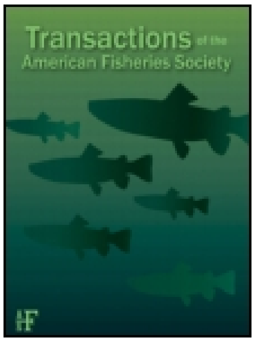

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[Article]

Ontogenetic Diet Shifts of Prickly Sculpin in the Lake Washington Basin, Washington

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Abstract.—We studied the ontogenetic diet shifts of prickly sculpin *Cottus asper* (the largest North American freshwater cottid) in the Lake Washington basin from a variety of habitat types, including fluvial and lacustrine. In all habitats, prickly sculpin progressively shifted to larger prey, such as fish and crayfish (Decapoda), as they increased in size. In offshore areas of Lake Washington, amphipods were the dominant prey by weight consumed by prickly sculpin of 75–124 mm total length (TL). Although generally uncommon numerically in the diet, fish (primarily small cottids) made up a large percentage of the diet by weight for prickly sculpin larger than 125 mm TL. In the lower end of the Cedar River, juvenile sockeye salmon *Oncorhynchus nerka* (23–30 mm TL) were most commonly observed in the diets of 50–99-mm prickly sculpin, while larger prickly sculpin tended to consume larger fish, including adult longfin smelt *Spirinchus thaleichthys*, lampreys *Lampetra* spp. (ammocoetes and adults), and small cottids. For each habitat type, diet overlap tended to decrease as size-classes became more dissimilar. Overall, the size of fish eaten was strongly related to prickly sculpin size, but the type of fish eaten influenced the relationship between prey size and predator size. The higher percentage contribution of fish to prickly sculpin diets seen here relative to other studies can be explained by the fact that (1) we collected many large prickly sculpin and sampled a wide variety of habitat types and (2) potential prey fish in the Lake Washington system are abundant and diverse. Our results, in combination with other research on the Lake Washington ecosystem, suggest that because of their size, abundance, wide range in habitat use, and breadth of diet, prickly sculpin are an especially important species in the food web of this system. Prickly sculpin are directly linked to the pelagic food web as both predators and prey, and they play a key role as benthic predators.

Freshwater sculpins *Cottus* spp., or cottids, are abundant throughout the cool- and coldwater ecosystems of North America. Cottids can have a dramatic effect on the population dynamics and life cycles of numerous other species because they are typically very abundant and can occupy a variety of habitat types (Foerster 1968; Brown et al. 1995; Foote and Brown 1998; Moyle 2002; Wydoski and Whitney 2003). They mostly feed on benthic invertebrates; fish usually constitute a minor part of their diets (Koster 1937; Northcote 1954; Bond 1963; Ebert and Summerfelt 1969; Andreasson 1971; Rickard 1980). Further, cottids can occupy trophic roles as both predators and prey and are trophically linked to both benthic and pelagic components of aquatic ecosystems (McDonald and Hershey 1992; Foote and Brown 1998). For example, in Lake Washington, prickly sculpin *C. asper* were linked to the pelagic community as prey for two large piscivores, the northern pikeminnow *Ptychocheilus oregonensis* and cutthroat trout *Oncorhynchus*

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clarkii (Eggers et al. 1978; Nowak et al. 2004; McIntyre et al. 2006), and to the benthic community as consumers of benthic invertebrates (Eggers et al. 1978; McIntyre et al. 2006).

One factor that helps define trophic effects of a predator is ontogenetic change in habitat use, diet, and foraging tactics (Keeley and Grant 2001; Nowak et al. 2004; Graeb et al. 2006). As a predator increases in size, it is able to capture and consume larger prey items and forage in a wider variety of habitats because its risk of being eaten is reduced (Hughes 1997). In addition, predators need to eat large prey relative to their body size so that growth efficiency does not decrease (Kerr 1971). As a result, larger size-classes of a predator are usually the most piscivorous (Mittelbach and Persson 1998; Nowak et al. 2004).

The prickly sculpin is the largest freshwater cottid in North America, attaining total lengths (TLs) greater than 230 mm (Tabor et al. 2006). It occurs in a wide variety of habitats and as a result of its large size, can ingest a broader range of prey than other freshwater cottids. Thus, ontogenetic diet shifts by this species are likely to be more pronounced than for other freshwater cottids.

Because prickly sculpin are abundant in Lake Washington (Eggers et al. 1978) and in the lower reaches of its major tributaries (Tabor et al. 2006), information on prickly sculpin diets for all size-classes and all occupied habitat types is needed to fully evaluate trophic effects, evaluate potential competitive effects, develop food web models, and help manage aquatic resources associated with this system. Typically, most diet analyses of prickly sculpin have not included larger size-classes (Millikan 1968; Broadway and Moyle 1978; Brown et al. 1995; Merz 2002) because either the larger fish were not present or the gear type limited sampling to shallow-water habitats. Additionally, diet analyses have not evaluated the full breadth of occupied habitats (deep benthos to fluvial; (Tabor et al. 2006).

The only detailed diet work conducted on prickly sculpin in the Lake Washington basin is from the late 1970s (Rickard 1980); however, sampling occurred primarily within the littoral zone and only limited diet information was obtained on the largest individuals (i.e., ≥150 mm TL). A number of major changes have occurred in Lake Washington that could affect the trophic relationships of prickly sculpin since Rickard's (1980) study was conducted (e.g., increase in water clarity, dramatic increase in *Daphnia* spp. abundance, higher water temperatures). Thus, it is not clear how well these historic diet data reflect current food web relationships. Climate change, reductions of sewage effluent, increased shoreline armoring in the lake and its tributaries, species introductions, altered drainage patterns, and other changes in land use practices have resulted in a highly altered lake ecosystem.

Our primary objective was to determine ontogenetic changes in the trophic ecology of prickly sculpin in the major habitat types they occupy in the Lake Washington basin. We were particularly interested in the importance of fish in prickly sculpin diets because of the large size of prickly sculpin in this system and the diverse and abundant prey fish community available. Over 40 species of fish, including six anadromous salmonid species, occur in the lower basin, where prickly sculpin reside. This allowed us the opportunity to evaluate the importance of piscivory by prickly sculpin in multiple habitat types in this system and to evaluate relationships between predator length, prey type, and prey size.

Study Site

The Lake Washington basin is approximately 1,570 km^2 and ranges in elevation from sea level to 1,650 m. The eastern 14% (by area) of the basin lies within the Cascade Range, while the rest is part of the Puget Sound lowlands. Much of the basin is heavily urbanized and has undergone numerous anthropogenic changes over the past 150 years. Over 1 million people inhabit the basin, including much of Seattle, Washington.

Within the Lake Washington basin, we collected prickly sculpin from four major habitats: (1) deep, benthic areas of Lake Washington; (2) shoreline areas of Lake Washington; (3) the lowest 1,700 m of the Cedar River; and (4) an off-channel pond on the Cedar River floodplain. Lake Washington is a large monomictic lake with a total surface area of 9,495 ha and a mean depth of 33 m. Surface water temperature ranges from 4°C to 6°C in winter to over 23°C in summer. The lake drains through the Lake Washington Ship Canal (LWSC), a 13.8-km waterway built to facilitate navigation between Lake Washington and Puget Sound. The Chittenden Locks, located at the downstream end of the LWSC, control the lake level. The Cedar River is the lake's largest tributary, accounting for about half of the mean annual surface flow into the lake (King County 1993); it enters the lake at the south end (Figure 1). Most of the natural production of anadromous salmonids in the Lake Washington basin occurs in the Cedar River. Cavanaugh Pond is a groundwater-fed, 3.8-ha, off-channel pond that enters the Cedar River at river kilometer (rkm) 10.3 (rkm 0 = Cedar River mouth) and is an important spawning area for sockeye salmon *O. nerka* (Hall and Wissmar 2004). The pond averages 2.0 m in depth (maximum = 3.1 m)

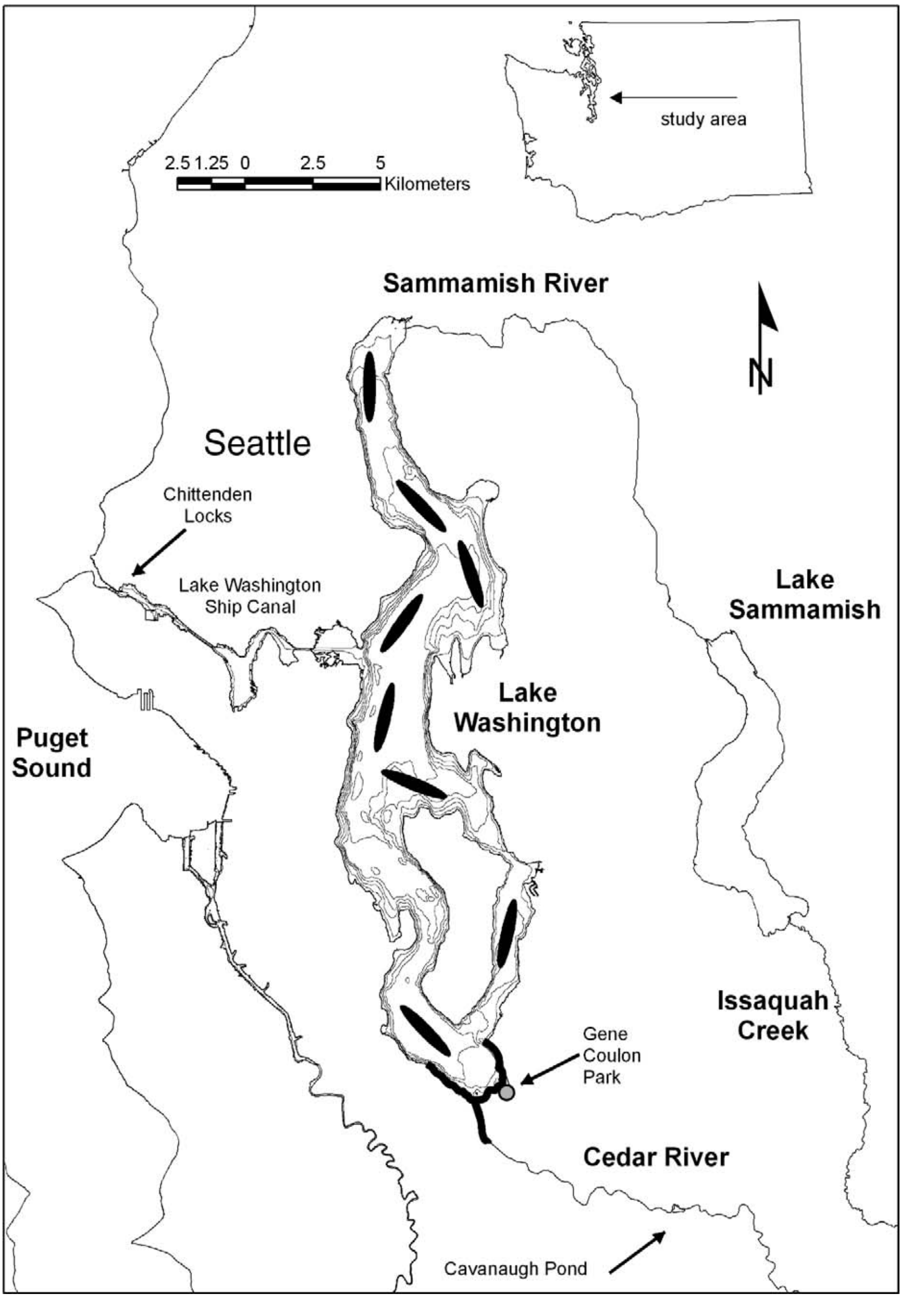

FIGURE 1.—Map of the lower Lake Washington basin, Washington, where prickly sculpin diets were examined. Filled ovals represent offshore areas where bottom trawls were conducted. Depth contours are in 9-m intervals. The lower Cedar River, south Lake Washington shoreline (indicated by bold lines), Cavanaugh Pond, and Gene Coulon Park were additional fish sampling areas.

and has surface water temperatures ranging from 3°C to 21°C (Hall and Wissmar 2004).

Four cottid species other than prickly sculpin inhabit the basin, including coastrange sculpin *C. aleuticus*, riffle sculpin *C. gulosus*, shorthead sculpin *C. confusus*, and torrent sculpin *C. rhotheus* (Tabor et al. 2006). Prickly sculpin are the dominant cottid in the benthic areas of Lakes Washington and Sammamish and in low-velocity areas of lower reaches of tributaries to the two lakes. Besides cottids, 21 native species and 20 introduced species currently inhabit the Lake Washington basin.

The sockeye salmon is an economically important species in the basin, supporting both recreational and commercial fisheries. It is by far the most abundant anadromous salmonid species in the basin, and sockeye salmon spawning occurs primarily in the Cedar River. As many as 60 million sockeye salmon fry (naturally and hatchery produced) annually migrate downstream to Lake Washington between January and June (Seiler et al. 2003). Hatchery releases of fry primarily occur in February, when the numbers of naturally produced fry are generally low; peak abundance of naturally produced sockeye salmon fry occurs in March. Peak spawning of sockeye salmon in Cavanaugh Pond occurs later than in the Cedar River (Hall and Wissmar 2004); subsequently, fry are not present in the pond until mid-April (J. Hall, Seattle Public Utilities, unpublished data).

The most abundant planktivore in the lake is the longfin smelt *Spirinchus thaleichthys*, which is adfluvial, semelparous, and almost always mature at age 2; these fish spawn primarily in the lower Cedar River in March. The number of spawning longfin smelt may be 10-fold higher during even-numbered years than during odd-numbered years (Moulton 1974). The most abundant introduced species in Lake Washington is the yellow perch *Perca flavescens*, which occurs in littoral and limnetic habitats.

Methods

Sculpin sampling.—A variety of collection methods were used to capture prickly sculpin throughout the range of occupied habitats. We used an otter trawl deployed by a 16.8-m commercial purse seiner (converted to a bottom trawler) to sample the deep, benthic areas of Lake Washington. The net mesh was 10 cm; the liner in the cod end was 32-mm stretch mesh. Sampling depth ranged from 9 to 62 m, and sampling occurred throughout the lake (Figure 1). The deep, benthic areas were sampled seasonally from spring 1998 to winter 2000. Each season was sampled twice; the exception was summer, which was sampled once. Sampling included both day and night trawling.

Boat electrofishing was used to collect prickly sculpin along a 4.6-km stretch of shoreline at the south end of Lake Washington once every 3 weeks from February to June in 1995–1997. Backpack electrofishing was conducted at night once every 3–4 weeks from February to May 1997 along the shore of Gene Coulon Park (Figure 1) to more effectively sample smaller prickly sculpin (<75 mm TL) inhabiting this area.

In the Cedar River, prickly sculpin were collected primarily from the lower 1,700 m of the river, because they are rare above this point. The lower 1,700 m was composed of two main sections: a convergence pool backwatered from the lake and a riffle immediately upstream. Prickly sculpin were collected along the shoreline of both habitat types with the use of either boat (only used in convergence pool) or backpack electrofishing equipment. Mid-channel areas were also sampled, but few prickly sculpin were collected. The lower end of the Cedar River was sampled once every 3 weeks from February to mid-June of 1995–2000.

Prickly sculpin were collected in Cavanaugh Pond at night by snorkeling, backpack electrofishing, or beach seining. Prickly sculpin were collected from one site at the outlet of the pond and from four sites along the pond's north shore, where sockeye salmon typically spawn (Hall and Wissmar 2004). Sampling was conducted once every 3 weeks from March to June 1997.

Diet analysis.—Prickly sculpin from each bottom trawl set were separated into four size-classes (75–99, 100–124, 125–149, and ≥150 mm TL; only one individual <75 mm TL was collected), and up to 20 fish of each size-class were measured, weighed, and sampled for stomach contents. Stomach samples for each size category were combined to facilitate processing of the large number of samples. Stomach contents of prickly sculpin from other locations were sampled individually. Because we were particularly interested in piscivory, we only sampled 50-mm or larger prickly sculpin because cottids below that size rarely consume fish.

Stomach contents were removed through gastric lavage as described by Foster (1977), saved on ice, and kept frozen for later laboratory analysis. In the laboratory, stomach contents were placed under a dissecting microscope and separated into major prey taxa. Insects and crustaceans were identified to the order level, whereas other invertebrate prey items were identified to the class level. Each prey group was blotted for 10 s on a paper towel and weighed (nearest mg).

Diet data were pooled by season, prickly sculpin size-class, and prey category. Seasons were winter (January–March), spring (April–June), summer (July–September), and fall (October–December). We pooled diet data across multiple years to give us a larger sample size and to overcome problems of unbalanced sampling during some years. To determine the importance of a particular prey taxon in the diet, we calculated percentage by weight (%*W*) and frequency of occurrence (FO) according to Liao et al. (2001). Lake Washington offshore samples were combined in the field, and FO could not be determined; however, we estimated the minimum and maximum FO of each type of fish in the diet. The minimum FO was based on the number of trawls in which the prickly sculpin diet contained the prey taxon of interest, and the maximum FO was based on the total number of prey fish observed in the diet samples (i.e., assuming each prickly sculpin only ate one individual of a particular taxon). On some survey dates, we recorded the number and type of ingested fish from each prickly sculpin and found that only one fish was present in each prickly sculpin stomach that contained fish ($n = 23$); thus, the maximum FO may be a reasonable approximation of the actual FO.

To compare the diet between size-classes, we calculated overlap index values using the following equation presented by Horn (1966):

$$C = 2\sum_{i=1}^{s} X_i Y / (\sum_{i=1}^{s} X_i^2 + \sum_{i=1}^{s} Y_i^2),$$

where C is the index value, s is the number of food categories, X_i is the proportion of the total diet of predator size-class X contributed by food category i, and Y_i is the proportion of the total diet of predator size-class Y contributed by food category i. Values of C can range from 0 (no overlap) to 1 (complete overlap).

Fish that were slightly digested were identified to species, whereas those in more advanced stages of digestion were identified to family, genus, or species from diagnostic bones, gill raker counts, pyloric caeca counts, or vertebral columns. Fish were individually weighed (nearest mg) and measured for fork length (FL) (nearest mm). If a FL could not be taken directly, the original FLs were estimated from measurements of standard length, nape-to-tail length, or diagnostic bones (Hansel et al. 1988; Vigg et al. 1991; Nowak et al. 2004). Additionally, we developed linear regressions for yellow perch measurements following the procedures of Hansel et al. (1988): FL = 4.32 + (1.45 × nape-to-tail length) and FL = −5.42 + (7.15 × cliethrum length) ($N = 16$; range = 35–160 mm FL; $r^2 > 0.99$). Linear regression analyses and analysis of variance (ANOVA) tests were used to compare the size of prickly sculpin with the size of ingested fish. The sizes of fish eaten by different prickly sculpin size-classes from Lake Washington offshore areas were compared with an ANOVA test and Tukey's post hoc honestly significant difference (HSD) test.

Results

Diet

In offshore areas of Lake Washington, amphipods (predominantly *Diporeia* [formerly *Pontoporeia*] *hoyi*) were the dominant prey by weight for prickly sculpin of the 75–99- and 100–124-mm TL classes. Amphipods were also consumed by the 125–149-mm TL class and by 150-mm and larger prickly sculpin but at a much smaller percentage of the diet by weight. Fish were uncommon in the diet of each size-class (Table 1) but made up the largest percentage of the diet by weight for prickly sculpin larger than 150 mm TL (Table 2). Most of the fish eaten by prickly sculpin in offshore habitats were small cottids (Table 1).

The dominant winter prey of prickly sculpin in nearshore areas were mysid shrimp *Neomysis mercedis* (Table 3), which were present in 34% of all stomach samples and were the dominant prey by weight for three predator size-classes (75–99, 100–124, and 125–149 mm TL). In spring, fish eggs (predominantly cottid eggs) comprised at least 40% of the prey biomass of each size-class larger than 75 mm TL (Table 3). Although fish eggs were also eaten in winter, they were eaten primarily by prickly sculpin larger than 150 mm TL. In winter and spring, the %*W* and FO (Table 2) of aquatic insects in the diet decreased as size-class increased. This was particularly noticeable for chironomids (small-bodied aquatic insects; Table 4).

Fish were more common numerically in the diets of prickly sculpin in littoral areas than in offshore areas; however, the fish percentage of the diet by weight was lower (Tables 2, 3). In both winter and spring, small cottids were the most important prey fish by weight for all size-classes but were more commonly observed in the larger size-classes. Threespine sticklebacks *Gasterosteus aculeatus* and yellow perch were only consumed by the two largest size-classes. Out of 420 stomach samples examined from littoral habitats, only 7 juvenile salmonids (6 sockeye salmon fry and 1 juvenile Chinook salmon *O. tshawytscha*) were observed and they represented only 1.4% of the overall diet by weight.

The main food item of smaller prickly sculpin size-classes in the Cedar River convergence pool was aquatic insects (Table 5). The diet FO and %*W* of aquatic insects in this habitat progressively decreased as prickly sculpin size increased. This was particularly noticeable for chironomids (Table 4). During winter and spring, the FO and %*W* of sockeye salmon fry declined as prickly sculpin size increased. Sockeye salmon fry were present in prickly sculpin diets at the following frequencies: 31% for the 50–99-mm TL class, 20% for 100–149-mm TL class, and only 6.5% for 150-mm and larger predators. Prickly sculpin larger than 100 mm TL in the convergence pool often consumed larger prey, including adult longfin smelt, cottids, lampreys (ammocoetes and adult western brook lampreys *Lampetra richardsoni* and river lampreys *L.*

TABLE 1.—Number of prey fish consumed and the minimum (min) and maximum (max) frequency of occurrence (FO; %) of prey fish found in four size-classes of prickly sculpin from offshore areas of Lake Washington, 1998–2000. Number of stomach samples examined, including empty stomachs, is indicated by *N*. Other fish were mostly unidentified and included both nonsalmonids and salmonids. Stomach samples at each trawling site were combined; thus, the exact FO of prey fish in the diet could not be determined.

Size-class and season	*N*	Sockeye salmon			Longfin smelt			Other sculpin			Yellow perch			Other fish		
		Number	Min	Max	Number	Min	Max	Number	Min	Max	Number	Min	Max	Number	Min	Max
75–99 mm TL																
Winter	230	0	0.0	0.0	0	0.0	0.0	1	0.4	0.4	0	0.0	0.0	0	0.0	0.0
Spring	315	0	0.0	0.0	3	0.6	1.0	1	0.3	0.3	0	0.0	0.0	0	0.0	0.0
Summer	134	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0
Fall	255	0	0.0	0.0	0	0.0	0.0	6	1.6	2.4	1	0.4	0.4	0	0.0	0.0
100–124 mm TL																
Winter	296	0	0.0	0.0	1	0.3	0.3	1	0.3	0.3	1	0.3	0.3	0	0.0	0.0
Spring	413	1	0.2	0.2	0	0.0	0.0	3	0.7	0.7	0	0.0	0.0	2	0.5	0.5
Summer	152	0	0.0	0.0	0	0.0	0.0	2	1.3	1.3	0	0.0	0.0	0	0.0	0.0
Fall	339	0	0.0	0.0	0	0.0	0.0	6	1.8	1.8	1	0.3	0.3	2	0.3	0.6
125–149 mm TL																
Winter	217	1	0.5	0.5	0	0.0	0.0	3	1.4	1.4	0	0.0	0.0	1	0.5	0.5
Spring	339	2	0.3	0.6	7	1.2	2.1	5	1.5	1.5	3	0.6	0.9	7	1.8	2.1
Summer	115	3	2.6	2.6	1	0.9	0.9	1	0.9	0.9	0	0.0	0.0	0	0.0	0.0
Fall	313	5	1.0	1.6	7	1.3	2.2	13	2.6	4.2	2	0.6	0.6	2	0.6	0.6
>150 mm TL																
Winter	108	1	0.9	0.9	0	0.0	0.0	10	6.5	9.3	2	0.9	1.9	2	1.9	1.9
Spring	160	6	1.9	3.8	9	3.1	5.6	4	2.5	2.5	4	1.9	2.5	1	0.6	0.6
Summer	37	3	5.4	8.1	1	2.7	2.7	5	8.1	13.5	0	0.0	0.0	0	0.0	0.0
Fall	98	6	4.1	6.1	6	4.1	6.1	18	9.2	18.4	0	0.0	0.0	1	1.0	1.0

ayresii), and crayfish (Decapoda). In March and April, many prickly sculpin larger than 125 mm TL preyed on adult longfin smelt, which constituted a large part of the diet by weight. The smallest prickly sculpin to ingest an adult longfin smelt (prey size = 85 mm FL) was a 102-mm individual.

The %*W* and FO (Table 5) of sockeye salmon fry in the diets of prickly sculpin inhabiting the riffle shoreline area also tended to decrease as predator size increased. The %*W* and FO of other fish (primarily cottids) tended to increase as prickly sculpin size increased; however, in contrast with the convergence pool, the FO and %*W* of aquatic insects were similar among predator size-classes.

In Cavanaugh Pond, small crustaceans (primarily amphipods) were common in the diet and made up a substantial portion of the diet by weight (Table 5). Aquatic insects were also common in the diet but made up a relatively small proportion of the diet by weight. The %*W* and FO of small crustaceans and aquatic insects did not change appreciably between size-classes. In the spring, sockeye salmon fry were present in 37% of all fish examined and made up over half of the diet by weight consumed by 100–124- and 125–149-mm prickly sculpin.

The level of diet overlap between size-classes varied with location and season; however, *C* tended to decrease as size-classes became more dissimilar. For example, the diets of 50–74-mm prickly sculpin generally had low overlap with the diets of 125–149-mm fish ($N = 8$; mean $C = 0.30$; range = 0.09–0.59) and 150-mm and larger fish ($N = 4$; mean $C = 0.04$; range = 0.01–0.10), whereas overlap was usually higher with the diets of the 75–99-mm ($N = 8$; mean $C = 0.69$; range = 0.30–0.94) and 100–124-mm ($N = 8$; mean $C = 0.48$; range = 0.25–0.69) TL classes.

Size of Ingested Fish

The relationship between prickly sculpin size and ingested fish size varied greatly among prey types. Lamprey and cottid lengths showed a strong positive relationship with predator length, although lampreys were considerably longer than cottids for a given predator length (Figure 2). There did not appear to be any relationship between sockeye salmon length ($N = 677$; $R^2 = 0.026$) or longfin smelt length ($N = 54$; $R^2 = 0.002$; ANOVA: $F = 0.11$, $P = 0.74$) and predator length. Prickly sculpin length was positively related to the size of all prey fish combined ($N = 936$; $R^2 = 0.34$; ANOVA: $F = 484$, $P < 0.001$).

We also examined the length of fish eaten by four prickly sculpin size-classes from offshore areas of Lake Washington. Overall, ingested fish size was significantly different among predator size categories (ANOVA: $P < 0.001$) and generally declined as predator size declined. Tukey's post hoc HSD test showed that

TABLE 2.—Seasonal diet (% by weight) of four prickly sculpin size-classes collected in offshore areas of Lake Washington, 1998–2000. Sample size (*N,* including empty stomachs) given for each season and size-class. Other crustaceans were primarily mysid shrimp for the three smallest size-classes and crayfish for the largest size-class.

Season and prey category	Size-class (TL, mm)			
	75–99	100–124	125–149	>150
Winter				
N	230	296	217	108
Sockeye salmon	0.0	0.0	2.3	0.1
Sculpin	2.4	0.5	31.6	68.2
Other fish	0.0	38.6	3.0	27.2
Amphipods	60.5	25.0	13.5	0.3
Other crustaceans	3.6	3.4	2.1	0.7
Other	33.5	32.5	47.5	1.3
Spring				
N	315	413	339	160
Sockeye salmon	0.0	0.9	21.8	41.5
Sculpin	19.5	4.6	3.1	11.3
Other fish	2.0	0.1	25.4	29.0
Amphipods	60.6	66.3	32.1	15.7
Other crustaceans	14.7	5.3	0.4	0.0
Other	3.2	22.9	17.3	2.4
Summer				
N	134	152	115	37
Sockeye salmon	0.0	0.0	7.1	9.6
Sculpin	0.0	2.7	0.6	13.3
Other fish	0.0	0.0	0.0	0.2
Amphipods	93.6	49.1	84.8	20.3
Other crustaceans	5.6	41.8	2.5	44.8
Other	0.8	6.3	4.9	11.7
Fall				
N	255	339	313	98
Sockeye salmon	0.2	0.0	28.2	18.3
Sculpin	29.5	17.0	34.5	44.3
Other fish	18.9	2.7	16.2	35.3
Amphipods	39.2	68.9	16.2	1.8
Other crustaceans	6.1	0.9	2.4	0.0
Other	5.9	10.5	2.5	0.4

significantly smaller fish were consumed by the 75–99-mm TL class than by the 125–149-mm ($P = 0.001$) or 150-mm and larger fish ($P < 0.003$). In addition, 100–124-mm predators consumed significantly smaller prey fish than did 150-mm and larger predators ($P = 0.001$).

Discussion

We observed a major ontogenetic diet shift in prickly sculpin: as they increased in size, they became more piscivorous. Although all sizes of prickly sculpin ate some fish, small invertebrates like aquatic insects were the most common prey of small predators and occurred infrequently in the diets of large predators. Large prickly sculpin instead preyed mostly on larger prey, including fish and crayfish. These results are consistent with other studies of freshwater cottids (Koster 1937; Northcote 1954; Minckley et al. 1963; Ebert and Summerfelt 1969; Starnes and Starnes 1985; Phillips and Kilambi 1996) and other freshwater piscivores (Mittelbach and Persson 1998; Nowak et al. 2004; McIntyre et al. 2006), indicating that predatory fish often become progressively more piscivorous as they increase in size. Because mouth gape width is a major constraint for the onset of piscivory in freshwater fish (Mittelbach and Persson 1998), we hypothesize that the significant increase in prickly sculpin gape during growth helps them capture and handle larger prey. Gape width in prickly sculpin increases from 6 mm in a 75-mm fish to 25 mm in a 200-mm fish (Patten 1971). In Lake Washington, therefore, many sizes and species of fish that are available to large prickly sculpin (>150 mm TL) are unavailable to smaller individuals.

Based on combined data from all habitats, prickly sculpin in the Lake Washington basin appear to become largely piscivorous at 125–149 mm TL or ages 4–5 (Rickard 1980). This pattern fits Keast's (1985) definition of a secondary piscivore as one that can take years to become piscivorous. Mittelbach and Persson (1998) also suggested that secondary freshwater piscivores switch to piscivory when they are about 100–180 mm TL. In comparison with specialist piscivores, which are highly piscivorous and structurally specialized, secondary piscivores like the prickly sculpin are never more than 30–40% piscivorous and are generally slow moving and nocturnal (Keast 1985).

There was a general tendency for prey size to increase as prickly sculpin size increased. Large prickly sculpin preyed on relatively large fish (i.e., adult longfin smelt) and infrequently consumed the smaller fish (i.e., sockeye salmon fry) that were eaten by smaller prickly sculpin. Additionally, small invertebrates (e.g., chironomids) were common in the diets of the 50–74-mm TL class but infrequent in the diets of fish larger than 125 mm TL. Some other studies of cottids have documented a positive relationship between prey size and predator size (Miller 1951; Andreasson 1971; Rickard 1980). Our results are consistent with bioenergetics analyses suggesting that to maintain high growth efficiency, predators must eat prey that are large relative to predator body size (Paloheimo and Dickie 1966; Kerr 1971; Wankowski and Thorpe 1979). Thus, many fish, such as prickly sculpin, consume larger prey as they increase in size.

Factors other than prey size, such as prey activity and behavior, also play important roles in cottid prey selection. Cottids, which are often nocturnal, rely on their lateral line system to locate moving prey (Hoekstra and Janssen 1985) and thus select for more active prey whose movements are easily detected (Kratz and Vinyard 1981). Other studies suggest that cottids generally ignore small individuals and select intermediate-sized and larger individuals when the prey

TABLE 3.—Seasonal diet (% by weight; %*W*) and frequency of occurrence (FO; %) of prey consumed by five prickly sculpin size-classes collected from nearshore areas of southern Lake Washington, 1998–2000. Sample size (*N*; including empty stomachs) is given for each season and size-class. Other crustaceans were mostly amphipods and isopods, except in the spring, for when this category was mostly made up of crayfish for the 124–149 and >150–mm classes.

Season and prey category	Size-class (TL, mm)									
	50–74		75–99		100–124		125–149		>150	
	%*W*	FO	%*W*	FO	%*W*	FO	%*W*	FO	%*W*	FO
Winter										
N	28		51		45		20		16	
Fish	6.8	10.7	19.3	9.8	28.2	13.3	26.1	30.0	32.1	31.3
Fish eggs	0.0	0.0	0.3	2.0	21.4	8.9	0.0	0.0	59.7	6.3
Aquatic insects	13.3	53.6	7.0	51.0	2.6	42.2	0.2	5.0	1.6	6.3
Mysid shrimp	9.4	25.0	36.8	49.0	23.2	31.1	35.3	15.0	1.5	31.3
Other crustaceans	5.0	53.6	14.4	60.8	5.9	42.2	13.0	50.0	3.3	25.0
Annelids	64.8	28.6	13.7	21.6	9.4	11.1	10.2	20.0	0.5	18.8
Other	0.7	14.3	8.5	41.2	9.3	37.8	15.2	40.0	1.3	28.6
Spring										
N	27		70		77		56		30	
Fish	7.8	3.7	10.0	4.3	4.3	3.9	9.6	17.9	23.4	20.0
Fish eggs	0.0	0.0	35.6	12.9	41.5	22.1	58.6	35.7	53.5	40.0
Aquatic insects	71.4	48.1	5.4	48.6	3.4	45.5	0.5	23.2	3.2	26.7
Mysid shrimp	0.0	0.0	0.2	1.4	0.1	1.3	0.0	0.0	0.1	6.7
Other crustaceans	10.6	55.6	6.5	47.1	7.0	46.8	11.6	46.4	9.2	46.4
Annelids	3.3	3.7	36.4	12.9	28.9	27.3	15.1	19.6	3.2	10.0
Other	6.9	25.9	5.9	27.1	14.8	42.9	4.6	48.2	7.4	43.3

are relatively small and slow moving (Gilson and Benson 1979; Newman and Waters 1984; Kraft and Kitchell 1986; Cuker et al. 1992). For larger, more mobile prey taxa (e.g., fish and crayfish), cottids may select small- to intermediate-sized individuals because capture success declines when larger individuals are targeted (Patten 1971; Juanes 1994).

Prickly sculpin diet varied greatly from season to season, largely in response to seasonal changes in prey availability. Cottids are generally regarded as opportunistic predators (Bond 1963; Jenkins and Burkhead 1994) and consume prey as it becomes locally abundant. Temporal changes in prickly sculpin diets in the Cedar River reflected the seasonal migration timing of sockeye salmon (Seiler et al. 2003), adult longfin smelt (Moulton 1974), and larval catostomids (Wydoski and Whitney 2003). Similarly, aquatic insects in the Cedar River become abundant in May

TABLE 4.—Percentage by weight (%*W*) and frequency of occurrence (FO; %) of chironomids in the stomachs of five prickly sculpin size-classes collected from four locations in the Lake Washington basin, 1995–2000. Only groups with at least 10 stomach samples were included.

Location, habitat, and season	Size-class (TL, mm)									
	50–74		75–99		100–124		125–149		>150	
	%*W*	FO	%*W*	FO	%*W*	FO	%*W*	FO	%*W*	FO
Lake Washington										
Nearshore										
Winter	17.6	55.9	4.6	43.4	1.1	31.1	0.2	5.0	0.0	0.0
Spring	9.0	37.5	2.2	36.0	0.7	27.3	0.1	10.7	0.1	13.3
Cedar River										
Convergence pool										
Winter	4.0	38.2	0.2	21.5	0.2	10.0	0.02	1.4	0.003	2.9
Spring	16.0	72.2	14.9	51.5	11.5	40.7	0.7	21.6	0.4	15.4
Riffle shoreline										
Winter	1.5	36.4	1.5	31.8	0.2	13.0				
Spring	15.3	48.1	10.2	40.9	1.0	36.2	0.6	45.5		
Cavanaugh Pond										
Winter	8.5	41.7	1.8	56.3						
Spring	9.5	65.4	6.5	60.0	2.3	56.3	1.2	47.4		

TABLE 5.—Seasonal diet (% by weight; %*W*) and frequency of occurrence (FO; %) of prey consumed by five prickly sculpin size-classes collected from two areas of the lower Cedar River (Feb–Jun 1995–2000) and Cavanaugh Pond (Feb–Jun 1997), Washington. Sample size (*N*; including empty stomachs) is given for each location, season, and size-class.

Location, season, and prey category	Size-class (TL, mm) 50–74		75–99		100–124		125–149		>150	
	%*W*	FO	%*W*	FO	%*W*	FO	%*W*	FO	%*W*	FO
Cedar River convergence pool										
Winter										
N	256		158		211		136		49	
Sockeye salmon fry	60.8	38.9	46.6	48.4	27.2	26.7	21.1	35.6	0.4	5.7
Longfin smelt	0.0	0.0	0.0	0.0	17.2	3.3	47.9	20.5	71.9	51.4
Sculpin	0.0	0.0	6.5	5.4	22.1	13.3	8.1	8.2	14.5	16.0
Other fish	0.1	1.4	1.4	3.2	0.9	5.0	8.1	11.0	1.5	8.0
Aquatic insects	19.6	66.0	12.3	69.9	8.7	65.0	1.8	30.1	1.6	37.1
Other	19.5	51.4	33.2	64.5	23.9	57.5	13.0	45.2	10.2	37.1
Spring										
N	279		325		305		138		59	
Sockeye salmon fry	37.5	38.7	26.0	36.7	12.9	25.0	2.2	19.3	0.2	9.6
Longfin smelt	0.0	0.0	0.0	0.0	10.0	1.2	29.7	9.1	13.6	5.0
Sculpin	0.0	0.0	1.9	2.4	3.6	4.7	12.9	11.4	10.3	9.6
Other fish	0.0	0.0	6.1	4.7	9.5	5.8	26.5	12.5	30.5	32.0
Aquatic insects	41.8	89.9	35.8	81.1	27.2	69.8	4.9	60.2	1.9	55.8
Other	20.7	43.7	30.2	50.3	36.8	57.6	23.8	45.5	43.5	69.2
Cedar River riffle shoreline										
Winter										
N	63		25		26		3			
Sockeye salmon fry	73.2	56.0	56.1	64.0	31.6	46.0	20.3	100.0		
Sculpin	0.0	0.0	3.0	4.0	27.1	19.0	0.0	0.0		
Other fish	0.0	0.0	13.4	4.0	0.0	0.0	0.0	0.0		
Aquatic insects	13.5	83.0	14.5	72.0	33.6	81.0	14.7	100.0		
Annelids	11.9	19.0	3.3	20.0	4.6	12.0	18.9	33.3		
Other	1.4	19.0	9.7	24.0	3.1	34.8	46.1	33.3		
Spring										
N	98		84		61		16		2	
Sockeye salmon fry	36.8	22.2	15.6	11.4	7.9	5.0	0.0	0.0	0.0	0.0
Sculpin	0.0	0.0	14.0	6.8	13.6	12.8	27.4	18.8	0.0	0.0
Other fish	1.5	3.7	1.4	4.5	13.3	7.0	0.3	6.3	0.0	0.0
Aquatic insects	42.1	88.9	38.5	75.0	31.8	87.2	31.8	75.0	6.5	100.0
Annelids	13.1	7.4	17.1	13.6	10.1	12.8	23.3	18.8	0.0	0.0
Other	6.5	37.0	13.4	35.0	23.3	48.0	17.2	62.5	93.5	50.0
Cavanaugh Pond										
Winter										
N	12		14		6		2			
Sockeye salmon fry	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0		
Fish eggs	46.4	8.3	3.6	12.5	0.0	0.0	0.0	0.0		
Aquatic insects	15.0	58.3	14.1	62.5	13.6	83.3	11.9	100.0		
Crustaceans	34.5	83.3	61.4	81.3	83.0	100.0	52.1	100.0		
Other	4.1	41.7	20.9	37.5	3.4	83.3	36.0	100.0		
Spring										
N	26		44		47		19			
Sockeye salmon fry	16.0	15.4	27.3	35.6	59.5	37.5	52.9	42.1		
Fish eggs	0.0	0.0	2.5	6.7	0.0	0.0	0.0	0.0		
Aquatic insects	25.4	84.6	20.1	75.6	10.3	81.3	6.2	78.9		
Crustaceans	54.0	88.5	34.1	88.9	24.3	87.5	25.9	78.9		
Other	4.6	34.6	16.0	55.6	5.9	68.8	15.0	78.9		

and June (Malick 1977) and were the main prey type of small prickly sculpin during that time. In Lake Washington, mysid shrimp are abundant nearshore primarily in winter (Chigbu et al. 1998) and were the main winter prey of prickly sculpin.

Diet analysis of prickly sculpin from various habitat types in the Lake Washington system found that fish were a more prevalent diet component than we had predicted based on results of previous research (Millikan 1968; Broadway and Moyle 1978; Rickard 1980; Brown et al. 1995; Merz 2002; Moyle 2002). One reason for the difference is that we collected a much larger size of prickly sculpin than did previous studies. Our samples contained 558 prickly sculpin that were 150 mm TL or larger, including 23 fish that were over 200 mm TL (maximum size = 236 mm TL).

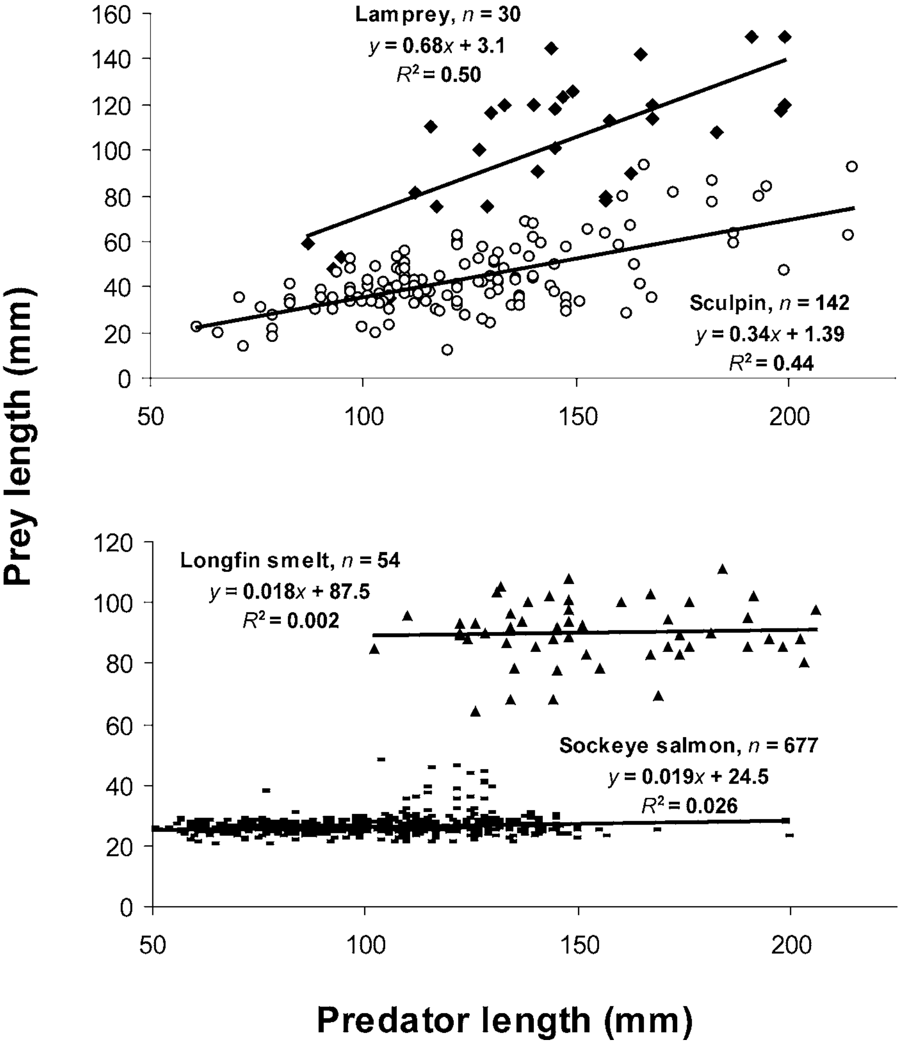

FIGURE 2.—Relation between prickly sculpin predator length and ingested fish length in samples from southern Lake Washington, Cedar River, and Cavanaugh Pond, Washington, 1995–2000. Prey groups are lampreys (adults and ammocoetes; solid diamonds), sculpins (open circles), longfin smelt (solid triangles), and sockeye salmon (dashes). Sample sizes and linear regression results are also given for each group.

Another explanation may be the wider range of sampled habitat types than was used in previous studies. Lastly, the high incidence of piscivory is probably at least partly attributable to the abundant fish fauna in the Lake Washington system. There are over 40 different fish species, several of which have large population sizes. This diversity and abundance of prey fish species appear to be unique within the geographical range of prickly sculpin (Wydoski and Whitney 2003).

Given their abundance and the wide variety of occupied habitats, prickly sculpin are one of the most important species in the food webs of the Lake Washington basin and have a significant effect on the population dynamics of a number of fish species in the basin. In general, prickly sculpin are considered to be obligate benthic feeders and important prey of a variety of piscivores. This is also true for Lake Washington, where prior food web analyses (Eggers et al. 1978; Mazur 2004; McIntyre et al. 2006) have considered prickly sculpin to be linked to the pelagic community by serving as prey for large piscivores, such as northern pikeminnow (Eggers et al. 1978) and cutthroat trout (Nowak et al. 2004). Our results expand on the recent results of McIntyre et al. (2006) and demonstrate that prickly sculpin are also directly linked to the pelagic food web as predators and thus have a significant effect on both pelagic and benthic communities.

Because of the large numbers of anadromous fish found in the Lake Washington basin, we were particularly interested in the role of prickly sculpin as predators of juvenile salmon (e.g., Hunter 1959; Foerster 1968; Patten 1971; Moyle 1977). Within the basin, the two primary instances of salmonid consumption by prickly sculpin both involved sockeye salmon (Cedar River and deep, benthic areas of the lake). However, our sampling design probably missed other, more local instances of predation on other species, such as juvenile coho salmon *O. kisutch* or cutthroat trout. In the lower Cedar River, predation on sockeye salmon fry was primarily exhibited by small- and intermediate-sized prickly sculpin. This may be partly explained by habitat use of large prickly sculpin. Because large cottids typically are found in deepwater habitats (Freeman and Stouder 1989; Koczaja et al. 2005; Tabor et al. 2006), their distribution may not overlap with sockeye salmon fry, which are usually in the middle of the channel in high water velocities (McDonald 1960) or along the shoreline in shallow water (Hartman et al. 1962; Tabor et al. 2004). Bioenergetic inefficiency of capturing sockeye salmon fry may have led to their low consumption by large prickly sculpin (Kerr 1971).

Once sockeye salmon fry enter Lake Washington, they spend much of their time at or near the bottom (Eggers et al. 1978), where they are vulnerable to the benthic-dwelling prickly sculpin. For example, benthic gill-net sets taken at the same time as our study indicated that sockeye salmon were often found within a few centimeters of the substrate (B.A.F., unpublished).

Much of the prickly sculpin diet in the lower Cedar River consisted of sockeye salmon fry; however, our results may not be representative of other river systems that are more pristine. Several anthropogenic changes (reduction of water velocities with dredging activities, flow management, and artificial lighting) have occurred in the Cedar River that may enhance prickly sculpin predation on sockeye salmon fry. Also, the presence of hatchery sockeye salmon fry in the Cedar River may also help increase prickly sculpin predation rates by extending the number of weeks for which fry are available and by increasing overall prey abundance.

Additionally, flow conditions may have contributed to the high observed predation levels on sockeye salmon fry. Survival of hatchery fry from rkm 35 to the lake can be less than 1% at 11 m^3/s but more than 60% at 28 m^3/s (Seiler and Kishimoto 1996). Most of our sampling was conducted when streamflows were maintained between 10 and 22 m^3/s. Because we took few samples at higher flow levels, our results are indicative only of low to moderate streamflow levels. Because predation rates can vary as a function of streamflow (Ginetz and Larkin 1976), the importance of sockeye salmon fry in prickly sculpin diets will vary depending on streamflow.

In conclusion, our results and those of other research on the Lake Washington ecosystem suggest that because of its size, abundance, wide range in habitat use, and breadth of diet, the prickly sculpin is a key species in the Lake Washington food web. We recommend that prickly sculpin be considered as having a broader ecosystem role than that of obligate benthic predator or as food for other piscivores. Assumptions about minimum size at piscivory should be reexamined, as we found that all size-classes of prickly sculpin larger than 50 mm TL ate fish. Further, because prickly sculpin consume fish with extremely different characteristics (e.g., body morphology and behavior), we recommend that investigators evaluate prickly sculpin size–prey size relationships for each prey type individually.

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