



Biology and ecology of *Nezumia liolepis* and *N. stelgidolepis* from the west coast of North America

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Nezumia liolepis and *Nezumia stelgidolepis* were collected during a National Marine Fisheries Service 1997 groundfish survey along the Pacific coast of North America. Bottom trawling was conducted from 188 to 1260 m depths. *Nezumia liolepis* were collected from 581 to 1247 m (3.4–5.7° C) and *N. stelgidolepis* from 285 to 555 m (6.0–8.4° C). The two species had distinct depth and temperature distributions and the majority of the specimens for each species came from narrow depth ranges. *Nezumia stelgidolepis* attains a larger pre-anal fin length (117 mm) than *N. liolepis* (83 mm), and age estimates from otolith ring counts indicate ages from 3 to 9 years for *N. liolepis* and 7 and 13 years for *N. stelgidolepis* from specimens collected. The gonads of *N. liolepis* were not reproductively active, and a single *N. stelgidolepis* possessed eggs of various sizes suggesting batch spawning. *N. liolepis* and *N. stelgidolepis* fed benthically, primarily on crustaceans such as amphipods, shrimp, mysids and polychaete worms. Although diet overlap was high, these two species appear to limit competition for resources by habitat separation.

Key words: *Nezumia*; grenadier; macrouridae; deep sea fish; age and growth; life history.

INTRODUCTION

The eastern North Pacific (southern California to the Bering Sea) has relatively few macrourid species when compared with other oceans (nominally 13 species in five genera, Iwamoto & Stein, 1974). Little is known of the life history of macrourids from the eastern North Pacific. A few common species of *Coryphaenoides* and *Albatrossia pectoralis* (Gilbert) have been studied (Novikov, 1970; Percy & Ambler, 1974; Stein & Percy, 1982; Wilson, 1982, 1988; Armstrong *et al.*, 1991; Andrews *et al.*, 1999; Buckley *et al.*, 1999; Drazen *et al.*, 2000) and scant ecological or biological information is available on eastern North Pacific species of *Nezumia*.

Nezumia species are slope dwelling benthopelagic macrourids represented by *N. liolepis* (Gilbert) (smooth grenadier) and *N. stelgidolepis* (Gilbert) (California grenadier) on the west coast of North America. *Nezumia* is a large genus (46 species) possessing ventral light organs (fossa), an anus located well anterior of the anal fin insertion, seven branchiostigal rays, bands of small teeth in both jaws, moderate to large-sized eyes, a relatively small swim bladder with two retia mirabilia, two gas glands, and a relatively small body size (to 45 cm L_T) (Cohen

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et al., 1990). *N. stelgidolepis* possesses many of the characters that define the genus. *N. liolepis* is a divergent member of the group and many of the distinguishing characters for *Nezumia* are absent or reduced (Iwamoto, 1979; Cohen *et al.*, 1990). Although they have little economic value in the eastern North Pacific, *Nezumia* share the habitat of the upper continental slope with many commercially important species where they may compete for resources. Specimens were collected to provide information on the ecology and biology of these two macrourid species.

METHODS

Nezumia liolepis and *N. stelgidolepis* were collected in October and November of 1997 during the west coast slope survey, from Point Conception, California, to Vancouver Island, British Columbia, by the National Marine Fisheries Service, Alaska Fisheries Science Center, Seattle, Washington. Depth stratified locations along the upper continental slope (188–1260 m depths) were trawled using a Nor'eastern bottom trawl with mudsweep gear. The net body was constructed of 127 mm stretched-mesh polyethylene netting and the codend was lined with a 32 mm stretched-mesh liner. The footrope was 37.4 m long and headrope 27.2 m. Net mensuration equipment was used to measure net spread (\bar{x} = 16.81 m) and height and a global positioning system (GPS) was used to determine distance fished. Catch per unit effort (CPUE) was expressed as the number of fish per hectare swept by the trawl (no. ha⁻¹) (Lauth, 1999).

Specimens of *Nezumia* were preserved in 10% formalin-sea water solution buffered with sodium bicarbonate and transferred to 70% ethanol after about 2 months. Total length (L_T , mm), pre-anal fin length (L_P , mm, Andrews *et al.*, 1999), total weight (W , 0.1 g) and sex were recorded. In the laboratory, stomachs, otoliths, and ovaries were removed and placed in 70% ethanol for later analysis.

DISTRIBUTION AND SPECIES ASSOCIATION

Distributional maps were constructed using the Arcview 3.1 software package. Comparisons of bottom depth and bottom temperature were examined using Statgraphics 4.0. Species associations were summarized by combining all hauls where *N. liolepis* or *N. stelgidolepis* were caught and then the percent biomass that each non-*Nezumia* species contributed to the total biomass from each haul was calculated.

AGE AND GROWTH

Pre-anal fin length is the more accepted and useful measure for macrourids (Atkinson, 1981, 1991; Andrews *et al.*, 1999) rather than total length due to the fragile nature of the long whip-like tail and tail regeneration. The L_P is measured from the tip of the snout to the insertion of the anal fin and is used throughout this study for comparisons. Pre-anal fin length frequencies and the $L_P - W$ and $L_P - L_T$ relationships were examined for each species using Statgraphics 4.0.

Sagittal otoliths were cut along the longitudinal axis using a Buehler Isomet saw and the cut surface of one-half was prepared by passing through an alcohol flame for several seconds, coating with a thin coat of mineral oil, and examining it under reflected light. Each narrow translucent band was assumed to represent an annual event and, therefore, age in years. A non-linear regression (von Bertalanffy growth model) was fitted to age-at-length data for *N. liolepis* using Statgraphics 4.0.

REPRODUCTIVE BIOLOGY

All ovaries were examined to determine the state of development. A single *N. stelgidolepis* possessed developing oocytes. The ovary was removed and weighed (nearest 0.001 g) and a sub-sample of the ovary was weighed and oocytes counted. The estimated number of developed oocytes was obtained using the gravimetric method. The diameter

of individual oocytes from the subsample was measured (nearest 0.01 mm) using a dissecting microscope and a computerized image analysis software package (Optimas 4.0). Samples of the developed ovary were prepared for histological examination by embedding the tissue in paraffin wax and taking slices approximately 6 μm thick. Sections were mounted on microscope slides and stained using a standard hematoxylin-eosin procedure. The sectioned oocytes were examined and classified into groups depending on their developmental stages (McDermott & Lowe, 1997). Oocytes fitting each category were measured a second time from sections and compared with the whole oocyte measurements.

FOOD HABITS

The contents of each stomach were rinsed with water, blotted, and weighed to the nearest 0.01 g. Prey were identified to the lowest taxa possible, and the number and weight (nearest 0.001 g) of each taxon were recorded. Specimens with everted stomachs or showing signs of regurgitation were not included in this analysis. Three statistics were calculated for each prey type to describe their contribution to the stomach contents: percent frequency of occurrence (%F) in non-empty stomachs, per cent numerical composition (%N) and per cent gravimetric composition (%W) (Hyslop, 1980; Bowen, 1983). The data were examined for dietary variation with predator size for both species. *Nezumia liolepis* samples were divided into size-groups of <60, 60–69, 70–79 and >79 mm L_p , and *N. stelgidolepis* samples were divided into size-groups of <80, 80–89 and >89 mm L_p . Dietary variation with predator density was examined for *N. liolepis*. Rocks, sand, and unidentified organic material were excluded from comparisons of prey composition.

RESULTS

Eighty-six specimens of *N. liolepis* and 23 specimens of *N. stelgidolepis* were caught during the 1997 west coast slope survey. A single haul off the central Washington coast (46°43'44" N; 125°03'56" W, depth 800 m) caught both species of *Nezumia* (two *N. liolepis* and one *N. stelgidolepis*). These specimens were not collected for verification and only 84 *N. liolepis* and 22 *N. stelgidolepis* were available for study.

DISTRIBUTION AND SPECIES ASSOCIATION

Nezumia liolepis and *N. stelgidolepis* were caught from Point Conception, California, to Washington State (Fig. 1). The two species segregated by depth with *N. liolepis* from 581 to 1247 m (\bar{x} =900 m) and *N. stelgidolepis* from 285 to 555 m (\bar{x} =465 m). Temperature was closely related to depth in the survey area. Consequently, the habitat occupied by these species also differed in temperature. *Nezumia liolepis* was collected at bottom temperatures of 3.4–5.7° C (\bar{x} =4.2° C) and *N. stelgidolepis* at 6.0–8.4° C (\bar{x} =6.7° C) (Fig. 2). More than 90% of the *N. liolepis* samples were captured in a depth range of 171 m (765–936 m) and a temperature range of 0.6° C (4.1–4.7° C), and 96% of *N. stelgidolepis* were captured in a narrow depth and temperature range of 101 m (454–555 m) and 1.2° C (6.0–7.2° C).

Nezumia liolepis were collected near Point Conception, California (35° N), northward to 43° N. Specimens of *N. stelgidolepis* were collected from the southernmost stations to at least 41° N and although effort north of 43° N was considerable, no confirmed *Nezumia* specimens were caught. In general, *Nezumia* was caught rarely as only 26 out of 182 (14.0%) hauls included them.

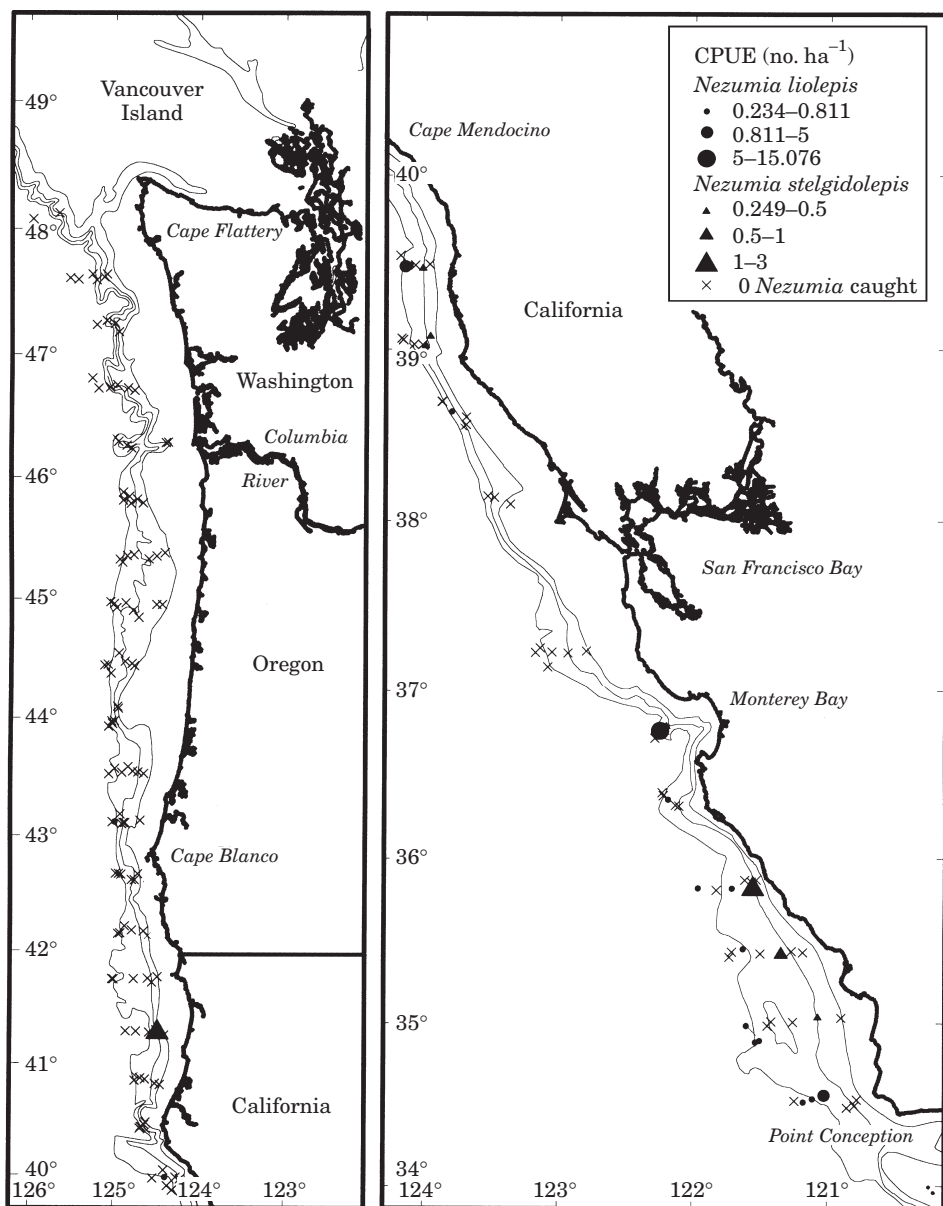


FIG. 1. Distribution of *Nezumia liolepis* and *Nezumia stelgidolepis* from the west coast of North America coded by CPUE (no. ha⁻¹). All trawled stations during the 1997 NMFS survey are included. Bathymetry lines are at 1000, 500, and 200 m, respectively.

Species composition of trawls where *N. liolepis* were caught consisted of 185 species of fish and invertebrates of which *Sebastobus altivelis* Gilbert, *Microstomus pacificus* (Lockington), and *Anoplopoma fimbria* (Pallas) comprised 59.7% of the total biomass and the remaining 172 species (93.0%) contributed <1.0% to the biomass ($\Sigma=10.6\%$ by weight) (Table I). Other macrourids

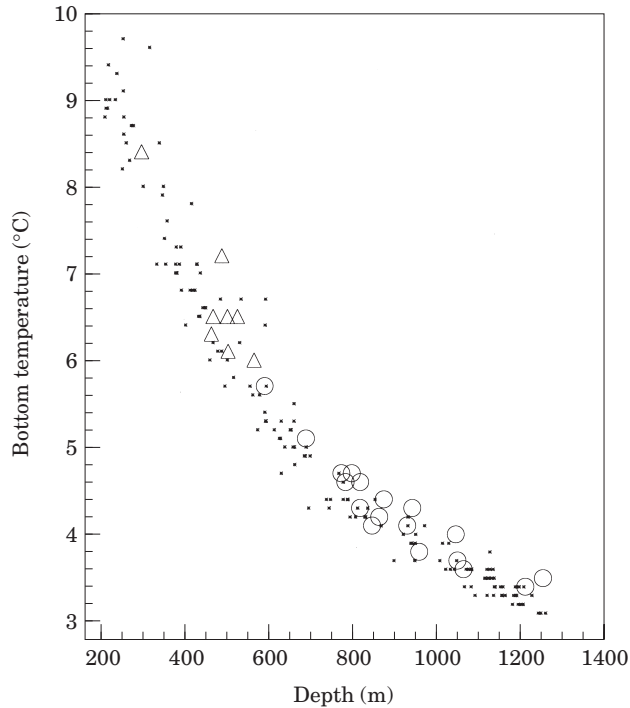


FIG. 2. Relationship between depth and temperature for all trawls conducted during 1997 with the distribution of *Nezumia* collections along these parameters. ○, *Nezumia liolepis*; △, *Nezumia stelgidolepis*; *, trawls with no *Nezumia* caught.

(*Coryphaenoides acrolepis* (Bean) and *Albatrossia pectoralis*) made up c. 10.0% of the biomass associated with *N. liolepis*.

Species composition of trawls where *N. stelgidolepis* were caught consisted of 142 species of fish and invertebrates of which *Merluccius productus* (Ayres), *Microstomus pacificus*, and *Anoplopoma fimbria* comprised 52.6% of the total biomass and the remaining 122 species (86.0%) contributed <1.0% to the biomass ($\Sigma=9.0\%$ by weight) (Table I). Other macrourid species (*C. acrolepis* and *A. pectoralis*) were rare in hauls with *N. stelgidolepis* and comprised only 0.3% of the total biomass caught.

AGE AND GROWTH

The relationship between L_T and L_P for *N. stelgidolepis* and *N. liolepis* was described by a linear model (Fig. 3, top) where L_P is c. 33% of L_T . The $L_T - L_P$ relationships were:

$$N. liolepis: L_T = 38.65 + 3.02 L_P \quad (r^2 = 81.8; n = 77; \text{s.e.} = 13.14)$$

$$N. stelgidolepis: L_T = 11.47 + 3.29 L_P \quad (r^2 = 87.9; n = 22; \text{s.e.} = 24.01).$$

The relationship between W (g) and L_P (mm) were also closely correlated for both species (Fig. 3, bottom). The $W - L_P$ relationships were:

TABLE I. Species associated with *Nezumia liolepis* and *Nezumia stelgidolepis* by gravimetric composition from all hauls combined where each *Nezumia* species was caught

<i>Nezumia liolepis</i>			<i>Nezumia stelgidolepis</i>		
Species name	Weight per cent (%W)	Cumulative weight per cent (%W)	Species name	Weight per cent (%W)	Cumulative weight per cent (%W)
<i>Sebastolobus altivelis</i>	18.15%	31.48%	<i>Merluccius productus</i>	31.09%	31.09%
<i>Microstomus pacificus</i>	18.15%	49.63%	<i>Microstomus pacificus</i>	14.20%	45.29%
<i>Anoplopoma fimbria</i>	10.07%	59.70%	<i>Anoplopoma fimbria</i>	7.31%	52.60%
<i>Coryphaenoides acrolepis</i>	5.81%	65.51%	<i>Glyptocephalus zachirus</i>	4.38%	56.98%
<i>Sebastolobus alascanus</i>	5.79%	71.30%	<i>Raja rhina</i>	3.73%	60.71%
<i>Alepocephalus tenebrosus</i>	3.93%	75.23%	<i>Sebastolobus altivelis</i>	3.51%	64.22%
<i>Chionoectes tanneri</i>	3.67%	78.90%	<i>Myoxoderma platyacanthum rhomaleum</i>	3.32%	67.54%
<i>Albatrossia pectoralis</i>	3.33%	82.23%	<i>Squalus acanthias</i>	3.12%	70.66%
<i>Embassichthys bathybius</i>	1.85%	84.08%	<i>Sebastes aurora</i>	2.86%	73.52%
<i>Thrissacanthias penicillatus</i>	1.78%	85.86%	<i>Sebastolobus alascanus</i>	2.14%	75.66%
<i>Bathybembix bairdii</i>	1.45%	87.31%	<i>Allocentrotus fragilis</i>	2.08%	77.74%
<i>Bothrocara brunneum</i>	1.04%	88.35%	<i>Apristurus brunneus</i>	1.96%	79.70%
<i>Brisaster townsendi</i>	1.02%	89.37%	<i>Paractinostola faeulentata</i>	1.61%	81.31%
172 incidental species (<1.00% each)	10.63%	100.00%	<i>Parmaturus xanthurus</i>	1.57%	82.88%
			Actinaria (order)	1.53%	84.41%
			<i>Lycodes cortezianus</i>	1.42%	85.83%
			<i>Brisaster townsendi</i>	1.39%	87.22%
			<i>Brisaster latifrons</i>	1.33%	88.55%
			Heart urchin unident	1.29%	89.84%
			<i>Bathyraja interrupta</i>	1.15%	90.99%
			122 incidental species (<1.00% each)	9.01%	100.00%

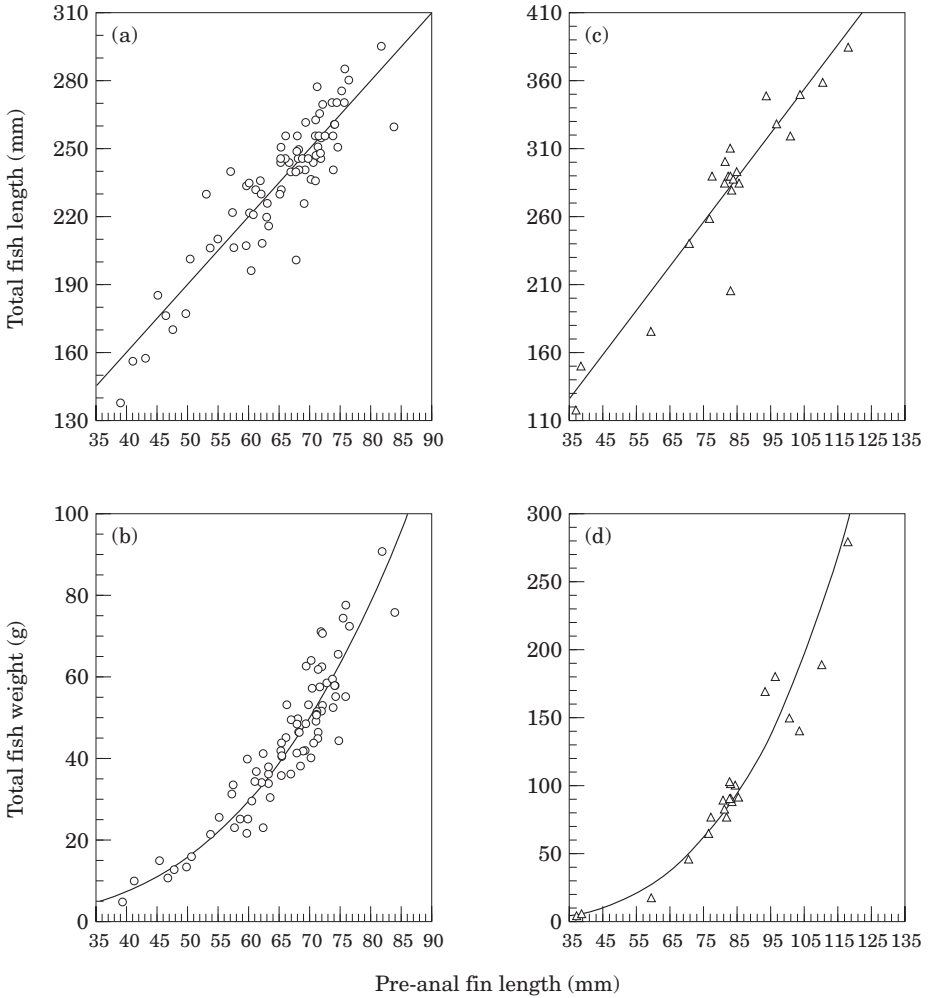


FIG. 3. Relationship between total fish length (L_T) and total fish weight (W) and pre-anal fin length (L_P) for *Nezumia liolepis* (a), (b) and *Nezumia stelgidolepis* (c), (d).

$$N. liolepis: W = 3.07 \times 10^{-5} L_P^{3.37} \quad (r^2 = 90.8; n = 77; \text{S.E.} = 0.16)$$

$$N. stelgidolepis: W = 2.19 \times 10^{-5} L_P^{3.45} \quad (r^2 = 97.5; n = 22; \text{S.E.} = 0.16)$$

N. stelgidolepis is a slightly larger species than *N. liolepis*, with little size difference between sexes for either species (Fig. 4).

Sagittal otoliths from *N. liolepis* showed regular, alternating hyaline and opaque bands from the core to the edge when sections were viewed under reflected light. Age frequency showed slight differences between the sexes (Fig. 5). Males were from 3 to 8 years old with a high proportion of 4- and 5-year-olds, and females were from 3 to 9 years old with a large mode at 4 years.

A von Bertalanffy growth curve was fitted to the age data for *N. liolepis* for both sexes combined (Fig. 6), yielding the parameters;

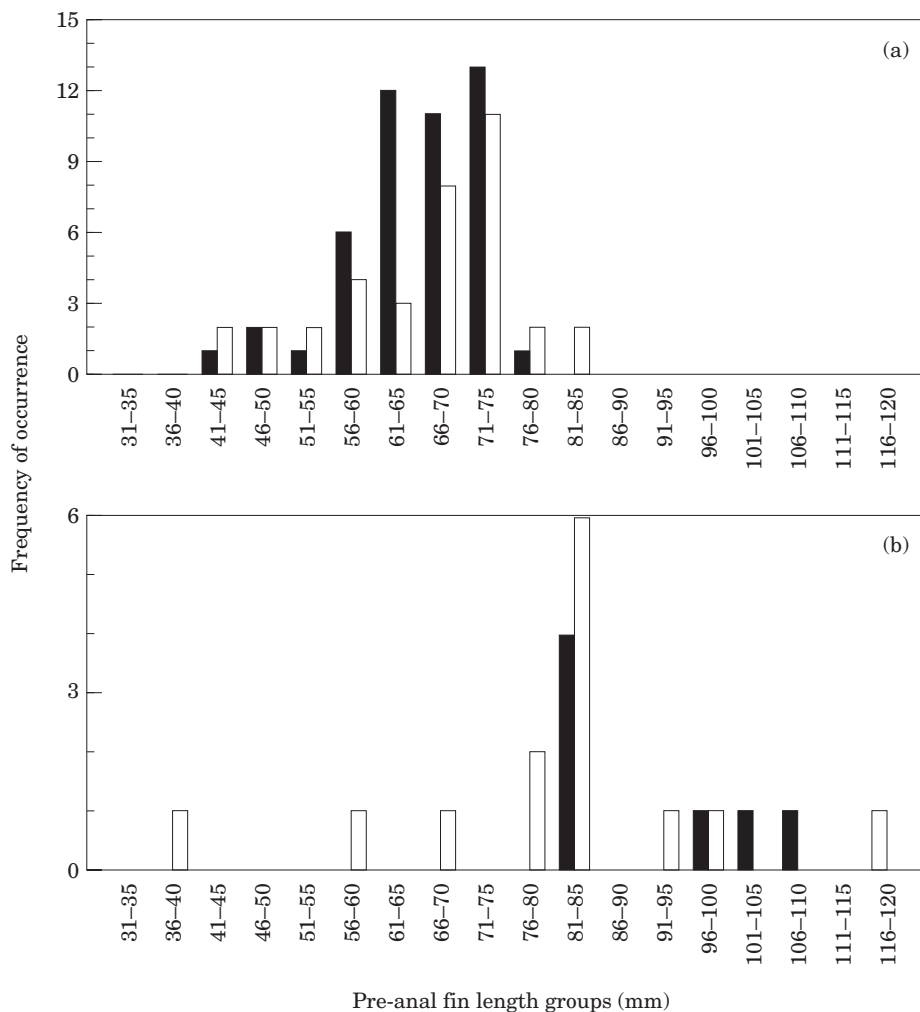


FIG. 4. Size-frequency distribution for male and female *Nezumia liolepis* (a) and *Nezumia stelgidolepis* (b).

$$L_P \infty = 68.44 \text{ mm (S.E.} = 2.19)$$

$$k = 0.70 \text{ (S.E.} = 0.38)$$

$$t_0 = 0.88 \text{ years (S.E.} = 1.19)$$

$$(r^2 = 0.19; n = 79).$$

Sagittal otoliths from *N. stelgidolepis* were examined also, but proved difficult to interpret, having many ring structures and no regular patterns discernible on most otoliths. The two interpretable otoliths had ring counts up to 13 for a 101.4 mm L_P male and 7 for a 79.7 mm L_P female.

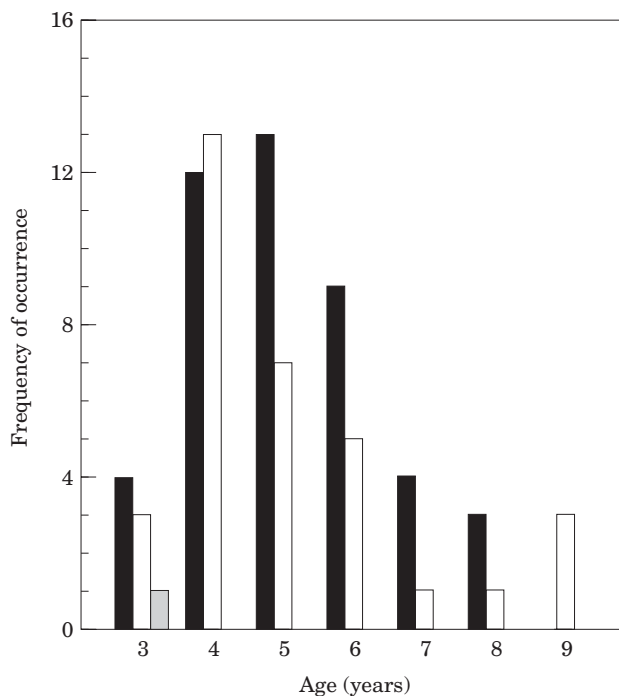


FIG. 5. Age-frequency distribution for *Nezumia liolepis* based on estimates from sagittal otolith ring counts. ■, Males; □, females; ▒, unsexed.

REPRODUCTIVE BIOLOGY

Examination of the gonads of all 84 specimens of *N. liolepis* and 21 specimens of *N. stelgidolepis* found only one *N. stelgidolepis* that displayed any ovarian development. The specimen was collected at 39°01'38" N; 123°59'47" W at a depth of 492 m. The single female (105 mm L_P , 382 mm L_T , 280.9 g W_T , and ovary weight 24.330 g) possessed ovaries with oocytes of various sizes. The size frequency histogram (Fig. 7) of oocytes suggests three potential modes ranging from 0.09 to 1.06 mm in diameter. The multi-modal size distribution suggests a batch spawning mode of reproduction with oocytes at various stages of development at a single moment. The sectioned oocytes measured ($n=75$) did not show a complete size correlation with whole oocyte frequency modal distributions due to the inability to detect the subtle oocyte stage changes. However, there were distinct developmental stages which could be categorized by size groups. Oocytes <0.20 mm diameter were undeveloped in the perinucleus stage; oocytes with some yolk present and cortical aveoli forming were from 0.20 to 0.50 mm; and oocytes in a late yolk to nearly hydrated states were >0.50 mm. The number of most developed oocytes (>0.50 mm yolked and partially hydrated) was estimated using the gravimetric method at *c.* 5489 for both ovaries.

FOOD HABITS

Seventy-seven of the *N. liolepis* did not have everted stomachs or show signs of regurgitation. Two stomachs were empty and 75 contained prey. The diet was

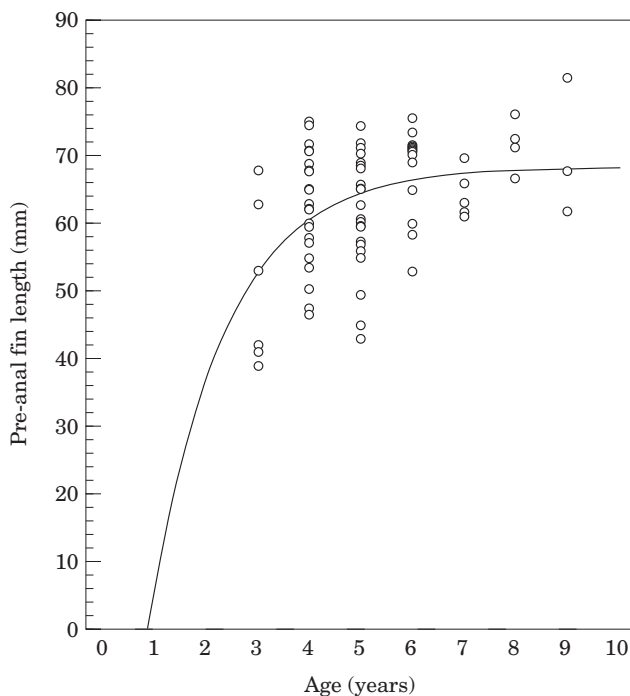


FIG. 6. Von Bertalanffy growth curve fitted to age estimates from sagittal otolith ring counts for *Nezumia liolepis*.

dominated by crustaceans in terms of %*F*, %*N*, and %*W* (Table II). The most important groups by %*F* were amphipods, shrimp, mysids and polychaetes, respectively. Similarly, the most important groups by %*N* were amphipods, shrimp, polychaetes and mysids, while gravimetrically, shrimp, amphipods, polychaetes and a myctophid (lanternfish) were the most important prey. All of the identified shrimp were of the family Hippolytidae.

Most *N. liolepis* ($n=55$) came from a single trawl location (36° N); therefore, they were compared with the 22 specimens collected from other locations. Mean stomach fullness was not significantly different (Student's *t*-test, $P=0.8$) between fish from 36° N (1.02% body weight) and other locations (0.95% body weight). Polychaetes were not important at 36° N (0.2%*W*, 12.7%*F*) but were important at other locations (35.5%*W*, 65.0%*F*). They occurred with a significantly lower frequency in stomachs of *N. liolepis* from 36° N than those from other locations (Fisher exact test, $P<0.01$) while the %*F* of amphipods, shrimp, other crustacea and fish were not significantly different (Fisher exact tests, $P=0.17$, 0.11, 0.11, and $P>0.5$; respectively). Rocks were found in the stomachs of eight *N. liolepis* from 36° N but in none from other locations.

The gravimetric composition of the *N. liolepis* diet changes with body size (Fig. 8). Amphipods decreased and larger prey, like shrimp and fish, increased with increasing predator size. The %*F* of shrimp and mysids increased rapidly with predator size while polychaetes, copepods, amphipods, and fish increased slightly (Fig. 9). The number of shrimp and amphipods eaten per occurrence also increased with predator size.

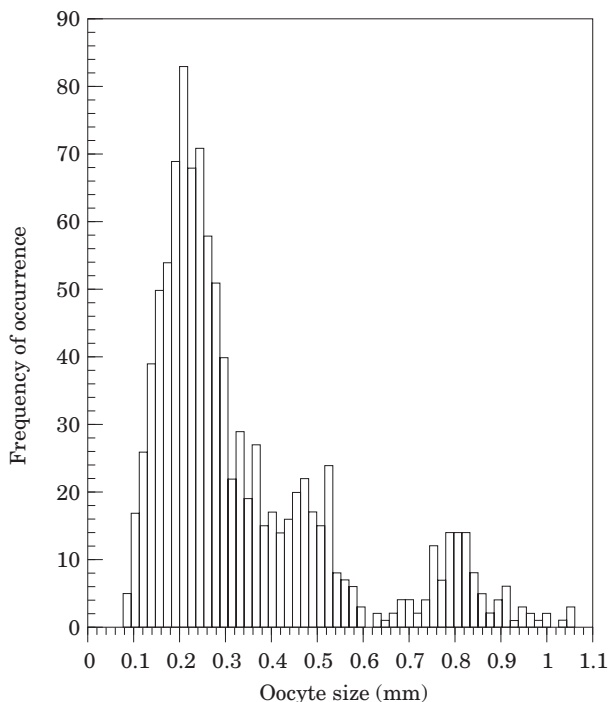


FIG. 7. Size-frequency distribution for a subsample of oocytes from a single *Nezumia stelgidolepis* ($n=1030$).

Seventeen of the *N. stelgidolepis* did not have everted stomachs or show signs of regurgitation. One of the stomachs was empty and 16 stomachs contained prey, mostly crustaceans (Table II). Amphipods, mysids and shrimp were the most important groups of crustaceans in the stomach contents by %*F* and %*N*. In order of gravimetric contribution, the crustaceans in the diet were dominated by shrimp, crabs, amphipods and mysids. Crabs and polychaete worms both increased in %*F*, %*N* and %*W* with increasing predator size (Fig. 10), and the single *Pasiphaea pacifica*, a pelagic shrimp (Butler, 1980), was found in a stomach from the smallest size-group.

DISCUSSION

During the 1997 west coast slope survey *N. stelgidolepis* and *N. liolepis* were more common south of 41° N than north. Studies off northern Oregon near the Columbia River (Alton, 1972; 1961–1966 in 91–2121 m) and off the central Oregon coast (Day & Pearcy, 1968; 1961–1962 in 40–1829 m) failed to catch any *Nezumia* spp. although up to four species of *Coryphaenoides* and *Albatrossia pectoralis* were caught. Stein & Pearcy (1982) reported collecting fewer than 30 *N. stelgidolepis* from 579 otter trawls off the Oregon coast in 200–5180 m between 1963 and 1976. The Alaska Fisheries Science Center's trawl surveys (1990–1997; 180–1284 m) from Point Conception, California, to Vancouver Island, B.C., caught *N. liolepis* rarely between 35° N and 46° N in 236–1284 m,

TABLE II. The stomach contents of *Nezumia loiepis* and *Nezumia stelgidolepis* sampled from the 1997 groundfish survey of the upper continental slope off Washington, Oregon and California. The per cent frequency of occurrence (%F), the per cent numerical composition (%N) and the per cent gravimetric composition (%W) are shown for each mutually exclusive prey category identified in the stomach contents

Prey name	<i>Nezumia loiepis</i>			<i>Nezumia stelgidolepis</i>		
	%F	%N	%W	%F	%N	%W
Foraminiferida (protozoan)	4.0	0.1	0.0	6.3	1.2	0.0
Polychaeta (worm)	26.7	3.4	7.6	18.8	5.6	3.5
Gastropoda (snail)	1.3	0.0	0.0	12.5	1.2	0.6
Bivalvia (clam and mussel)	4.0	0.1	0.1	6.3	0.6	0.2
Cephalopoda (squid and octopus)	2.7	0.1	0.0	6.3	0.6	0.1
Crustacea, unidentified	90.7	2.9	17.7	100.0	13.0	18.9
Ostracoda	1.3	0.0	0.0			
Calanoida (copepod)	8.0	0.3	0.0			
Peracarida Mysidacea (mysid)	36.0	2.5	0.9	56.3	15.5	7.1
Cumacea (cumacean)	16.0	1.4	0.3	6.3	0.6	0.0
Isopoda (isopod)	4.0	0.1	0.3	6.3	0.6	0.0
Amphipoda (amphipod)	96.0	77.4	18.1	62.5	23.6	9.4
Decapoda (shrimp and crab)	2.7	0.1	0.1			
Natantia (shrimp)	37.3	2.7	5.0	50.0	11.8	2.8
Caridea (shrimp)	6.7	0.3	1.4			
<i>Pasiphaea pacifica</i> (shrimp)				6.3	0.6	8.3
Hippolytidae (shrimp)	21.3	1.4	5.6	18.8	3.1	3.0
<i>Spirontocaris</i> sp. (shrimp)	14.7	1.0	17.0	18.8	1.9	12.3
<i>Lebbeus</i> sp. (shrimp)	2.7	0.1	0.1			
<i>Eualus</i> sp. (shrimp)	2.7	0.1	0.8			
<i>Eualus macrophthalma</i> (shrimp)	9.3	0.5	3.5			
<i>Crangon</i> sp. (shrimp)				6.3	1.2	9.9
Reptantia (crab)				6.3	1.2	5.3
Paguridae (hermit crab)				6.3	1.2	7.2
<i>Chionoecetes</i> sp. (Tanner crab)	2.7	0.1	0.1			
Osteichthyes Teleostei (bony fish)	2.7	0.1	0.0	18.8	3.7	0.5
Myctophidae (lanternfish)	1.3	0.0	6.3			
Unidentified eggs	8.0	1.2	0.4			
Unidentified tube	5.3	0.2	0.1	6.3	0.6	0.2
Unidentified worm-like organism	1.3	0.0	0.0			
Unidentified organic material	97.3	3.1	13.7	100.0	10.6	9.9
Sand	2.7	0.1	0.2			
Rocks	10.7	0.4	0.9	12.5	1.2	0.9
Total stomachs (empty)	77 (2)			17 (1)		
Total number of items		2358			161	
Total weight of contents			31.1 g			7.3 g

and *N. stelgidolepis* commonly from *c.* 34° N to 45° N in 284–1099 m, with few records for either species north of 45° N. However, the identification of these two species may be confused for any records not collected and verified. Both species also may have been misidentified as young *Coryphaenoides acrolepis*, which are caught commonly in the areas surveyed.

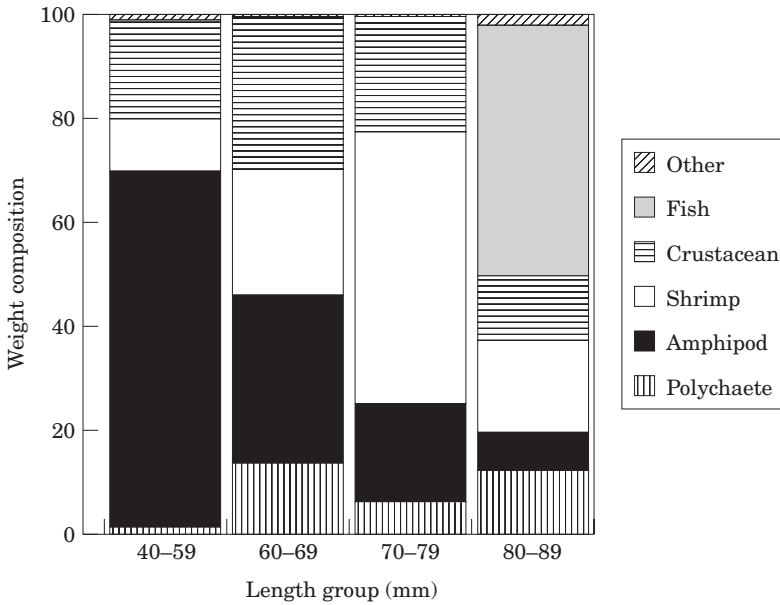


FIG. 8. Gravimetric composition of the stomach contents of *Nezumia liolepis* by length groups of 40–59, 60–69, 70–79 and 80–89 mm pre-anal fin length with sample sizes of 9, 30, 30 and 6 fish, respectively. ‘Crustacean’ includes all crustaceans that are not shrimp or amphipods.

Both species had limited depth ranges and distributions and were not locally abundant during the 1997 survey, with the exception of a single haul (36° N, Monterey Canyon), in which 55 individuals of *N. liolepis* were collected. There

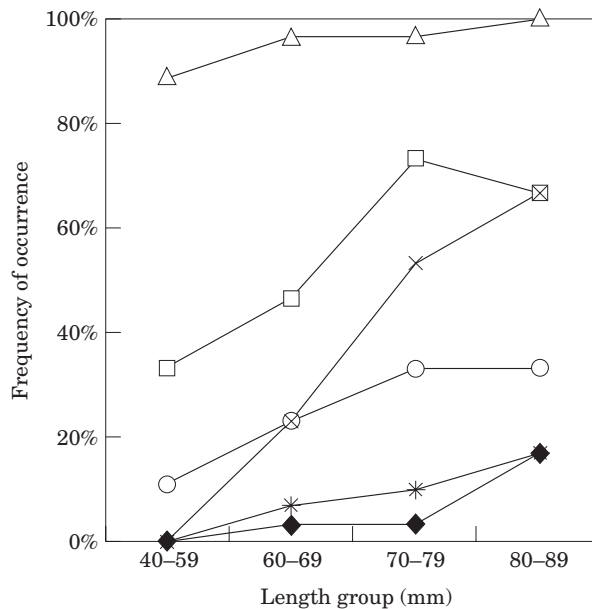


FIG. 9. Frequency of occurrence of prey types found in the stomachs of *Nezumia liolepis* by size groups of 40–59, 60–69, 70–79 and 80–89 mm pre-anal fin length with sample sizes of 9, 30, 30 and 6 fish, respectively. ○, Polychaete; *, copepod; ×, mysid; △, amphipod; □, shrimp; ◆, fish.

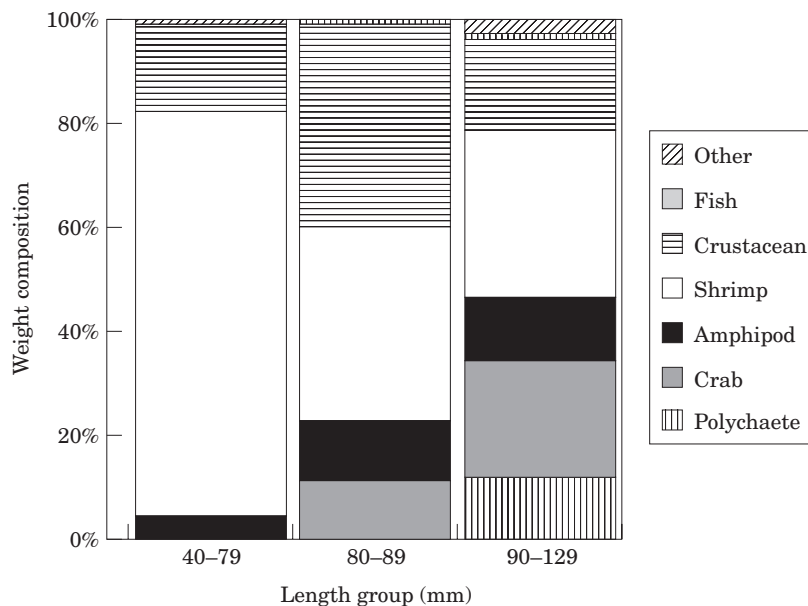


FIG. 10. Gravimetric composition of the stomach contents of *Nezumia stelgidolepis* by length groups of 40–79, 80–89 and 90–129 mm pre-anal fin length with sample sizes of 5, 8 and 3 fish, respectively. 'Crustacean' includes all crustaceans that are not shrimp, amphipods or crabs.

was a mix of unripe males ($n=30$) and females ($n=25$) from this haul indicating that reproductive activity was probably not responsible for this aggregation or high density of individuals. It is possible that *N. liolepis* has a strong preference for a particular type of habitat that was encountered at this station on the north side of Monterey Canyon. The lack of polychaetes and the presence of rocks in the stomachs of *N. liolepis* from this station indicate that the substratum may be more rocky than at the other locations where fewer *N. liolepis* were caught. If *N. liolepis* have a preference for rocky habitat, they may be undersampled because of the difficulty in trawling in these areas.

McLellan (1977) has suggested that smaller, slope-dwelling macrourids have more restricted geographic ranges due to the availability of resources. *Nezumia bairdi* (Goode & Bean) was widely distributed around Newfoundland but was concentrated in a narrow depth range of 500 to 700 m and temperature range of 3.0 to 8.0°C (Savvatimsky, 1989). Present data suggest that *N. liolepis* and *N. stelgidolepis* have narrow depth and temperature ranges also and have patchy distributions due to their possible substratum preferences.

Preliminary analysis of distributional data from the NMFS 1999 west coast slope survey was similar to that of 1997. In 1999 *Nezumia liolepis* occurred from 797 to 1043 m (3.7–4.2°C, $n=83$) and *N. stelgidolepis* from 432 to 651 m (4.7–6.5°C, $n=44$). As in 1997, the two species were separated completely by depth (and temperature) and were never collected together in the same trawl during the 1999 survey. Although the depth ranges for the two species overlap across years, they do not appear to co-occur.

Age estimates for *N. liolepis*, and limited evidence for *N. stelgidolepis*, suggest relatively rapid growth rates and a low maximum age (9 for *N. liolepis* and 13 for

N. stelgidolepis) for *Nezumia* species from off California. *Nezumia bairdi* from Atlantic waters appear similar to *N. liolepis* and *N. stelgidolepis* in many ecological and biological aspects and reached similar ages (3–11 years) with similar growth rates (Savvatimsky, 1989). Minimum L_p s and ages (Figs 4 and 5) of 35–40 mm and 3 years, suggest the lower limit of recruitment to the bottom trawl used for capture. However, many juvenile *Coryphaenoides acrolepis* (20–40 mm L_p) were captured in trawls with *Nezumia* species in 1997, casting doubt on net efficiency as a single factor for lack of capture. Given the pelagic nature of the juvenile period for many macrourid species (Marshall, 1965; Merrett, 1978, 1989; Stein, 1980; Stein & Percy, 1982), it can be speculated that *N. liolepis* and *N. stelgidolepis* remain in the water column through the juvenile period and recruit to the bottom at c. 3 years of age and 35 mm L_p .

Nezumia liolepis during October and November 1997 showed no evidence of gonadal development and most ovaries in the resting state. The single *N. stelgidolepis* with active ovaries suggests batch spawning spanning autumn, in common with other *Nezumia* species (D'Onghia *et al.*, 1999). However, all other *N. stelgidolepis* had ovaries in the resting state resulting in only a tentative conclusion for time of spawning for this species. The spawning season for *Nezumia* appears to be highly variable from winter-spring (*Nezumia sclerorhynchus* (Valenciennes); Sanzo, 1933) to summer-fall (*Nezumia bairdi*; Bigelow & Schroeder, 1953) to year-round (*Nezumia aequalis*, Günther, Relin-Orsi & Wurtz, 1979; Carrasson & Matallanas, 1989; Massuti *et al.*, 1995; Coggan *et al.*, 1999; and *Nezumia sclerorhynchus*, D'Onghia *et al.*, 1999).

The food habits of other macrourid genera in the eastern North Pacific have been described (Novikov, 1970; Percy & Ambler, 1974; Buckley *et al.*, 1999; Drazen *et al.*, 2000). Within the Macrouridae, *Nezumia* spp. are relatively poor swimmers with small mouths and this restricts many species to a more specialized diet than larger macrourids that can feed on both small and large prey (McLellan, 1977). While present results did not indicate a specialized diet, they did show a diet lacking larger prey (such as squid, large crustaceans and fishes) that are common in the diets of larger *A. pectoralis* and *Coryphaenoides* spp. from the same region (Percy & Ambler, 1974; Buckley *et al.*, 1999; Drazen *et al.*, 2000). However, the diet of small *C. acrolepis* ($L_p < 150$ mm) is similar to that of *N. liolepis* and *N. stelgidolepis* (Drazen *et al.*, 2000). Analysis of multiple years of trawling from the eastern North Pacific suggests that, for the depth ranges where *N. liolepis* occurs, similar sized *C. acrolepis* decrease in abundance and reappear in larger numbers at greater depths, where *N. liolepis* is less abundant (unpubl. data). This disjunct depth distribution for juvenile *C. acrolepis* may lessen the likelihood of intraspecific competition for food, given the similarity in diets of *Nezumia* spp. and *C. acrolepis*.

The diets of *N. liolepis* and *N. stelgidolepis* were also similar to the diets of other species of *Nezumia*. In the Atlantic Ocean, the diets of *N. sclerorhynchus* (Marques & Almeida, 1998), *N. aequalis* (Macpherson, 1979; Hoffmann, 1982; Mauchline & Gordon, 1984; Carrason & Matallanas, 1989; Marques & Almeida, 1998), and *N. bairdi* (Savvatimsky, 1989; Langton & Bowman, 1980) consist primarily of polychaetes, amphipods, shrimp and other epibenthic organisms. In the western Pacific Ocean, the diet of *N. condylura* was mostly euphausiids and polychaetes, with some prawns (parenthetically referred to as mysids; Okamura,

1970). Based on the large portion of polychaetes in the diet, Okamura (1970) concluded that *N. condylura* was bathydemersal and prowled for food in the mud. The large proportion of euphausiids in the diet was thought to result from diurnal consumption when vertically migrating euphausiids were near the continental slope. Interactions of this type are documented for benthic rockfishes feeding on euphausiids in the eastern North Pacific (Genin *et al.*, 1988).

The number of *N. stelgidolepis* sampled was small and inferences about the diet should be considered preliminary. *N. stelgidolepis* became increasingly demersal in its foraging habits with increasing size (Fig. 10). However, further studies would be required to see if the consumption of pelagic prey (*P. pacifica*) was due to pelagic foraging, scavenging of a carcass, or simply the proximity of the prey to the seafloor, as was suggested for *N. condylura* (Okamura, 1970).

Changes in the diet with increasing predator size were defined better for *N. liolepis*. The decline in the gravimetric proportion of amphipods with increasing size (Fig. 8) was attributable to an increase in the consumption of other prey types, most notably shrimp and mysids (Fig. 9), rather than a decrease in the number of amphipods consumed. As *N. liolepis* get larger, the physical limit on the size of prey that they can ingest increases, but the frequency of occurrence of smaller prey types does not decrease (Fig. 9).

Overall, the diets of *N. liolepis* and *N. stelgidolepis* were dominated by crustaceans, particularly shrimp (%W) and amphipods (%N). The large number of amphipods consumed is probably attributable to their relative abundance, ease of capture and small size. Polychaetes, amphipods, and hippolytid shrimp were more important (%W) to *N. liolepis* while mysids, crabs, and non-hippolytid shrimp (*P. pacifica* and *Crangon* spp.) were more important to *N. stelgidolepis*. Although the overlap in the diet based on gross taxonomic groupings is fairly high, it is doubtful that there is much competition for food between these two macrourids because of their disparate depth distributions.

The wide, overlapping depth ranges reported for these two species of *Nezumia* is in contrast to the narrow, distinct depth ranges indicated by this single survey. Confusion surrounding the identification of these species and coverage of wide depth ranges by trawls may play a role in the distributions reported previously. However, it is recognized that this single survey does not encompass interannual and seasonal differences that may occur, and does not match the large number of trawls taken in previous years. Also, *N. liolepis* may have been caught rarely because it had a strong association with steep and rocky habitat that was not easily trawled. *Nezumia liolepis* appears to be fast-growing, and some evidence suggests that this is also true for *N. stelgidolepis*. Both species fed on benthic and epibenthic fauna. A batch spawning reproductive strategy appears common among *Nezumia* species, as was found for *N. stelgidolepis*. However, surveys in other seasons would be necessary to establish the spawning cycle.

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