Abstract—The threaded sculpin (Gymnocanthus pistilliger) is distributed in the North Pacific from Norton Sound south to Southeast Alaska and west to Russia and Japan. It reaches its greatest abundance in the eastern Bering Sea in Bristol Bay where it is typically found in waters less than 50 m deep. Alaska Fisheries Science Center groundfish surveys in the eastern Bering Sea have estimated densities of up to 102 fish per hectare (catch per unit of effort, CPUE) for 1997 and 1998. Population estimates for 1997 were 111.20 million and for 1998 were 51.70 million. The population estimate drop is reflected in length-frequency data that suggest a complete lack of 2-year-old fish for 1998. Gymnocanthus *pistilliger* is a short-lived species (age estimates from otoliths range up to 10 years for males and up to 9 years for females), and the maximum size is 161 mm and 201 mm total length for males and females, respectively. During June, when specimen collections were made, ovaries are in the resting stage and contain some residual eggs from a previous spawning. The diet of G. pistilliger changes from predominantly gammarid amphipods and polychaetes to crangonid shrimp and fish with increased total length. Comparisons with studies from the western North Pacific on G. pistilliger suggest biological differences between populations, which may reflect adaptation to different habitats.

Biology and ecology of threaded sculpin, *Gymnocanthus pistilliger,* in the eastern Bering Sea

Gerald R. Hoff

National Marine Fisheries Service Alaska Fisheries Science Center 7600 Sand Point Way NE Seattle, Washington 98115 E-mail address: jerry.hoff@noaa.gov

Gymnocanthus pistilliger (Pallas), the threaded sculpin, is a small marine cottid that inhabits waters from Southeast Alaska north to Norton Sound and west to Russia and Japan (Wilson. 1973). It is found in shallow waters (<50 m) over soft sandy to muddy bottoms and is the most abundant cottid in the Bristol Bay region (>15 m) of the eastern Bering Sea. Gymnocanthus pistilliger may compete for resources with juvenile stages of commercially important flatfish in the shallow bays and nearshore areas used as nursery grounds (Grigorev and Fadeev, 1995). Although G. pistilliger is an abundant species, little life history information is available on Bristol Bay populations. The present study reports on the ecology and biology of G. pistilliger from Bristol Bay, Alaska, and compares it to ecology studies conducted on western North Pacific populations.

Methods

Specimens of *G. pistilliger* were collected in June of 1997 and 1998 during the National Marine Fisheries Service, Alaska Fisheries Science Center (AFSC), eastern Bering Sea survey. The survey area extended from the Alaska Peninsula north to Nunivak and St. Matthew Islands, and west to the 200-m shelf break (Fig. 1). Trawls were conducted on a grid of 356 fixed stations (20 nmi

20 nmi) fished during daylight hours throughout the Bering Sea survey area. Thirty-minute trawls towed at 3.0 knots were conducted at each station. The shallowest depth surveyed was 15 m in Bristol Bay and the deepest was 178 m near the shelf edge. Trawling was conducted with the AFSC 83-112 eastern trawl, which is a low-opening twoseam trawl with a 26.5-m headrope and 34.1-m cable footrope (Rose and Walters, 1990) wrapped with rubber stripping and chain hangings that contact the bottom while the trawl is towed. Height and width measurements of the net were recorded with an acoustic SCANMAR net mensuration system. Global positioning system was used to record latitude and longitude data at the start and end of the trawl in order to determine distance fished.

The entire catch was sorted to species, enumerated and weighed, or a weighed subsample was used if there was a very large catch. Catch per unit of effort (CPUE) was calculated as number of fish per hectare (no./ha) by dividing the number of fish caught for each haul by the estimate of the area swept (net width distance fished). Gymnocanthus pistilliger occurred in the survey area only at stations less than 50 m in depth (Fig. 1); therefore only this area was used for calculating population estimates. A population estimate was calculated by first determining a mean CPUE from all hauls combined (<50 m) and then expanded to the area. The biomass estimates were calculated in a similar manner by using weight in metric tons. The population and biomass estimates were made under the assumption that all fish in the path of the trawl were caught and were a representative sample for each station grid. However, given that there may be gear selectivity for fish size and given the patchy nature of fish distributions, the populations and biomass stated in this study are best estimates.

In May of 1995 and June of 1988–91 exploratory trawling was conducted in the shallow bays (<30 m) within Bristol

Manuscript accepted 2 June 2000. Fish. Bull. 98:711–722 (2000).



Figure 1

Map of the area in the eastern Bering Sea surveyed by the National Marine Fisheries Service. All stations (+) shown were trawled in 1997 and 1998. Map includes contour lines at 50-, 100-, and 200-m depths.

Bay by the National Marine Fisheries Service. Trawling methods, population, and density estimates were performed as described above.

Gymnocanthus pistilliger samples collected during 1997 and 1998 were preserved at sea by freezing or by preserving in a 10% formalin-seawater solution buffered with sodium bicarbonate. Frozen samples were partially thawed, and total length (TL, in mm), standard length (SL, in mm), total fish weight (TFW, in mg), gonad weight (GW, in mg), and sex were recorded. Sagittal otoliths were removed and placed in 50% ethanol. Parameters from formalin-preserved specimens with stomachs and ovaries removed were recorded in a similar manner and placed in 50% ethanol.

Dark bands on otoliths were evident under reflected light and were counted by the break-and-burn method to ensure inclusion of all ring structures. Length at age was described by using nonlinear regression to fit the von Bertalanffy (1957) growth model for male and females separately with pooled data from the two years.

The von Bertalanffy growth curve is

$$L_t = L_{\infty} [1 - e^{-K(t-t_0)}].$$

Fish numbers for length-frequency samples were combined for all hauls by sex and year. The relationships of total fish length (TL) to total fish weight (TFW) were investigated with the model

$$TFW(g) = a TL(mm)^b.$$

Ovaries were removed and weighed to the nearest milligram from formalin-preserved fish. The gonosomatic index (GSI) was calculated from TFW and ovary weight was calculated as

100(ovary weight/TFW).

Stomach contents were recorded to the lowest practical taxon, and enumerated and weighed to the nearest milligram. For analysis, prey items were grouped into seven logical or taxonomic categories (Table 1). *Gymnocanthus pistilliger* were grouped into four length groups (<100 mm, 100–124 mm, 125–149 mm, and 150–201 mm TL). Percent frequency of occurrence, total count, and total weight were calculated for individual prey items and for each prey item group. Statistical analysis and graphing were conducted with the computer programs Statgraphics 2.0 and Sigma-Plot 4.0, and distributional maps were produced with the software Arcview 3.0.

Table 1

Diet composition of *Gymnocanthus pistilliger*. Prey items are grouped into major taxonomic or similar groups and frequency of occurrence (freq.), total count, and total weight percentages were calculated for both individual items and for groups. (Total lengths 73-201 mm, n=93).

Prey items	Frequency of occurrence	Total count	Total weight
Wormlike organisms			
Polychaeta	47.19	1.21	14.27
<i>Echiur</i> us sp.	7.87	0.36	1.43
Opheliidae	2.25	0.03	0.48
Annelida	1.12	0.01	0.01
Goniadae	1.12	0.07	0.08
Total	52.81	1.69	16.26
Amphipoda			
Gammaridea	82.02	92.74	15.43
Caprellidea	2.25	0.04	0.05
Amphipoda unidentified	1.12	0.03	0.26
Total	83.15	92.84	15.74
Shrimp	00.10	02.01	10.11
Shrimp Crangonidae	32.58	0.7	31.23
Total	32.58	0.7 0.7	31.23 31.23
	02.00	0.7	31.23
Other Crustacea		0.02	
Ostracoda	1.12	0.06	0.01
Mysidacea	1.12	0.01	0.03
Cumacea	17.89	0.4	0.47
Isopoda	1.12	0.01	0.07
Euphausiacea	1.12	0.01	0.02
Crustacea unidentified	1.12	0.01	0.07
Total	21.35	0.52	0.67
Mollusca			
Gastropoda	10.11	0.27	0.64
Naticacea	2.25	0.04	0.99
Bivalvia	31.46	1.39	1.5
<i>Clinocardi</i> um sp.	1.12	0.01	1.1
Octopus sp. (beaks)	2.25	0.03	0.01
Total	39.33	1.75	4.24
Fish			
Lumpenus sp.	1.12	0.01	2.24
Ammodytes hexapterus	4.49	0.07	12.03
Teleostei unidentified	2.25	0.03	1.24
Total	7.87	0.12	15.5
Miscellaneous			
Forminifera	3.37	0.07	0.02
Anthozoa	2.25	0.03	0.05
Urochordata	1.12	0.03	0.03
unidentified eggs	10.11	0.48	0.06
organic material unidentified	85.39	1.15	12.28
wood	1.12	0.01	0.19
rocks	38.2	0.51	2.61
sand	4.49	0.06	1.06
material unidentified	1.12	0.00	0.04
Total	88.76	2.37	16.35
10001	00.10	2.01	10.00

Results

Distribution

The distribution of *G. pistilliger* during the 1997 and 1998 eastern Bering Sea surveys was limited to depths <50 m;

areas of highest concentration were located around southern Kuskokwim and Togiak Bays for both survey years (Fig. 2). In 1997, *G. pistilliger* were caught in 60% of the trawls <50 m (n=86 for each year), compared with 51% in 1998. The 1997 CPUE ranged from 0.19 to 101, with a mean of 15.81 (SD=22.78); the population estimate for



the entire survey area was 110.24 million fish and the biomass estimate was 4254 metric tons (t). The 1998 CPUE ranged from 0.1 to 55 with a mean of 7.37 (SD=5.23); the population estimate was 51.70 million fish and the biomass estimate was 1956 t.

The distribution of females and males differed by depth (Fig. 3) with the proportion of females decreasing with

depth. Catch rates at depth indicated that *G. pistilliger* inhabited nearshore areas and were most abundant in the shallowest depths covered by this survey (Fig. 4).

Trawling in Kuskokwim Bay and Togiak Bays resulted in mean CPUEs of 6 and 24 for each bay, respectively (n=9trawls per bay, CPUEs of 1 to 17, SD=5.54 for Kuskokwim Bay; CPUEs of 1 to 79, SD=30.32 for Togiak Bay). During



these years, catches peaked in Togiak Bay (CPUEs of 71 to 79) at some of the shallowest depths trawled (13–15 m). Trawls conducted in Togiak Bay again in 1995, during late May, resulted in densities up to 249 at 19.8 m in depth (n=28 trawls, CPUEs from 4 to 249, $\bar{x}=65.68$, SD=74.68, depth range: 4–30 m).

Age and growth

A von Bertalanffy growth curve was fitted to pooled lengthat-age data for 1997b and 1998 and analyzed separately for males and for females (Fig. 5). The growth models were the following:

males
$$L_t = 165.5 \ [1-e^{-0.375299 \ (t + 0.0704311)}]$$

(n=395, r²=0.78, SE=8.08);
fomelog $L_t = 222.8 \ [1 \ e^{-0.228048 \ (t + 0.226626)}]$

temales $L_t = 223.8 [1-e^{-0.228048 (t+0.220026)}]$ (n=595, r²=0.84, SE=9.85).

Females grew faster than males, and by three years of age, a difference in length at age was established (Fig. 5). Females reached >200 mm TL and a maximum age of 9

years; males reached 160 mm and a maximum age of 10 years.

Age groups from 1997 consisted of 2- to 10-year-old fish; the strongest age group was 4 years (>50% of individuals) and there were large groups of 2- and 3-year-old fish. In 1998 however, ages ranged from 3 to 9-year-old fish. The strongest age group (>50% of individuals) was 5 years. Two-year-old fish were absent (Fig. 6). Length-frequency histograms (Fig. 7) for 1997 and 1998 male and female *G. pistilliger* show the age modes as well as the age groups that were absent in 1997 and 1998.

Weight-length relationships for males and females and between years showed no significant difference (P>0.05) and were pooled for analysis (Fig. 8). The pooled weight-length equation was statistically significant (P<0.01, r^2 =0.97, n=992):

$$TFW (gm) = 2.40317 \quad 10^{-6}TL (mm)^{3.30692}.$$

Ovaries were not developed in June when fish were collected; few large females contained residual eggs from the previous spawning. The GSI ranged from 0.5% to 1.9% for fish collected from 1997 (females n=108, 70–190 mm TL).



Diet

A total of 32 different prey items were identified from 93 stomachs of fish collected in 1997 (Table 1). Frequency of occurrence analysis indicated that gammarid amphipods and polychaete worms were the most common prey items; crangonid shrimp and bivalves were encountered less frequently. Similarily prey total count indicated that gammarid amphipods were the most numerous prey items encountered but no other single item was found in large numbers. Crangonid shrimp predominated by total weight; Pacific sandlance (*Ammodytes hexapterus*), gammarid amphipods, and polycheates were secondarily important and were of approximately equal weight.

The relation between fish size and diet composition showed a shift from predominantly small benthic amphipods to increasingly larger prey items, such as crangonid shrimp and fish with increased fish TL (Fig. 9). Total diet weight proportion showed similar trends; crangonid shrimp and fish became more important and gammarid amphipods decreased in diet weight proportion as fish increased in TL (Fig. 10).

Discussion

Distribution

Gymnocanthus pistilliger is abundant in the spring to early summer (May and June) near the mouth of Kuskokwim and Togiak Bays and throughout the shallow areas of Bristol Bay. This area is characterized by relatively shallow water (<50 m) and has a sandy to muddy bottom (McDonald et. al, 1981). The Togiak River and Kuskokwim River discharge large amounts of fresh water into the shallow estuarine environment creating fluctuating temperatures and salinities; thus, during winter the entire area may be covered in thick ice sheets. Gymnocanthus *pistilliger* may move in and out of the shallow local bays seasonally to sustain a suitable habitat. However the nearshore distribution was difficult to assess for G. pistil*liger* from the present study owing to limited sampling in very shallow coastal waters and single season collections. The timing of spawning movements, however, may significantly affect population estimates if the species moves between depths seasonally and may help to explain a 50% decline in fish from 1997 to 1998. Although water temperature is often associated with fish movements, there was no significant difference between the means (t-test P=0.18) in bottom water temperatures in the survey area <50m in depth for the two years sampled (1997, \bar{x} =4.22°C, SD=1.88; 1998, \bar{x} =4.48°C, SD=0.87).

Vdovin et al. (1994) suggested that *G. pistilliger* remains within shallow water and except for spawning, probably remains in the nearshore area most of the year. Spawning migrations in winter resulted in both sexes aggregating in deeper bay areas of Peter the Great Bay (Vdovin et al., 1994); however, the proportion of females increased with increasing depth (a depth range of 80 to 110 m was maintained during spawning) (Tokranov, 1987; Vdovin et al., 1994).

If Bristol Bay populations are similar to Peter the Great Bay populations, then at the time of capture (June) *G. pistilliger* has already spawned and dispersed in the nearshore areas. Females probably migrate to join the males in the deeper part of Bristol Bay (around 50 m depth) during late winter to early spring to spawn, although it is unlikely that Bristol Bay populations reach the spawning depths of populations in Peter the Great Bay. Distributional data from Alaska indicate that *G. pistilliger* are rarely found deeper than 50 m, except occasionally in coastal areas of the Gulf of Alaska (Hoff, unpubl. data).

Age and growth

Age data gathered from otoliths suggest that G. pistil*liger* is short lived (to 10 years), the females exhibit faster growth, and that this species reaches a maximum size of 205 mm for females and 160 mm for males. The age structure of western Bering Sea populations has shown older populations than those for Bristol Bay (a strong mode from 7 to 9 years (range 3-13 years) and a larger maximum size of 270 mm TL for females and 220 mm TL for males (Tokranov, 1987). Length-at-age data for fish collected off Kamchatka (Tokranov, 1987) were similar to those reported in the present study, suggesting that similar aging techniques were used and similar growth rate estimates were calculated for the two populations of G. *pistilliger*. Therefore, different size composition and age groups for eastern Bering Sea and western Pacific populations appear real.

The ovaries from females collected in June from Bristol Bay were deflated and a few large females contained residual eggs from a previous spawn. Wilson (1973) stated that *G. pistilliger* spawn in spring but provided no evidence for this. Ovaries collected from eastern Bering Sea popula-



tions in June of 1997 suggest that *G. pistilliger* is a late winter to early spring spawner. Tokranov (1987) reported that *G. pistilliger* spawn in winter, are single batch spawners in shallow waters, and produce adhesive eggs.



Diet

Gymnocanthus pistilliger preys upon benthic amphipods, polychaetes, crangonid shrimp, and fish. A diet shift from amphipods to shrimp and fish with increased body size represents the sculpin's ability to capture and ingest larger prey items with increased body size, an ability that lessens the likelihood of intraspecific competition and increases efficiency in feeding.

Tokranov (1985) reported on the diets of *G. pistilliger* from off the western coast of the Kamchatka Peninsula. He found diets consisted mainly of polychaete and *Echiurus* (~70% frequency and weight) and amphipods (contributing little to the diet). *Gymnocanthus pistilliger* from Kamchatka increasingly consumed mollusks, decapods, and juvenile capelin as it grew, and polychaetes and *Echiurus* decreased as important items in the diet. Tokranov (1985) also found a shift to larger prey items with increasing fish size.

Commercially important flatfish also use shallow waters in Bristol Bay as spawning and nursery grounds (Fadeev, 1968; Grigorev and Fadeev, 1995). The diet composition of G. pistilliger overlaps with that of flatfish species, such as Limanda aspera (yellowfin sole), Limanda proboscidea (long-head dab), Pleuronectes bilineatus (rock sole), and Pleuronectes quadrituberculatus (Alaska plaice), where competitive interactions may occur. These flatfish diets also consist of benthic amphipods, polychaetes, and *Echi*urus (>50% by weight) (Livingston et al., 1986; Brodeur and Livingston, 1988; Corcobado-Onate, 1991; Lang et al., 1995). However, Holladay and Norcross (1995) found that these flatfish species exhibit a diverse diet (10-57 groups) and show diet preferences based on substrate. Dietary shifts such as these may lessen the likelihood of prey competition in densely populated areas such as Bristol Bay.

Gymnocanthus pistilliger is also potentially an important resource to larger predators because of its small size







and relative abundance. Pacific cod from Bristol Bay have been found to occasionally feed on *G. pistilliger*.¹ Bearded seals, *Erignathus barbatus*, whose distribution overlaps with *G. pistilliger*, consume sculpin species (>80% by volume) (Lowry et al., 1980) and may exploit *G. pistilliger*. However, many feeding studies on seals do not document which species of sculpins were found as prey items.

Gymnocanthus pistilliger is an abundant, short-lived cottid species occurring in shallow waters of the Bristol Bay area. Owing to its great abundance, it may make up an important part of the biomass resource in its range. There are distinct biological differences, such as male-to-female ratios with depth, maxi-

¹ Buckley, T. 1998. Personal commun. Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.



mum depth, maximum age and size, and diet preferences between western and eastern North Pacific populations. The eastern Bering Sea and Kamchatka shelf habitats have different currents, salinities, sediment types, shelf area, and temperatures (Pavlov and Pavlov, 1996) and these different oceanographic features may be reflected in the local adaptation patterns of *G. pistilliger* in this area.

Smith et. al (1997) reported on the biology of *Gymnocan*thus tricuspis, a congener of *G. pistilliger*, which is abundant in the Chukchi Sea and Norton Sound, Alaska (Allen and Smith, 1988). The two species of *Gymnocanthus* are very similar and probably occupy the same ecological niche in different environments. Smith et. al (1997) reported similar ages up to 9 years of age and similar densities and interannual variations in populations of *G. tricuspis* as were found for *G. pistilliger*. The ecological importance of *Gymnocanthus* throughout its range is not well understood but undoubtedly significant because of its high abundance and role as prey and competitive predator.

Acknowledgments

I would like to thank the crew and scientific parties of the vessels *Arcturus* and *Aldebaran* for their efforts in collecting

data and in collecting biological specimens. I would also like to thank the reviewers Troy Buckley, Bill Gale, Doug Markle, Dave Somerton, Gary Stauffer, and Gary Walters and the unidentified journal reviewers. All gave many helpful suggestions that improved the content of the manuscript.

Literature cited

- Allen, M. J., and G. B. Smith.
 - 1988. Atlas and zoogeography of common fishes in the Bering Sea and Northeast Pacific. U.S. Dep. Commer., NOAA Tech. Report NMFS-66, 151 p.
- Brodeur, R. D., and P. A. Livingston.
 - 1988. Food habits and diet overlap of various eastern Bering Sea Fishes. U.S. Dep. Commer., NOAA Tech. Memo. NMFS/NWC-127, 76 p.
- Corcobado-Onate, F.
 - 1991. Food and daily ration of the rock sole *Lepidopsetta bilineata* (Pleuronectidae) in the eastern Bering Sea. Mar. Biol. 108:185–191.
- Environmental Systems Research Institute.

1996. Arcview GIS, ver. 3.0. Environmental Systems Research Institute, Redlands, CA, 614 p.

Fadeev, N. S.

1968. Comparative outline of the biology of flatfishes in the southeastern part of the Bering Sea and condition of their

resources. In Soviet fisheries investigations in the northeast Pacific, part IV (P.A. Moiseev, ed.), p. 112–129. Translated from Russian by Isr. Prog. Sci. Transl., 1968. [Avail. Natl. Tech. Inf. Serv., Springfield, VA, as TT 67-51206.]

Grigorev, S. S., and N. S. Fadeev.

1995. Distribution of Alaska plaice, flathead sole, and Bering flounder eggs in the eastern Bering Sea during April–July, 1988–1990. In Proceedings of the international symposium on North Pacific flatfish p. 89–100. Alaska Sea Grant College Program Report 95-04, Univ. Alaska, Fairbanks, AK.

Holladay, B. A., and B. L. Norcross.

1995. Diet diversity as a mechanism for partitioning nursery grounds of pleuronectids. In Proceedings of the international symposium on North Pacific flatfish, p. 177–204. Alaska Sea Grant College Program 95-04, Univ. Alaska Fairbanks, AK.

Jandell.

1995. Sigmaplot 4.0. Jandell Scientific, P.O. Box 7005, San Rafael, CA 94912-7005.

Lang, G. M., P. A. Livingston, and B. S. Miller.

- 1995. Food habits of three congeneric flatfishes: yellowfin sole (*Pleuronectes asper*), rock sole (*P. bilineatus*), and Alaska plaice (*P. quadrituberculatus*) in the eastern Bering Sea. In Proceedings of the international symposium on North Pacific flatfish, p. 225–246. Alaska Sea Grant College Program 95-04, Univ. Alaska Fairbanks, AK.
- Livingston, P. A., D. A. Dwyer, D. L. Wencker, M. S. Yang, and G. M. Lang.
- 1986. Trophic interactions of key fish species in the eastern Bering Sea. Int. North Pac. Fish. Comm. Bull. 47:49–65. Lowry, L. F., K. J. Frost, and J. J. Burns.

Lowry, L. F., K. J. Frost, and J. J. Burns.

1980. Feeding of bearded seals in the Bering and Chukchi Seas and trophic interaction with Pacific walruses. Arctic 33(2):330-342.

Manugistics.

1997. Statgraphics Plus 2.1. Manugistics, Inc. Rockville, MD, 822 p.

1981. Bivalve mollusks of the southeastern Bering Sea. In

The eastern Bering Sea shelf: oceanography and resources, vol. 2 (D. W. Hood and J.A. Calder, eds.), p. 1155–1204. U.S. Dep. Commer., NOAA., Washington, D.C.

- Pavlov, V. K., and P. V. Pavlov.
 - 1996. Oceanographic description of the Bering Sea. In Ecology of the Bering Sea: a review of Russian literature (O. A. Mathisen and K. O. Coyle (eds.), p. 1–96. Univ. Alaska Sea Grant College Program Report 96-01, Univ. Alaska. Fairbanks, AK.

Rose, C. S., and G. E. Walters.

1990. Trawl width during bottom trawl surveys: causes and consequences. *In* Proceedings of the symposium on application of stock assessment techniques to gadids (L.-L. Low, ed.), p. 57–67. Int. North Pac. Fish. Comm. Bull. 5.

Smith, R. L., W. E. Barber, M. Vallarino, J. Gillispie, and

A. Ritchie.

1997. Population biology of the arctic staghorn sculpin in the northeastern Chukchi Sea. *In* Fish ecology in Arctic North America (J. Reynolds, ed), p. 133–139. Am. Fish. Soc. Symp. 19.

Tokranov, A.M.

- 1985. Feeding in species of sculpins of the genus Gymnocanthus (Cottidae) from Kamchatka waters. J. Ichthyol. 25(4):46-51.
- 1987. Reproduction of sculpins of the genus *Gymnocanthus* (Cottidae) in the coastal waters of Kamchatka. J. Ichthyol. 28(3):124–128.
- Vdovin, A. N., G. V. Shvydkii, N. I. Afanas'eva, V. I. Rachkov, and N. M. Skokleneva.
 - 1994. Spatial and temporal variability of distribution of staghorn sculpin in Peter the Great Bay. Russian J. Ecol. 25(4):53–59.

von Bertalanffy, L.

1957. Quantitative laws in metabolism and growth. Q. Rev. Biol. 2:217–231.

Wilson, D. E.

1973. Revision of the cottid genus *Gymnocanthus*, with a description of their osteology. M.S. thesis, Univ. British Columbia, Vancouver, Canada, 223 p.

McDonald, J., H. M. Feder, and M. Hoberg.