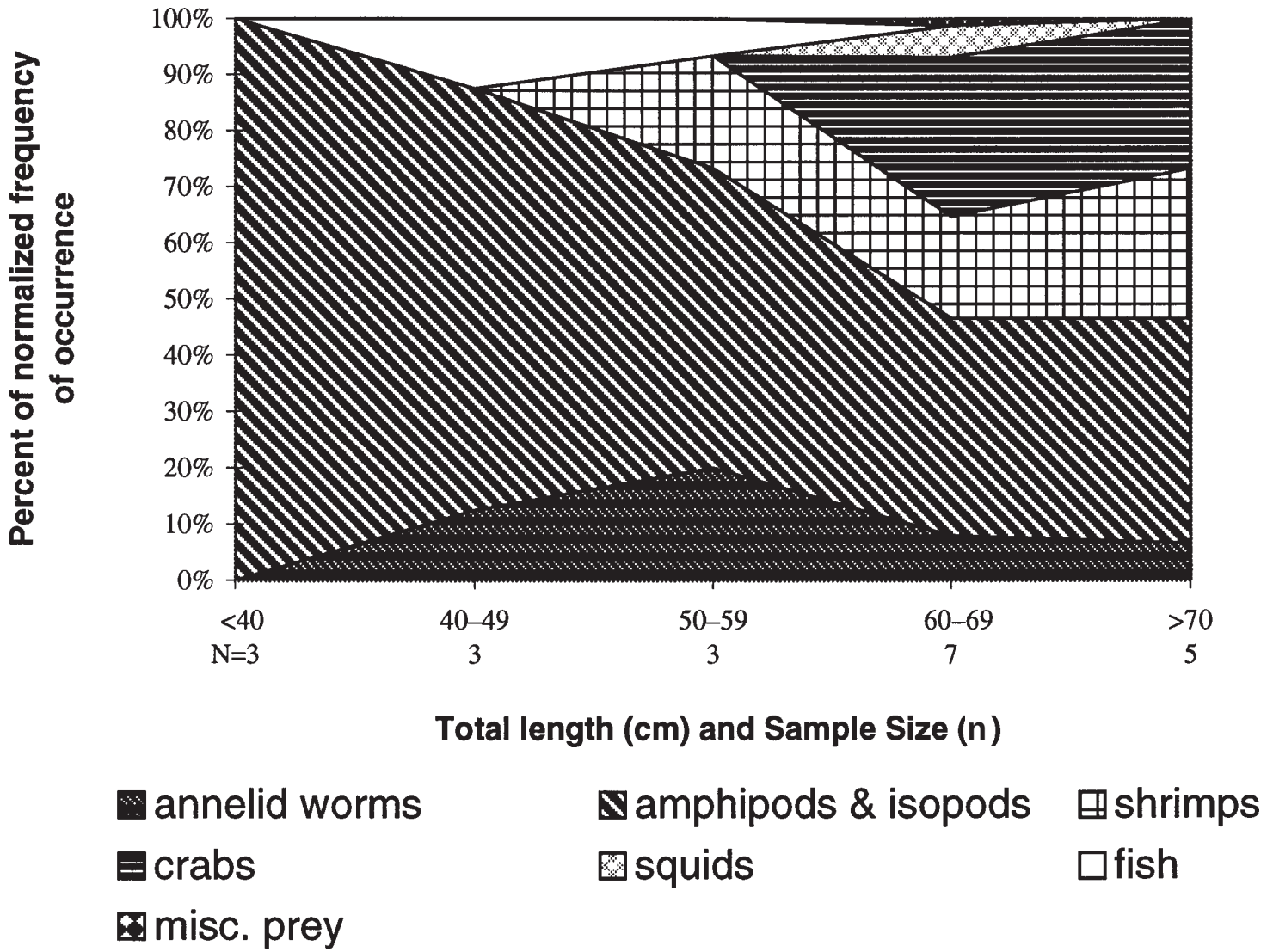

Figure 2G. Diet of Okhotsk skates in terms of normalized frequency of occurrence by body length categories.

Table 4. Frequency of occurrence (FO) of stomach contents of whiteblotched skates (612 stomachs examined, 70 empty) from Pacific waters off the northern Kuril Islands and southeastern Kamchatka in 1996.

	Stomachs Occurring In	
Taxa	Nr Stomachs	FO (%)
Amphipoda (amphipods)	183	29.9
Berryteuthis magister (red squid)	175	28.6
Pandalidae (pandalid shrimps)	78	12.7
Teleostei (unidentified)	75	12.2
Chionoecetes opilio (snow crab)	35	5.7
Pleurogrammus monopterygius (Atka mackerel)	29	4.7
Paguridae (hermit crabs)	25	4.1
Octopoda (octopuses)	24	3.9
Polychaeta (polychaet worms)	22	3.6
Unidentified organic material	22	3.6
Oligochaeta (oligochaet worms)	12	2.0
Teuthida (squid)	10	1.6
Triglops scepticus (spectacled sculpin)	9	1.5
Theragra chalcogramma (walleye pollock)	8	1.3
Fish eggs	8	1.3
Leuroglossus schmidti (northern smoothtongue)	7	1.1
Crangonidae (crangonid shrimps)	6	1.0
Stenobrachius leucopsarus (northern lampfish)	6	1.0
Mysidacea (mysids)	4	0.6
Belonella borealis (squid)	4	0.6
Nematoda (roundworms)	3	0.5
Gonatopsis borealis (boreopacific gonate squid)	3	0.5
Malacocottus zonurus (darkfin sculpin)	3	0.5
Isopoda (isopods)	2	0.3
Protomyctophum thompsoni (northern flashlightfish)	2	0.3
Sebastes borealis (shortraker rockfish)	2	0.3
Lithodes aequispina (golden king crab)	1	0.2
Bivalvia (clams)	1	0.2
Gallyteuthis phyllura (squid)	1	0.2
Arctozenus rissoi (ribbon barracudina)	1	0.2
Stenobrachius nannochir (garnet lampfish)	1	0.2
Coryphaenoides cinereus (popeye grenadier)	1	0.2
Zaprora silena (prowfish)	1	0.2
Hemilepidotus gilberti (sculpin)	1	0.2

Small Alaska skates (<50 cm) consumed mainly amphipods (Figure 2F) but with increasing skate size, fewer amphipods were consumed. The larger skates ate mostly large crustaceans (shrimps, snow crabs, and hermit crabs) and squids and octopuses. The largest Alaska skates (>90 cm) ate mainly fish and cephalopods.

Okhotsk skate <40 cm ate mainly small crustaceans (amphipods and isopods; Figure 2G). With increasing size, shrimps and annelid worms became more frequent in their diet and the FO of amphipods and isopods gradually declined. Large crustaceans (hermit crabs and snow crabs) and squids occurred in the stomachs of individuals >60 cm. Total FO of small food items (worms, isopods and amphipods) and large prey (squids, snow crabs and hermit crabs) in stomachs of the largest individuals (length > 70 cm) were almost the same.

Table 5. Frequency of occurrence (FO) of stomach contents of *Bathyraja matsubarai* (308 stomachs examined, 69 empty) from Pacific waters off the northern Kuril Islands and southeastern Kamchatka in 1996.

Taxa	Stomachs Occurring In	
	Nr Stomachs	FO (%)
Chionoecetes opilio (snow crab)	96	31.2
Berryteuthis magister (red squid)	47	15.3
Teleostei (unidentified)	39	12.7
Unidentified organic material	22	7.1
Pandalidae (pandalid shrimps)	17	5.5
Paguridae (hermit crabs)	11	3.6
Liparidae (unidentified snailfish)	9	2.9
Octopoda (octopuses)	8	2.6
Malacocottus zonurus (darkfin sculpin)	8	2.6
Lithodes aequispina (gold king crab)	7	2.3
Stenobrachius leucopsarus (northern lampfish)	5	1.6
Elassodiscus tremebundus (snailfish)	5	1.6
Oligochaeta (oligochaet worms)	4	1.3
Polychaeta (polychaet worms)	3	1.0
Amphipoda (amphipods)	2	0.6
Myctophidae gen. sp. (unidentified myctophid)	2	0.6
Pleurogrammus monopterygius (Atka mackerel)	2	0.6
Crangonidae (crangonid shrimps)	1	0.3
Gastropoda (snails)	1	0.3
Chauliodus macouni (Pacific viperfish)	1	0.3
Lampanyctus jordani (brokenline lampfish)	1	0.3
Protomyctophum thompsoni (northern flashlightfish)	1	0.3
Stenobrachius nannochir (garnet lampfish)	1	0.3
Gasterosteus aculeatus (threespine stickleback)	1	0.3
Icelus canaliculatus (porehead sculpin)	1	0.3
Careproctus zachirus (snailfish)	1	0.3
Fish eggs (unidentified)	1	0.3

DISCUSSION

Feeding characteristics of fishes can be divided into 3 basic groups (Anonymous 1961; Nikol'sky 1974): (1) Plantfeeders, which consume phytoplankton, algae, detritus, etc.; (2) zoophages, which include zooplanktophages, benthophages, and predators; and (3) omnivores, which consume both plants and animals.

Stomach content analysis of the 7 *Bathyraja* species considered here showed the presence of different feeding types, which may change with increasing body size (Table 9). The Aleutian skate, Alaska skate, whiteblotched skate, and *B. matsubarai* are predators. Adults consumed mainly fishes, cephalopods and large crustaceans (shrimps, snow crabs, and hermit crabs). Sandpaper, Okhotsk, and probably whitebrow skates are benthophages; they are primarily crustacean specialists that feed predominately on amphipods, although the diet of whitebrow skate includes shrimps and snow crabs.

Adults of various *Bathyraja* skates consumed a broad spectrum of benthic food items, but the low level of overlap in diet composition indicates low feeding competition between the species. On the other hand, juvenile *Bathyraja* skates (except *B. matsubarai*) all consume amphipods and worms. Competition is probably strongest between the species during the younger life stages.

Rajid skate diets in other oceans show similar results. In other rajid skate communities, as well as in the region considered here, predatory and benthophage

Table 6. Frequency of occurrence (FO) of stomach contents of whitebrow skates (18 stomachs examined, 4 empty) from Pacific waters off the northern Kuril Islands and southeastern Kamchatka in 1996.

Taxa	Stomachs Occurring In	
	Nr Stomachs	FO (%)
Amphipoda (amphipods)	6	33.3
Chionoecetes opilio (snow crab)	5	27.8
Pandalidae (pandalid shrimps)	4	22.2
Elassodiscus tremebundus (snailfish)	1	5.5
Protomyctophum thompsoni (northern flashlightfish)	1	5.5

species diets consist of the same groups of forage organisms: worms, isopods, amphipods, shrimps, spider crabs, hermit crabs, cephalopods, and fishes (Holden and Tucker, 1974; Ajayi 1982; Abdel-Aziz 1986; Gordon and Dunkan 1989; Ebert et al. 1991; Smale and Cowley 1992). Likewise, in other regions, prey is influenced by skate size. Larger skate species are predatory on fishes; smaller skate species are benthophagic, consuming worms, amphipods, mysids, isopods, and etc. Mid-sized skates consume both small and large crustaceans and occasionally cephalopods and fishes.

The feeding behavior of skates is of special interest. Skates are typical representatives of the benthic ichthyofauna and their diets consist mainly of benthic prey. However, we occasionally found mesopelagic squids (*Belonella borealis, Galiteuthis phyllura*) and mesopelagic fishes (northern smoothtongue *Leuroglossus schmidti*, Pacific viperfish *Chauliodus macouni*, ribbon barracudina *Arctozenus rissoi*, scaly wearyfish *Scopelosaurus harryi*, and various myctophids) in their stomachs. We also found salmon, which in the summer inhabit the upper 50-m layer of the ocean (Ogura 1994), and threespine stickleback *Gasterosteus aculeatus*, which can be observed near the sea surface, far from the coasts and over deep depths (Zyuganov 1991). Most pelagic prey were in a slightly digested condition making it unlikely that they were consumed as the trawl was being retrieved. I therefore believe that, at least within our study area,

Table 7. Frequency of occurrence (FO) of stomach contents of Alaska skates (19 stomachs examined, 1 empty) from Pacific waters off the northern Kuril Islands and southeastern Kamchatka in 1996.

Taxa	Stomachs Occurring In	
	Nr Stomachs	FO (%)
Amphipoda (amphipods)	4	21.0
Octopoda (octopuses)	3	15.8
Pleurogrammus monopterygius (Atka mackerel)	3	15.8
Chionoecetes opilio (snow crab)	2	10.5
Berryteuthis magister (red squid)	2	10.5
Triglops scepticus (spectacled sculpin)	2	10.5
Teleostei (unidentified fish)	2	10.5
Crangonidae (crangonid shrimps)	1	5.3
Paguridae (hermit crabs)	1	5.3
Teuthida (squid)	1	5.3
Leuroglossus schmidti (northern smoothtongue)	1	5.3
Theragra chalcogramma (walleye pollock)	1	5.3
Hemilepidotus gilberti (sculpin)	1	5.3
Allocareproctus jordani (snailfish)	1	5.3

Table 8. Frequency of occurrence (FO) of stomach contents of Okhotsk skates (91 stomachs examined, 8 empty) from Pacific waters off the northern Kuril Islands and southeastern Kamchatka in 1996.

	Stomachs Occurring In	
Taxa	Nr Stomachs	FO (%)
Amphipoda (amphipods)	59	64.8
Chionoecetes opilio (snow crab)	26	28.6
Crangonidae (crangonid shrimps)	16	17.6
Oligochaeta (oligochaet worms)	11	12.1
Pandalidae (pandalid shrimps)	7	7.7
Paguridae (hermit crabs)	3	3.3
Teuthida (squid)	3	3.3
Isopoda (isopods)	2	2.2
Berryteuthis magister (red squid)	2	2.2
Teleostei (unidentified)	2	2.2
Polychaeta (polychaet worms)	1	1.1
Unidentified organic material	1	1.1

Table 9. Total length (TL), body weight (W), and average stomach fullness indices (ASFI) of some deep-benthic skates from Pacific waters off the northern Kuril Islands and southeastern Kamchatka.

	Sample Size		ASFI	Total Length (cm)			Weight (kg)		
Skate Species	Males	Females	(units)	All	Males	Females	All	Males	Females
Aleutian	88	79	1.99						
Mean				91.7	93.6	89.6	6.57	6.47	6.64
SE				1.2	2.1	2.5	0.44	0.53	0.66
Range				33–122	39–121	33–122	0.14–14.10	0.26–11.50	0.14–14.10
Whitebotched	325	297	2.56						
Mean				66.3	68.7	70.9	2.95	2.91	3.00
SE				0.8	1.7	1.5	0.19	0.28	0.27
Range				17–113	17–113	22–102	0.40–9.50	0.55–9.50	0.40–7.30
B. matsubarai	189	119	1.74						
Mean				84.3	83.9	84.6	3.61	3.39	3.88
SE				0.3	0.5	0.4	0.16	0.14	0.30
Range				60–98	60–98	60–94	1.70–6.50	1.80–4.60	1.80–4.60
Sandpaper	110	161	3.00						
Mean				42.2	41.1	45.2	0.65	0.45	0.88
SE				0.8	1.0	1.6	0.05	0.04	0.08
Range				17–72	17–62	17–72	0.25–2.60	0.30–1.40	0.25–2.60
Okhotsk	52	39	2.84						
Mean				55.9	59.0	60.9	1.41	1.25	1.53
SE				0.8	1.7	1.6	0.06	0.08	0.08
Range				29–73	34–70	29–73	0.15–2.45	0.20–1.90	0.15–2.45
Alaska	11	8	2.89						
Mean				88.3	78.4	88.4	5.61	3.29	6.90
SE				3.7	8.6	7.6	1.00	1.16	1.25
Range				28–107	28–103	35–107	0.16–9.90	0.16–6.20	0.36–9.90
Whitebrow	11	7	2.44						
Mean				53.5	55.7	51.2	0.97	1.07	0.93
SE				2.5	5.3	3.4	0.15	0.33	0.17
Range				29–72	34–72	29–65	0.13–1.92	0.24–1.92	0.13–1.60

skates feed in the water column and in some cases even near the surface.

Berestovsky (1989) also found some pelagic fishes in skate stomachs from in the North Atlantic. However, Berestovsky concluded that skates could not feed in the water column because of their morphology and suggested that pelagic fishes traumatized by trawls in the fishing grounds were subsequently preyed upon by skates. I doubt this conclusion is correct. The ability of skates to hunt in the water column and even reach the sea surface is well known (Parin 1971). Moreover, we find it impossible to consider pelagic fishes as a casual component of skates diets because neritc, epi, and mesopelagic fishes play a rather essential role in feeding of rajid skates in various regions of the world ocean. For example, in the Black Sea sprat, horse mackerel, and anchovy are important components in the diet of *Raja clavata* (Lushnikova and Kirnosova 1990). In the northwest Atlantic myctophids, herring, and mackerel occur in the diet of thorny skate *Raja radiata* rather frequently (Templeman 1982; Robishaud et al. 1991). Diets of many skates in South African waters consist of myctophids, anchovy, and pilchard (Ebert et al. 1991; Smale and Cowley 1992). Some skates in British waters eat sprat, herring, and sardine (Holden and Tucker 1974). Prey of pelagic fishes is also known to include rajid skates as well as other benthic batoid fishes, including some stingrays (Devadoss 1978) and guitarfishes (Abdel-Aziz et al. 1993).

Changes in diet composition of skates with changes in size are inherent to all species of the family Rajidae. These changes are expressed most sharply for predatory species, the juveniles eating mainly small benthic food items and the adults mainly large crustaceans, cephalopods, and fishes. Juvenile benthophagic skates consume mainly small crustaceans (mysids, isopods, amphipods, etc.), whereas the adults consume larger crustaceans (shrimps, snow crabs and hermit crabs). The largest individuals occasionally consume cephalopods and fishes. Similar diets among of various size groups of rajid skates have been reported from other regions of the world oceans (Holden and Tucker 1974; Ajayi 1982; Templeman 1982; Abdel-Aziz 1986; Ezzat et al. 1987; Ebert et al. 1991; Smale and Cowley 1992; Pedersen 1995).

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