

**William D. Muir** and **George T. McCabe Jr.**, National Marine Fisheries Service, Fish Ecology Division, Northwest Fisheries Science Center, 2725 Montlake Boulevard East, Seattle, Washington 98112

**Michael J. Parsley**, U.S. Geological Survey, Biological Resources Division, Western Fisheries Research Center, Columbia River Research Laboratory, 5501A Cook-Underwood Road, Cook, Washington 98605

and

**Susan A. Hinton**, National Marine Fisheries Service, Fish Ecology Division, Northwest Fisheries Science Center, 2725 Montlake Boulevard East, Seattle, Washington 98112

## Diet of First-Feeding Larval and Young-of-the-Year White Sturgeon in the Lower Columbia River

### Abstract

In some Snake and Columbia River reservoirs, adult white sturgeon (*Acipenser transmontanus*) are common but few juvenile fish are found, indicating a lack of spawning success or poor survival of larvae. In contrast, recruitment of young-of-the-year white sturgeon to juvenile and adult stages is successful in the unimpounded Columbia River downstream of Bonneville Dam. The availability and size of preferred prey during the period when white sturgeon larvae begin exogenous feeding could be an important determinant of year-class strength. To explore this issue, we examined the diet composition of 352 larval and young-of-the-year white sturgeon collected from 1989 through 1991 in the lower Columbia River. Samples were collected downstream from Bonneville Dam and upstream from the dam in Bonneville and The Dalles Reservoirs. Fish that ranged in size from 15 to 290 mm in total length fed primarily on gammarid amphipods (*Corophium* spp.) during all months. This diet item became increasingly important to all sizes of white sturgeon examined as they grew. The length of *Corophium* spp. eaten by larval and young-of-the-year white sturgeon increased with increasing fish length ( $r^2 = 45.6\%$ ,  $P < 0.0001$ ). Copepods (Cyclopoida), Ceratopogonidae larvae, and Diptera pupae and larvae (primarily chironomids) were also consumed, especially at the onset of exogenous feeding. A small percentage of white sturgeon were found with empty stomachs during June (1.6% downstream from Bonneville Dam) and July (4.5% downstream and 2.6% in the reservoirs). Diets of larval and young-of-the-year white sturgeon from both impounded and free-flowing sections of the Columbia River were similar and we found no evidence of larval starvation in the areas investigated, areas currently supporting healthy white sturgeon populations.

### Introduction

Construction of dams along the Columbia and Snake Rivers has fragmented populations of white sturgeon, *Acipenser transmontanus*. The population of white sturgeon in the unimpounded Columbia River downstream from Bonneville Dam is currently robust and supports substantial sport and commercial fisheries (DeVore et al. 1995). However, upstream from Bonneville Dam population levels vary, with some reservoirs supporting relatively large populations and others having very few white sturgeon (Cochner et al. 1985, Beamesderfer et al. 1995, Anders and Richards 1996). In some reservoirs, adult white sturgeon are common but few juvenile fish are found, indicating a lack of spawning success or poor survival of larvae (Cochner et al. 1985, Beamesderfer et al. 1995). In the three reservoirs above Bonneville Dam, successive year-class failures and poor recruitment to

young-of-the-year have been found (Parsley and Beckman 1994).

For many fish species, year-class strength is largely dependent on larval survival (Houde 1987, Miller et al. 1988). The two major causes of larval mortality in nature are starvation and predation, and these are most likely interrelated (Hunter 1981, Houde 1987). The availability and size of preferred prey at the onset of exogenous feeding could be an important determinant of white sturgeon year-class strength in the Columbia River. If insufficient adequately-sized prey are available, growth rates would be reduced and mortality would be increased due to greater vulnerability to predation and starvation. The objective of our study was to describe the diet composition of exogenously feeding white sturgeon larvae and young-of-the-year collected downstream from Bonneville Dam and those collected upstream in the reservoirs created by Bonneville and The Dalles Dams.

## Methods

### Fish Collection

All larval and young-of-the-year (YOY) white sturgeon examined in this study were captured with trawls fished on the bottom. In the unimpounded reach downstream from Bonneville Dam (Figure 1), the National Marine Fisheries Service fished a 3.0-m beam trawl or a 7.9-m semiballoon shrimp trawl from late June through October 1990, and from late June through September 1991 (McCabe and Tracy 1994). In Bonneville and The Dalles Reservoirs, U.S. Fish and Wildlife Service (now the U.S. Geological Survey) fished either a 6.9-m high-rise trawl or a 3.0-m beam trawl to capture larval and YOY white sturgeon from July through October 1989 and 1990 (Parsley et al. 1993). The trawls were towed upstream along the bottom, for 2 to 20 minutes per set for the beam trawl and 5 to 15 minutes for the shrimp and high-rise trawls. Information on abundances of collected white sturgeon eggs, larvae, and juveniles, and their relation to water depth, flow, substrate type, and other factors are reported by McCabe and Tracy (1994) and Parsley et al. (1993).

White sturgeon larvae were collected downstream from Bonneville Dam from River Kilometer (Rkm) 45 to 232 from May through late July, a distribution that suggested wide dispersal after hatching (McCabe and Tracy 1994). Young-of-the-year white sturgeon were collected from June through October downstream from Bonneville Dam between Rkm 45 and 211 (Figure 1). Upstream from Bonneville Dam (Rkm 234), young-of-the-year were collected from July through October from Rkm 242 in Bonneville Reservoir to Rkm 343 in The Dalles Reservoir.

### Stomach Analysis

Larval and YOY white sturgeon were measured (total length) in the field, placed in a 4% buffered formaldehyde solution, and later transferred to vials containing 70% ethanol for storage. After weighing each fish, we removed its stomach surgically and examined the contents using a 10X binocular dissecting microscope. Food items were identified to the lowest practical taxon (usually species), but grouped at a higher taxonomic level for analysis. The percent frequency of occurrence and percent numbers of each food category were

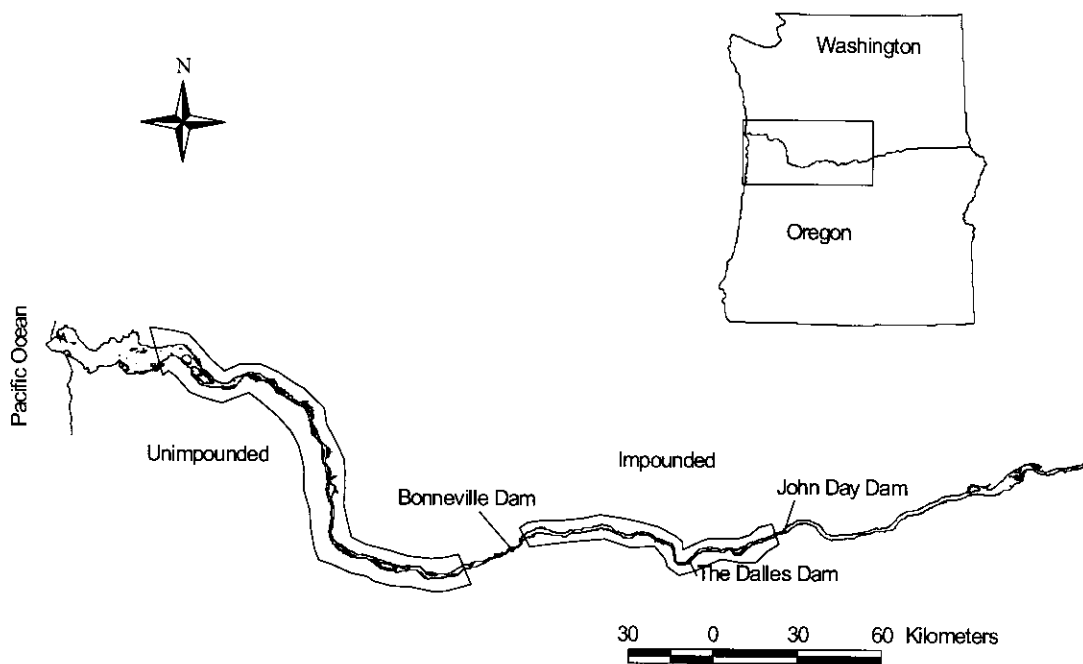


Figure 1. Lower Columbia River showing approximate locations where larval and young-of-the-year white sturgeon were captured for food habits analysis from 1989 through 1991.

then calculated. Weights of individual food items were not taken because of their small sizes. Data were stratified by month (with September and October combined) and by area (upstream and downstream from Bonneville Dam).

*Corophium* spp. (gammarid amphipods) found in stomachs of fish captured downstream from Bonneville Dam were measured to the nearest 0.1 mm (excluding antennae) using a lens micrometer, and a mean length of *Corophium* spp. consumed was calculated for each fish. The relationship between fish length and *Corophium* spp. length was then explored using linear regression.

A mean stomach fullness value (Terry 1977) ranging from one (empty) to seven (distended) was calculated for each month. Although subjective, this measure provided a useful, qualitative indication of feeding success.

## Results

A total of 352 larval and YOY white sturgeon stomachs were examined; 203 from fish captured downstream from Bonneville Dam, and 149 from fish captured in Bonneville and The Dalles Reservoirs (Table 1). There was little difference in diet between years, so the years were combined for this analysis. Since few fish were sampled from The Dalles Reservoir (11) and their diet was similar to those from Bonneville Reservoir, the data from the two reservoirs were also combined. Fish ranged in size from 15 to 290 mm in length, with the average length increasing each month.

During June, 20.3% of the fish sampled downstream from Bonneville Dam contained some yolk, a proportion that declined to 8% during July (Table 2). Empty stomachs were found in 1.6% (1) of the fish examined during June and 4.5% (4) during July (Table 2). No yolk sacs or empty stomachs were found in fish collected from August through October downstream from Bonneville Dam. In Bonneville and The Dalles Reservoirs, no fish were sampled in June and no fish with yolk sacs were sampled during any month (Table 3). Empty stomachs were found in 2.6% (1) of the fish sampled during July in these reservoirs, while no empty stomachs were found from August through October.

The shortest larval white sturgeon exhibiting exogenous feeding in this study were 21 mm in length. One 21-mm fish captured downstream from Bonneville Dam contained yolk material and exogenous food. The smallest fish containing exogenous food and no yolk was also 21 mm in length. Fish still containing yolk material ranged from 15 to 22 mm in length. All larvae found with empty stomachs and no yolk ranged from 20 to 22 mm in length. No empty stomachs were found in fish > 22 mm in length.

First-feeding white sturgeon (those captured during June and July) consumed *Corophium* spp., copepods (Cyclopoida), Ceratopogonidae larvae, and Diptera pupae and larvae (primarily chironomids). Other food items were eaten, but less frequently (Tables 2 and 3). *Corophium* spp.

TABLE 1. Lengths and weights of larval and young-of-the-year white sturgeon sampled each month from 1989 through 1991 in the Columbia River. Stomach fullness values ranged from one (empty) to seven (distended). Standard errors are in parentheses.

Month	N	Mean Length (mm)	Mean weight (g)	Mean stomach fullness
Downstream from Bonneville Dam				
June	64	25.9 (0.77)	0.1 (0.01)	4.1
July	88	38.7 (2.28)	4.6 (4.05)	4.6
August	31	115.8 (6.12)	7.3 (1.15)	5.1
Sept/Oct	20	208.7 (12.11)	37.8 (4.61)	4.6
Overall	203	63.2 (4.37)	6.9 (1.96)	4.5
Upstream from Bonneville Dam				
July	38	51.7 (3.50)	1.2 (0.21)	5.3
August	76	103.6 (3.79)	7.3 (0.84)	5.4
Sept/Oct	35	181.8 (7.46)	34.6 (4.59)	5.4
Overall	149	108.8 (4.65)	12.1 (1.55)	5.4

TABLE 2. Food habits of larval and young-of-the-year white sturgeon (by month) collected from the Columbia River downstream from Bonneville Dam, 1990 and 1991.

Food type	June n = 64		July n = 88		August n = 31		Sept/October n = 20		Overall n = 203	
	Number (%)	Frequency* (%)	Number (%)	Frequency* (%)	Number (%)	Frequency* (%)	Number (%)	Frequency* (%)	Number (%)	Frequency* (%)
Oligochaeta							<0.1	5.0	<0.1	0.6
Bivalvia	0.7	4.0			<0.1	3.2	0.3	35.0	0.2	5.6
Ostracoda			0.5	2.6			0.2	20.0	0.2	3.4
<i>Neomysis mercedis</i>	0.2	2.0	1.3	16.9	4.5	58.1	0.5	45.0	1.9	23.0
<i>Ramellogammarus</i> spp.	1.2	10.0	0.3	6.5	0.2	12.9	0.1	20.0	0.3	10.1
<i>Corophium</i> spp.	45.2	68.0	57.2	83.1	87.2	100.0	96.8	100.0	83.1	83.7
<i>Daphnia</i> spp.			0.2	2.6	0.3	9.7			0.1	2.8
Cyclopoida	31.0	30.0	17.2	24.7	0.7	9.7			5.4	20.8
Ceratopogonidae larvae	7.7	22.0	14.9	53.2	2.1	51.6	0.2	30.0	4.1	41.0
Diptera larvae and pupae	13.6	52.0	8.4	68.8	4.9	77.4	1.7	55.0	4.7	65.2
Ephemeroptera	0.2	2.0			<0.1	3.2			<0.1	1.1
Isopoda							<0.1	10.0	<0.1	1.1
Hemiptera							<0.1	5.0	<0.1	0.6
Empty stomachs	1.6		4.5		0.0		0.0		2.5	
With yolk sac	20.3		8.0		0.0		0.0		9.8	

\* Frequency of occurrence

TABLE 3. Food habits of young-of-the-year white sturgeon (by month) collected from the Columbia River upstream from Bonneville Dam, 1989 through 1991.

Food Type	July n = 38		August n = 76		Sept/October n = 35		Overall n = 149	
	Number (%)	Frequency* (%)	Number (%)	Frequency* (%)	Number (%)	Frequency* (%)	Number (%)	Frequency* (%)
Oligochaeta					<0.1	2.9	<0.1	0.7
Bivalvia					0.2	14.3	0.1	3.4
<i>Neomysis mercedis</i>	3.8	29.7	2.9	21.0	10.8	62.9	6.9	33.1
<i>Ramellogammarus</i> spp.	2.8	16.2	1.2	36.8	0.8	40.0	1.1	32.4
<i>Corophium</i> spp.	85.3	97.3	95.1	98.7	87.8	97.1	90.9	98.0
Cladocera	0.4	5.4	0.3	14.5	<0.1	5.7	0.2	10.1
Cyclopoida	4.6	8.1			<0.1	2.9	0.3	2.7
Ceratopogonidae larvae			<0.1	1.3			<0.1	0.7
Diptera larvae and pupae	3.0	24.3	0.4	13.2	0.2	22.9	0.5	18.2
Ephemeroptera					<0.1	2.9	<0.1	0.7
Insecta					<0.1	2.9	<0.1	0.7
Empty stomachs	2.6		0.0		0.0		0.7	
With yolk sac	0.0		0.0		0.0		0.0	

\*Frequency of occurrence

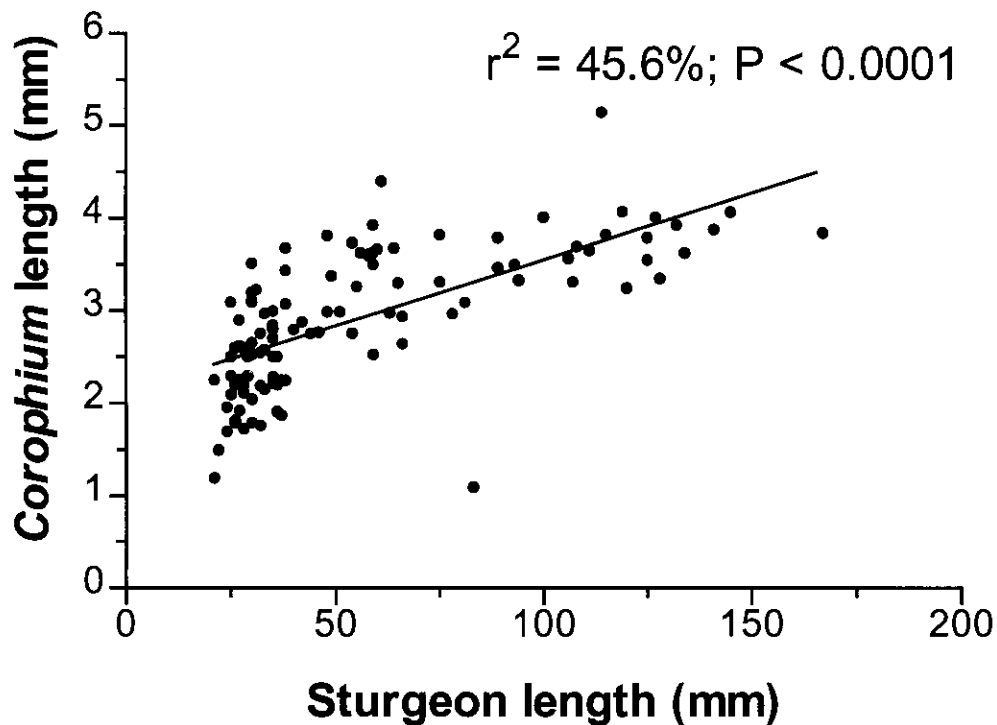


Figure 2. The relationship between the length (mm) of *Corophium* spp. found in larval and young-of-the-year white sturgeon stomachs and white sturgeon total length (mm) downstream from Bonneville Dam, 1990 and 1991.

had the highest percent number and percent frequency of occurrence in larvae and YOY white sturgeon stomachs each month in fish sampled downstream from Bonneville Dam and in the reservoirs (Tables 2 and 3). Downstream from Bonneville Dam, the proportion of the diet composed of *Corophium* spp. increased each month, and *Corophium* spp. were found in 100% of the stomachs from August through September/October (Table 2). In the reservoirs, *Corophium* spp. were found in > 97% of the fish examined in all months (Table 3). The length of *Corophium* spp. eaten downstream from Bonneville Dam increased significantly with increasing fish length ( $r^2 = 45.6\%$ ,  $P < 0.0001$ ) (Figure 2). The *Corophium* spp. eaten by white sturgeon were primarily *C. salmonis*, although *C. spinicornis* were also consumed.

Mean stomach fullness values ranged from 4.1 (26-50% full) in June to 5.1 (50-75% full) in August downstream from Bonneville Dam, averaging 4.5 in this reach (Table 1). In the reservoirs, mean stomach fullness ranged from 5.3 to 5.4, averaging 5.4.

### Discussion

*Corophium* spp. were the dominant prey consumed by larval and YOY white sturgeon captured from both impounded and free-flowing sections of the Columbia River during this study, and were important in the diet of first-feeding fish. Mortality of larval fish is often greatest during the period of transition from endogenous to exogenous feeding (Hjort 1926). It is unknown when "irreversible starvation" or the "point-of-no-return" (May 1974) occurs for larval white sturgeon that are deprived of food. Exogenous feeding generally begins 8 to 14 days post-hatch, depending on water temperatures (Conte et al. 1988). Post-yolk-sac larval white sturgeon metamorphose into juveniles with a full complement of fin rays and scutes after about 25 to 30 days (authors, unpublished data). During this time, fish actively feed on the substrate, but they do not have complete swimming capabilities. Priegel (1970) found that larval walleye (*Stizostedion vitreum vitreum*) were dependent on sufficient currents to carry them downriver to areas with suitable food within three

to five days of hatch. If river velocities were not sufficient, their yolks were depleted prior to entering habitat suitable for their primary prey, and they starved. Presumably, larval white sturgeon would fare similarly if appropriate food is not available at the onset of exogenous feeding.

*Corophium* spp. were also the most important prey for juvenile and sub-adult white sturgeon collected downstream from Bonneville Dam in the Columbia River (Muir et al. 1988, McCabe et al. 1993) and for YOY white sturgeon collected in the San Joaquin River, California (Schreiber 1962). The diets of YOY for other sturgeon species vary from primarily prey of benthic origin to planktonic origin (Kasumyan and Kazhlayev 1993, Ross and Bennett 1997). Post-larval lake sturgeon (*Acipenser fulvescens*) fed primarily on cladocerans and dipteran larvae in a Wisconsin lake (Kempinger 1996). Cladocerans and dipteran larvae were also eaten by white sturgeon larvae in our study, but were not the predominant prey. Food habit studies of larger white sturgeon have found that the dietary importance of fish and larger invertebrates increases with increasing fish size (Semakula 1963, Radtke 1966, Semakula and Larkin 1968, McKechnie and Fenner 1971).

The availability of *Corophium* spp. could play a key role in the survival of larval and YOY white sturgeon in the Columbia River and could possibly explain the apparent poor survival of larvae and YOY in some Snake and Columbia River reservoirs that apparently have successful spawning but poor recruitment (Parsley and Beckman 1994). Downstream from Bonneville Dam, YOY white sturgeon were captured primarily between Rkm 45 and 166, with few collected in the 68 km of river immediately downstream from Bonneville Dam at Rkm 234 (McCabe and Tracy 1994). They were found primarily on sand substrates, which are the predominant substrates in the lower Columbia River downstream from Bonneville Dam and in Bonneville Reservoir (Parsley and Beckman 1994). Sturgeon prefer sandy bottoms, where they can feed efficiently using their ventral barbels and protrusible mouths to suck prey from the substrate; they avoid vegetation, uneven substrates, and silt (Levin 1988, Sbikin and Bibikov 1988).

White sturgeon spawning in the Columbia River system occurs during high flows that disperse eggs and larvae downstream. Brannon et al. (1985) reported that white sturgeon larvae held in aquaria

swam up in the water column for about a five-day period after hatching, then settled to the bottom where they stayed if food was present. If food was not found, larvae again swam to the surface. This behavior would increase their downstream displacement and is thought to be a mechanism for dispersal to suitable habitats. Nilo et al. (1997) suggested that lake sturgeon year-class strength in the Saint Lawrence River was determined in the first few months of life, and that climatic and hydrological conditions in June, while larvae were dispersing from spawning grounds and exogenous feeding began, were the critical elements. Stevens and Miller (1970) found a direct relationship between river flow and white and green sturgeon (*A. medirostris*) larval abundance in the Sacramento-San Joaquin Delta, California although river flow may have influenced their sampling efficiency to some degree.

The larval and smallest YOY white sturgeon examined in this study selected the smallest *Corophium* spp. This would be expected since sturgeon larvae are gape-limited and unable to handle larger prey. The spring and early summer timing of white sturgeon larvae coincides with the presence of juvenile *Corophium* spp. in the size range useable by larvae. Although little is known about *Corophium* spp. populations in the Columbia River, especially in reservoirs, most populations studied have produced offspring twice yearly in spring and fall (Higley et al. 1984). The distribution and density of *Corophium* spp. populations are related to sediment size, and their abundance would most likely vary throughout the reservoirs and downstream from Bonneville Dam (Higley et al. 1984, McCabe et al. 1997). Reservoirs typically change from coarse sediment or cobble in their upper reaches to fine sand or silt downstream (Vannote et al. 1980). Therefore, the degree to which white sturgeon larvae successfully disperse to suitable habitats could be dependent on the magnitude of spring flows, the effect of channel morphometry on velocities within each reservoir, and the length and sediment characteristics of each reservoir.

As post-larval size (especially mouth gape) and swimming performance increase, the range of suitable food sizes and types increases (Blaxter 1969). Rapid growth from the larval stage increases swimming performance and decreases predation risk and size-related vulnerability to predators in bloater (*Coregonus hoyi*) (Rice et al. 1997).

Swimming speed (sustained and burst) increases with larval length, giving larger larvae an advantage to capture food or avoid predation (Miller et al. 1988). Survival of striped bass larvae (*Morone saxatilis*) was related to prey availability, with greatest mortality occurring when endogenous energy sources (yolk and oil) were exhausted (Eldridge et al. 1981). Species having larger larvae, such as white sturgeon, may have a longer window to find prey, due to their relatively large size and available energy reserves. This could increase survival in environments where prey availability is patchy (Miller et al. 1988).

Sturgeon have high fecundity, with white sturgeon in the lower Columbia River found to produce from 98,200 to 699,000 eggs per female (DeVore et al. 1995), with potentially even more eggs produced by the largest spawners with estimates as high as 4.7 million eggs per female (Moyle 1976). Therefore, substantial mortality during the egg and larval stages is expected. Miller and Beckman (1996) observed white sturgeon eggs in the stomachs of four common fish species collected downstream from The Dalles, John Day, and McNary Dams in the Columbia River. Although no larvae or YOY were found in these predator stomachs during their study, their sampling occurred immediately downstream from spawning areas from which most larvae would have already been displaced. Some predation farther downstream during this life stage would be likely. Anders (1996) reported that a substantial number of naturally produced white sturgeon eggs collected from the Kootenai River, Idaho during 1994 and 1995, were recorded from stomach contents of native predatory fishes. Anders and Richards (1996) reported finding one white sturgeon larvae in the stomach of a northern pike-minnow, *Ptychocheilus oregonensis*.

## Literature Cited

- Anders, P. J. 1996. Kootenai River fisheries studies. Annual Progress Report A: Natural spawning of white sturgeon (*Acipenser transmontanus*) in the Kootenai River. Report to Bonneville Power Admin., Portland, Oregon.
- Anders, P. J., and D. L. Richards. 1996. Implications of ecosystem collapse on white sturgeon (*Acipenser transmontanus*) in the Kootenai River, Idaho, Montana and British Columbia. Pages 27-40 *In* S. Dorshov, F. Binkowski, T. Thuemler, and D. MacKinlay (editors) Culture and Management of sturgeon and Paddlefish Symposium Proceedings, July 14-18, 1996. American Fisheries Society Symposium.
- Beamesderfer, R. C. P., T. A. Rien, and A. A. Nigro. 1995. Differences in the dynamics and potential production of impounded white sturgeon populations in the lower Columbia River. *Transactions of the American Fisheries Society* 24:857-872.
- Blaxter, J. H. S. 1969. Development: eggs and larvae. Pages 177-252 *In* W. S. Hoar and D. J. Randall (editors), *Fish Physiology*, Vol. III. Reproduction and Growth. Academic Press, New York and London.
- Brannon, E. S., A. Setter, M. Miller, F. Utter, and W. Hershberger. 1985. Columbia River white sturgeon (*Acipenser transmontanus*) early life history and genetics study. Report to Bonneville Power Admin., Portland, Oregon.

In this study, larval and YOY white sturgeon diets from adjacent impounded and free-flowing sections of the Columbia River were similar and no evidence of larval starvation was found. The fish were sampled from areas that currently support healthy populations of white sturgeon. Thus, larval starvation may not be a determinant of year-class strength in these areas. Capturing starving or dead larval white sturgeon in reservoirs lacking robust populations would be difficult because they would most likely already be scavenged or preyed upon. In reservoirs that contain adult white sturgeon, but lack YOY and juveniles, determining if suitable food resources exist for survival of post-yolk-sac larvae would be a logical research direction. In reservoirs found lacking suitable food resources to support early sturgeon life stages, management options to enhance white sturgeon populations should be considered, including the release of older juvenile hatchery fish or supplementation with older juveniles collected elsewhere. Older white sturgeon would be able to utilize a wider variety of food items. Releases would need to be made in suitable locations within each reservoir and at a size sufficient to utilize available food resources.

## Acknowledgements

We thank Lawrence Davis, Maurice Laird (deceased), Dennis Umphres, Roy Pettit, Steve Duke, Cal Sprague, Milton Hunter (deceased), Nicole Ricci, Joe Warren, and Lance Beckman for their assistance in field sampling and laboratory work and John Williams, David Damkaer, Paul Anders, and Jim Congleton for reviewing this manuscript. This study was funded primarily by the Bonneville Power Administration under Project 86-50.

- Cochnauer, T. G., J. R. Lukens, and F. E. Partridge. 1985. Status of white sturgeon, *Acipenser transmontanus*, in Idaho. Pages 127-133 *In* F. P. Binkowski and S. I. Doroshov (editors). North American Sturgeons: Biology and Aquaculture Potential. W. Junk, Dordrecht, The Netherlands.
- Conte, F. S., S. I. Dorshov, P.B. Lutes, and E. M. Strange. 1988. Hatchery Manual for the White Sturgeon *Acipenser transmontanus*. Publication 3322. Division of Aquaculture and Natural Resources, University of California, Oakland. 104 p.
- DeVore, J. D., B. W. James, C. A. Tracy, and D. A. Hale. 1995. Dynamics and potential production of white sturgeon in the unimpounded lower Columbia River. *Transactions of the American Fisheries Society* 124:845-856.
- Eldridge, M. B., J. A. Whipple, D. England, M. J. Bowers, and B. M. Jarvis. 1981. Effects of food and feeding factors on laboratory-reared striped bass larvae. *Transactions of the American Fisheries Society* 110:111-120.
- Higley, D. L., R. L. Holton, and D. L. Brooker. 1984. Literature review of the amphipod genus *Corophium* with emphasis on the two west coast species *C. salmonis* and *C. spinicornis*. Report to U.S. Army Corps of Engineers, Portland District.
- Hjort, J. 1926. Fluctuations in the year class of important food fishes. *Journal du Conseil* 1:5-39.
- Houde, E. D. 1987. Fish early life dynamics and recruitment variability. *American Fisheries Society Symposium* 2:17-29.
- Hunter, J. R. 1981. Feeding ecology and predation of marine fish life stages of cod and other fishes. Pages 533-562 *In* R. Lasker (editor), *Marine Fish Larvae: Morphology, Ecology and Relation to Fisheries*. University of Washington Press, Seattle.
- Kasumyan, A. O., and A. A. Kazhlayev. 1993. Formation of searching behavioral reaction and olfactory sensitivity to food chemical signals during ontogeny of sturgeons (*Acipenseridae*). *Journal of Ichthyology* 33:51-65.
- Kempinger, J. J. 1996. Habitat, growth, and food of young lake sturgeons in the Lake Winnebago system. *Wisconsin North American Journal of Fisheries Management* 16:102-114.
- Levin, A. V. 1988. Characteristics of feeding behavior of juvenile Russian sturgeon, *Acipenser gueldenstaedti*, in relation to food availability. *Voprosy Ikhtiologii* 1:110-116.
- May, R. C. 1974. Larval mortality in marine fishes and the critical period concept. Pages 3-19 *in* J. H. S. Blaxter (editor), *The Early Life History of Fish*. Springer-Verlag, New York.
- McCabe, G. T., Jr., R. L. Emmett, and S. A. Hinton. 1993. Feeding ecology of juvenile white sturgeon (*Acipenser transmontanus*) in the lower Columbia River. *Northwest Science* 67:170-180.
- McCabe G. T., Jr., S. A. Hinton, and R. L. Emmett. 1997. Benthic invertebrates and sediment characteristics in main channel habitats in the lower Columbia River. *Northwest Science* 71:45-55.
- McCabe, G. T., Jr., and C. A. Tracy. 1994. Spawning and early life history of white sturgeon, *Acipenser transmontanus*, in the lower Columbia River. *Fishery Bulletin* 92:760-772.
- McKechnie, R. J., and R. B. Fenner. 1971. Food habits of white sturgeon, *Acipenser transmontanus*, in San Pablo and Suisun Bays, California. *California Fish and Game* 57:209-212.
- Miller, A. L., and L. G. Beckman. 1996. First record of predation on white sturgeon eggs by sympatric fishes. *Transactions of the American Fisheries Society* 125:338-340.
- Miller, T. J., L. B. Crowder, J. A. Rice, and E. A. Marschall. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. *Canadian Journal of Fisheries and Aquatic Science* 45:1657-1670.
- Moyle, P.B. 1976. *Inland Fishes of California*. University of California Press, Berkeley, 405 p.
- Muir, W. D., R. L. Emmett, and R. J. McConnell. 1988. Diet of juvenile and subadult white sturgeon in the lower Columbia River and its estuary. *California Fish and Game* 74:49-54.
- Nilo, P., P. Dumont, and R. Fortin. 1997. Climatic and hydrological determinants of year-class strength of St. Lawrence River lake sturgeon (*Acipenser fulvescens*). *Canadian Journal of Fisheries and Aquatic Science* 54:774-780.
- Parsley, M. J., and L. G. Beckman. 1994. White sturgeon spawning and rearing habitat in the lower Columbia River. *North American Journal of Fisheries Management* 14:812-827.
- Parsley, M. J., L. G. Beckman, and G. T. McCabe, Jr. 1993. Spawning and rearing habitat use by white sturgeon in the lower Columbia River downstream from McNary Dam. *Transactions of the American Fisheries Society* 122:217-227.
- Priegel, G. R. 1970. Reproduction and early life history of the walleye in the Lake Winnebago region. *Technical Bulletin* 45. Wisconsin Department of Natural Resources, Madison.
- Radtke, L. D. 1966. Distribution of smelt, juvenile sturgeon, and starry flounder in the Sacramento-San Joaquin Delta with observations on the food of sturgeon. Pages 115-129 *in* J. L. Turner and D. W. Kelly (editors), *Ecological Studies of Sacramento-San Joaquin Delta, Part 2. Fishes of the Delta*. California Department of Fish and Game Bulletin 136. 168 p.
- Rice, J. A., L. B. Crowder, and F. P. Binkowski. 1997. Evaluating potential sources of mortality for larval bloater (*Coregonus hoyi*): starvation and vulnerability to predation. *Canadian Journal of Fisheries and Aquatic Science* 44:467-472.
- Ross, R. M., and R. M. Bennett. 1997. Comparative behavior and dietary effects in early life phases of American sturgeon. *Fisheries Management and Ecology* 4:17-30.
- Sbikin, Y. N., and N. I. Bibikov. 1988. The reaction of juvenile sturgeons to elements of bottom topography. *Voprosy Ikhtiologii* 3:473-477.

- Schreiber, M. R. 1962. Observations on the food habits of juvenile white sturgeon. *California Fish and Game* 48:79-80.
- Semakula, S. N. 1963. The age and growth of the white sturgeon (*Acipenser transmontanus* Richardson) of the Fraser River. British Columbia, Canada. M.S. Thesis, University of British Columbia, Vancouver, B.C. 115 p.
- Semakula, S. N., and P. A. Larkin. 1968. Age, growth, food, and yield of the white sturgeon (*Acipenser transmontanus*) of the Fraser River. British Columbia. *Journal of Fisheries Research Board of Canada* 25:2589-2602.
- Stevens, D. E., and L. W. Miller. 1970. Distribution of sturgeon larvae in the Sacramento-San Joaquin River system. *California Fish and Game* 56:80-86.
- Terry, C. 1977. Stomach analysis methodology: still lots of questions. Pages 87-92 *In* C. A. Simenstad and S. J. Lipovsky (editors), *Fish Food Habits Studies*. 1<sup>st</sup> Pacific Northwest Technical Proceedings, October 13-15, 1976. University of Washington FRI. No 8103. Div. Mar. Resources, Washington Sea Grant, WSG-WO 77-2.
- Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Science* 37:130-137.

*Received 26 July 1999*

*Accepted 16 December 1999*