AN ABSTRACT OF THE THESIS OF

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Title: Utilization of the Columbia River Estuary by American shad, Alosa sapidissima (Wilson)

Abstract Approved: Signature redacted for privacy.

Dr. Robert Holton, Ph.D.

The migrations, distribution, and feeding of American shad, Alosa sapidissima (Wilson), were studied from February 1980 through January 1981 in the Columbia River Estuary, an important rearing zone for young-of-the-year shad. Sampling was performed with purse seine, beach seine, and otter trawl.

Adult shad and large numbers of juveniles from the 1979 spawning (age group I) entered the estuary from the ocean in May 1980. Adults continued on their upstream migration while age group I juveniles appeared to congregate in the estuary, joining those (age group I) that had over-wintered there. Many young-of-the-year shad (age group 0) reached the estuary on their seaward migration in September 1980, during which time most of the age group I juveniles migrated back to the ocean. By January 1981, large numbers of young-of-the-year shad migrated to the ocean, although a few remained in the estuary.

The stomachs of 26 adult shad and 503 juveniles were analyzed. Adults did not appear to feed during their upstream migration, but juvenile shad fed extensively. Diet varied with season, gear type, and salinity zone. Calanoid copepods were important throughout the year, but Corophium salmonis and Neomysis mercedis were important during

fall, winter, and spring. Freshwater prey were consumed during summer and fall. The most important of these were *Daphnia* spp., Chironomidae larvae and pupae, and Trichoptera adults for shad feeding in shallow water near beaches.

UTILIZATION OF THE COLUMBIA RIVER ESTUARY BY AMERICAN SHAD, *ALOSA SAPIDISSIMA* (WILSON)

by

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I. INTRODUCTION

The American shad, *Alosa sapidissima* (Wilson), is one of the largest members of the herring family, Clupeidae. Native to the Atlantic Coast of North America, the shad was introduced into California's Sacramento River in 1871, and into Oregon's Columbia, Snake, and Willamette rivers in 1885 and 1886 (Craig and Hacker, 1940). Its populations have since grown and spread along the West Coast; from Todos Santos Bay, Baja California, to Cook Inlet and Kodiak Island, Alaska (Hart, 1973).

On the East Coast of America, there has historically been commercial and sport fisheries for shad, but pollution, construction of dams without fishways, and overfishing resulted in the reduction of the populations (Leim, 1924; Sykes and Lehman, 1957; Walburg, 1960; Walburg and Nichols, 1967). Since the early 1900's, the Columbia River has supported one of the largest Northwest shad fisheries, reaching, between 1946 and 1950, a peak of 841 thousand pounds (Craig and Hacker, 1940; Cleaver, 1951; Park, 1978). In recent years, however, marketing problems and regulations designed to prevent excessive incidental catches of salmonids, have contributed to the decline of the fishery, despite increasing populations (Hasselman, 1966; Young, 1971; Robinson, 1974, 1976; Parks, 1978). Although shad are sought after on the Atlantic Coast, they have never been widely accepted as a food fish in Pacific Coast states (Craig and Hacker, 1940; Parks, 1978).

Since its introduction, the upstream population of shad in the Columbia River has greatly increased. Counts of shad ascending the fish ladders at Bonneville Dam (236 km) averaged less than 16,000 before 1960, and in 1980, over 900,000 shad were counted (U.S. Army Corps Engineers, [1981?]). Furthermore, because Bonneville Dam allows shad to pass through the locks, the actual upstream spawning population may be considerably larger than the counts indicate.

An anadromous fish, shad spend most of their life in the ocean and migrates into freshwater rivers to spawn. On the Atlantic Coast, rivers supporting the largest numbers of spawning shad are tributaries to large estuaries, where great numbers of juvenile shad feed and mature (Leim, 1924).

Adult shad begin to enter the Columbia River during April (Coutant and Becker, 1968). On both the Pacific and Atlantic coasts of North America, the peak of the spawning run occurs at river temperatures of about 18.5°C (Leggett and Whitney, 1972). On the Atlantic Coast, there is a south to north seasonal progression of runs beginning as early as November in Florida, and as late as June in Canada (Walburg, 1960).

Chittenden (1973) found that in the Delaware River, non-tidal pools were the preferred habitat for nurseries, but that brackish waters may be more important rearing zones when large year classes overflow from the freshwater nurseries. He further stated that the importance of brackish waters probably depends on the young's rate of seaward dispersal and the proximity of brackish water to the chief spawning grounds. In the Columbia River, adult shad have been reported passing over McNary Dam (409 km), and even as far from the ocean as 622 km, passing over the Lower Granite Dam on the Snake River (U. S. Army Corps Engineers, [1981?]). The major spawning areas, nevertheless, are thought to be throughout the lower river below Bonneville Dam (Cleaver, 1951; Coutant and Becker, 1968). The importance of the Columbia River Estuary to American shad has not, however, been clearly documented.

The seaward migration of young-of-the-year shad generally occurs when the river temperature has decreased to less than 15.5°C (Leggett and Whitney, 1972). Coutant and Becker (1968) suggested that in the lower Columbia River, young-of-the-year shad may be present for many months due to the long spawning period and the far upstream extent of the spawning grounds. The age of seaward migrating shad is variable, but Leim (1924) found that young-of-the-year shad up to 55mm long were caught slightly less than two months after spawning.

Juvenile shad feed opportunistically (Domermuth and Reed, 1980), generally utilizing the most available food organisms (Walburg, 1956; Levesque and Reed, 1972). In Atlantic rivers, insects are the most important food for shad during summer and fall (Walburg, 1956; Massmann, 1963). Crustaceans, notably copepods and cladocerans, are also very important (Leim, 1924; Domermuth and Reed, 1980; Walburg, 1956; Watson, 1968). In the Columbia River Estuary, preliminary studies indicate that juvenile shad feed on amphipods, calanoid copepods, cladocerans, and insects (Durkin et al., 1979). In the Sacramento-San Joaquin River system, juvenile shad feed on mysids, copepods, larval fish, and amphipods (Ganssle, 1966). In the same system, Stevens (1966) found copepods and cladocerans in the stomachs of the few juveniles examined.

Because estuaries are important to man, fulfilling transportational, industrial, recreational, and other needs, its use may have a great effect on the distribution and abundance of America shad. The Delaware River provides an interesting example. Pollution of the estuary greatly decreased dissolved oxygen levels during the summer making the estuary inadequate not only as a rearing area, but also as a passageway for shad (Chittenden, 1969). Almost total mortality was reported for juveniles passing through the estuary under those conditions. Decreased water temperatures and increased river discharge restored the dissolved oxygen in the estuary to suitable levels in the fall, however. As a result, areas further upstream now dominate as the chief spawning grounds because the longer migration distances result in later spawning and therefore a later young-of-the-year seaward migration. These juveniles, then, would migrate through the estuary when conditions were more suitable for their survival (Chittenden, 1976a). Thus, only a small portion of the former spawning grounds now contributes to fish production, resulting in the drastic declines in shad abundance in the Delaware River (Chittenden, 1975). This example illustrates that knowledge of a fish's distribution and habitat requirements is important to manage an estuarine system properly.

The purpose of this study was to determine when and where American shad occupy the Columbia River Estuary, and to describe their feeding habits in the estuary.

II. MATERIALS AND METHODS

A. Field Work

American shad were collected from February 1980 through January 1981 in cooperation with a National Marine Fisheries Service non-salmonid study under contract with the Columbia River Estuary Data Development Program (CREDDP). The estuary was defined for the program as the first 74 km of the river (CREDDP, 1980), an area that includes the entire salt intrusion as well as some freshwater areas under tidal influence.

We sampled 16 stations with purse seine, 22 stations with otter trawl, and 11 stations with beach seine monthly (Figure 1). Sampling was usually performed during the first half of each month (CREDDP, 1981 (Figure 1]); the time of sampling was generally influenced by tidal conditions. The trawl was fished on the bottom for five minutes in an upstream direction with flood or slack tide. Purse seine sets were made during all tidal stages, with the net held open in an upstream direction for five minutes. The beach seine sampled the subtidal habitat at low tide, fishing a 180° arc back to the beach.

The 200 m X 10 m purse seine consisted of stretched mesh sizes ranging from 12 to 20 mm. The beach seine was 50 m long and 4 m deep with a mesh of design similar to that of the purse seine. The 8 m otter trawl consisted of 38 mm stretched mesh overall with a 12 mm stretched mesh cod-end liner. A 12.2 m twin diesel engine vessel was used to operate the purse seine and trawl, and smaller, outboard engine vessels were used with the beach seine. The time of day, tidal condition, depth, and surface and bottom salinities and temperatures were recorded for each set.

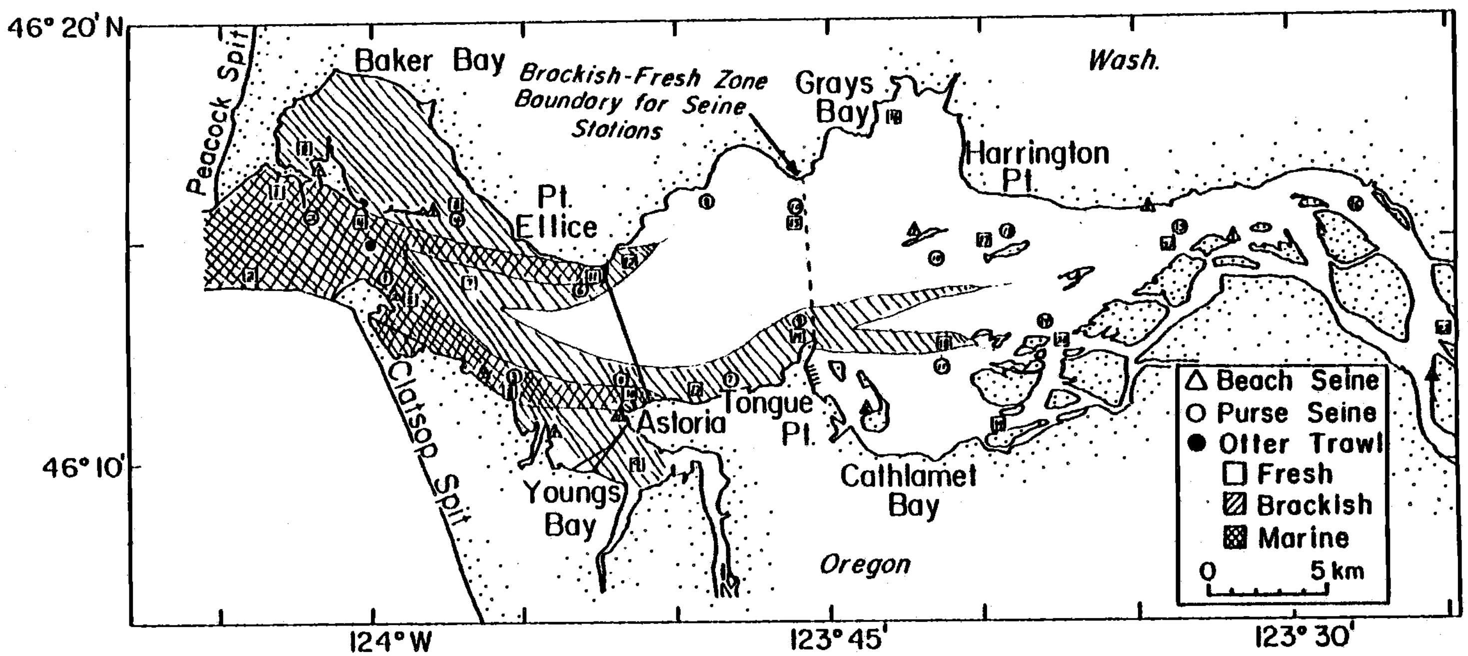

Figure 1. Sampling stations and salinity zones in the Columbia River Estuary.

After capture, fish were removed from the net and placed into a holding tank. Up to 45 shad were selected by dip-net, measured and weighed. Five additional shad for stomach analysis were injected in the stomach with 10% formaldehyde solution buffered to a pH of 7 with $NaHCO_3$ and measured and weighed in the laboratory. Thus up to 50 shad were individually measured and weighed per station. Any remaining shad were counted and weighed in bulk.

In May, the entire shad catch was measured at one purse seine station and no statistical difference was found between the mean lengths of the total catch and the five shad subsampled for stomach analysis ($t=1.110$; $df=106$; $p=0.05$). This test was performed monthly for catches at the same station (if catches at that station were less than 25, a nearby station with larger catches was used), but comparing the five shad subsampled with the 50 measured shad instead of the entire catch. Results were similar; no statistical difference between the mean lengths (Appendix V).

Diel sampling was performed 22 April, 21 May, 19 June, and 22 July 1980 at purse seine Station 6, and trawl station 11 (Figure 1). Simultaneous purse seine and trawl sampling efforts occurred every two hours in a 24 hour period through one complete tidal phase (semi-diurnal mixed tide). The monthly period chosen for diel sampling was during minimal tidal exchange to provide the best use of equipment and maximum safety. Five shad per set were selected for stomach analysis as previously described (when caught).

Different age groups, when caught, were separated by length frequency distributions in which modes were quite distinct for each age group (Table I). Any sexually mature shad was considered adult ('A'). Because the annuli are laid down during winter, shad are considered to enter the next age group in January (Cating, 1953).

B. Laboratory Work

At the laboratory, shad taken for stomach analysis were measured, weighed, and dissected. The stomachs were excised at the gullet and pyloric sphincter and stored in 70% alcohol for later analysis. Stomachs were opened under a dissecting microscope, and the contents were washed into a watch glass. Prey items were identified to the lowest taxon possible, counted and separated, and blot-dry weighed to 0.1 mg on a fine-mesh screen with a Mettler Type H6T balance. Tremendous numbers of copepods often occurred in the stomachs. When their numbers (or of any other small prey) exceeded a few hundred, a subsample was prepared after separating out those larger prey not requiring subsampling. The stomach contents were diluted with alcohol to a volume that would result in a 1.0 ml subsample that contained at least 50 individuals of the prey being subsampled. The diluted stomach contents were magnetically stirred and a Hansen-Stempel pipette was used to take the subsample. If the subsample did not contain at least 50 individuals, another 1.0 ml aliquot was added to the first. Subsample prey counts and weights were then multiplied by the dilution factor. The weights of all the prey groups, and any unidentifiable material were added to get a total stomach content weight.

Table I. Monthly mean fork length of each age group in shad catches (Feb. 1980-Jan. 1981) (mm)

	'O'			'I'			'II'			'A'		
MONTH	N	$\overline{X}$	SD	N	$\overline{X}$	SD	N	$\overline{X}$	SD	N	$\overline{X}$	SD
February	---	---	---	259	106.0	11.0	---	---	---	---	---	---
March	---	---	---	195	112.8	11.4	---	---	---	---	---	---
April	---	---	---	125	108.6	12.3	---	---	---	---	---	---
May	---	---	---	276	137.0	17.6	16	271.1	23.5	10	400.9	41.0
June	---	---	---	357	154.2	13.8	7	270.9	24.2	6	462.7	23.5
July	---	---	---	126	179.4	15.6	5	282.0	12.3	4	413.0	48.9
August	7	46.4	5.3	386	202.8	13.2	5	306.6	32.4	8	413.4	35.4
September	238	59.9	11.5	170	205.7	14.6	---	---	---	1	485	---
October	399	75.9	15.4	13	222.9	13.3	1	345	---	2	419.5	7.8
November	752	83.6	11.1	11	232.2	22.3	---	---	---	---	---	---
December	565	80.0	8.6	1	212	---	---	---	---	---	---	---
January[1]	301	88.6	12.2	8	234.4	20.4	---	---	---	---	---	---

[1] Month that shad are elevated to the next age group

C. Data Analysis

For the analysis of the feeding data, months were combined into the four seasons (fall: Sept., Oct., Nov. 1980; winter: Feb. and Dec. 1980, Jan. 1981; spring: March, April, May 1980; summer: June, July, August 1980). Stations were combined into zones (Figure 1) based on the predominant salinity regime throughout the year. Because the trawl was fished on the bottom, the stations were affected by bottom salinities. Thus, otter trawl stations were combined into three zones: marine (salinity varies with the tide but was usually greater than 15 o/oo), brackish (salinity varies with the tide but was usually less than 15 o/oo), and fresh (beyond the extent of the salt wedge; salinity was usually less than 1.0 o/oo). Purse seine and beach seine stations were combined into two zones: brackish and fresh, as defined above.

Stomach samples were organized into groups by gear type, salinity zone, season, and approximate age. To allow for comparison between the four seasons with increasing fish length the approximate chronological age based on the time shad first reach the estuary was used instead of the age groups. These groups of stomachs can be seen in Table II. Subyearling shad are denoted as 'S', yearling shad are denoted as 'Y', and adult shad (sexually mature) are denoted as 'A'. All stomachs collected during spring were analyzed. Subsamples were taken from those stomachs collected during winter, summer, and fall with a Hewlett Packard 34C one-million random number generator.

The feeding data are presented as the percentage of the identifiable prey weight represented by each prey (% Wt.), and the percentage of the fish in the group that consumed that prey (% frequency occurrence). The percentage of the total stomach content weight that was identifiable as prey is also presented (see Figures 3 and 4).

Table II. Feeding group sample sizes.

Gear & Salinity Zones	Fall '80			Winter '80/81			Spring '80			Summer '80		
	'S'	'Y'	'A'	'S'	'Y'	'A'	'S'	'Y'	'A'	'S'	'Y'	'A'
Purse Seine												
Brackish	20	23	1	30	---	---	61	6	1	65	11	4
Fresh	15	16	1	15	---	---	5	---	7	31	---	12
Beach Seine												
Fresh	---	---	---	---	---	---	20	---	---	9	---	---
Otter Trawl												
Marine	9	---	---	20	---	---	6	---	---	---	---	---
Brackish	19	---	---	45	---	---	7	---	---	---	---	---
Fresh	6	---	---	7	---	---	12	---	---	---	---	---

III. CATCH RESULTS

Monthly catches in each gear type, and their distribution by salinity zone (purse seine and otter trawl catches only) are shown in Figure 2 (see Figure 1 for the location of the salinity zones). Table III shows the monthly age group composition of those shad that were measured.

American shad were caught predominantly in the water column with the purse seine. Shad of age group I (from the 1979 spawning) dominated the catches during winter 1980. During February through August 1980, they were caught almost entirely in brackish water. Small numbers of adult shad were caught during May through October, as were shad of age group II (from the 1978 spawning). Before May only shad of age group I were caught. The first large catches of young-of-the-year shad (age group 0) were in September 1980, although four individuals were caught in August. By October, most of the age group I shad had apparently migrated to the ocean, after which the purse seine catches were dominated by young-of-the-year shad caught principally in fresh water. During November and December, the catches of shad were very much larger than they had been in previous months, apparently due to a surge of young-of-the-year shad migrating to the ocean. During this period, shad were caught throughout the estuary in brackish and fresh waters. In January 1981, the catches of shad, now of age group I, were much smaller and almost entirely in the brackish water areas.

Shad were caught near the bottom throughout the year by means of the otter trawl, although during the summer, the catches were extremely low (Figure 2; Table III). Shad of age group I were caught mostly

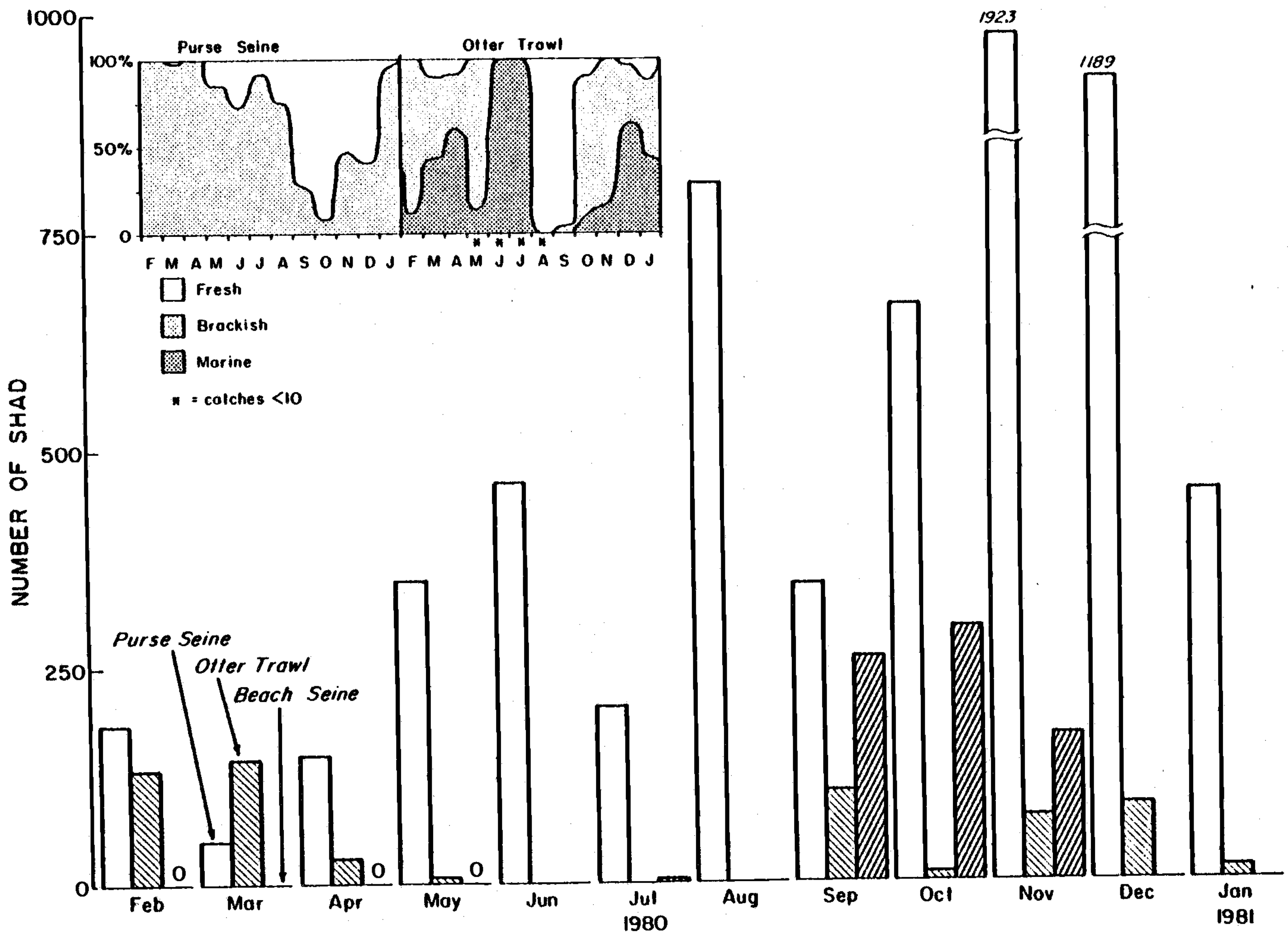

Figure 2. Monthly catches for purse seine, otter trawl, and beach seine. Insert shows the monthly percent of the catch in each salinity zone for the purse seine and otter trawl catches.

Table III. Monthly age composition of shad catches (Feb. 1980-Jan. 1981) (* = total catch of age group)

Month	Purse Seine						Otter Trawl				Beach Seine			
	Total	#Meas.	'0'	'I'	'II' *	'A'*	Total	#Meas.	'0'	'I'	Total	#Meas.	'0'	'I'
February	185	158	0	158	0	0	133	101	0	101	0	0	0	0
March	51	51	0	51	0	0	143	143	0	143	1	1	0	1
April	149	96	0	96	0	0	29	29	0	29	0	0	0	0
May	350	295	0	269	16	10	7	7	0	7	0	0	0	0
June	462	365	0	352	7	6	1	1	0	1	4	4	0	4
July	228	129	0	120	5	4	1	1	0	1	5	5	0	5
August	806	401	4	384	5	8	2	1	0	2	4	4	3	1
September	347	220	49	170	0	1	104	54	54	0	260	135	135	0
October	669	291	275	13	1	2	10	10	10	0	295	114	114	0
November	1923	552	542	10	0	0	75	73	72	1	169	138	138	0
December	1189	456	455	1	0	0	137	108	108	0	2	2	2	0
January[1]	448	290	0	282	8	0	16	16	0	16	3	3	0	3

[1] month that shad are elevated to the next age group.

during February through April 1980 predominantly in marine and brackish waters. In September 1980, 100 of the 104 young-of-the-year shad caught were found in the upper estuary, in fresh water. After September, however, young-of-the-year shad were caught only in marine and brackish waters. Because of the very low catches of shad in the summer in the otter trawl, there are no samples for feeding analysis representing the summer months.

Catches of shad in the beach seine were totally in fresh water. Very low numbers of age group I shad were caught from March through August 1980. Large numbers of young-of-the-year shad (age group 0) were caught during September through November (Figure 2; Table III).

IV. FEEDING RESULTS

A. Purse Seine

The stomachs of all but one (N=26) adult shad were either empty or with very small amounts of prey or unidentifiable material lodged in the convolutions of the stomach wall. Remnants of calanoid copepods, Cirripedia larvae, Corophium salmonis (Amphipoda, Corophiidae), and juvenile Corbicula manilensis (Bivalvia, Corbiculidae) were identified, however. The one exception was a stomach from a spent female caught in August which was packaged with over eight grams (2032 individuals) of Neomysis mercedis (Mysidacea, Mysidae) juveniles.

Subyearling (S) shad, in brackish water (Figure 3a), fed mostly on calanoid copepods (predominantly Eurytemora spp.) during fall, 1980. In the winter and spring of 1980, however, Corophium salmonis was the most important prey species, representing 96.5% and 80.0%, respectively, of the identifiable prey biomass. During summer, calanoid copepods were most important in terms of biomass. During this period the biomass of Corophium salmonis dropped to only 1.0% of the identifiable prey biomass. Large percentages of the prey weight were fish during fall and summer, but in each case only one shad consumed fish (therefore the sample probably is not adequately represented).

Yearling (Y) shad (Figure 3b), during fall 1980, fed primarily on Daphnia spp. (Cladocera, Daphnidae) in fresh water, although Chironomidae larvae and purpae (Insecta, Diptera) were also consumed. In brackish water, unlike subyearling shad, yearlings fed heavily on Neomysis mercedis. Calanoid copepods were also an important prey group. Crangon franciscorum (Decapoda, Caridae) represented the largest percentage of the

Figure 3. Stomach contents of shad caught in the purse seine and beach seine.

A. Purse seine, subyearlings, brackish water.

B. Purse seine, yearlings, brackish and fresh water.

C. Purse seine, subyearlings, fresh water.

D. Beach seine, fresh water.

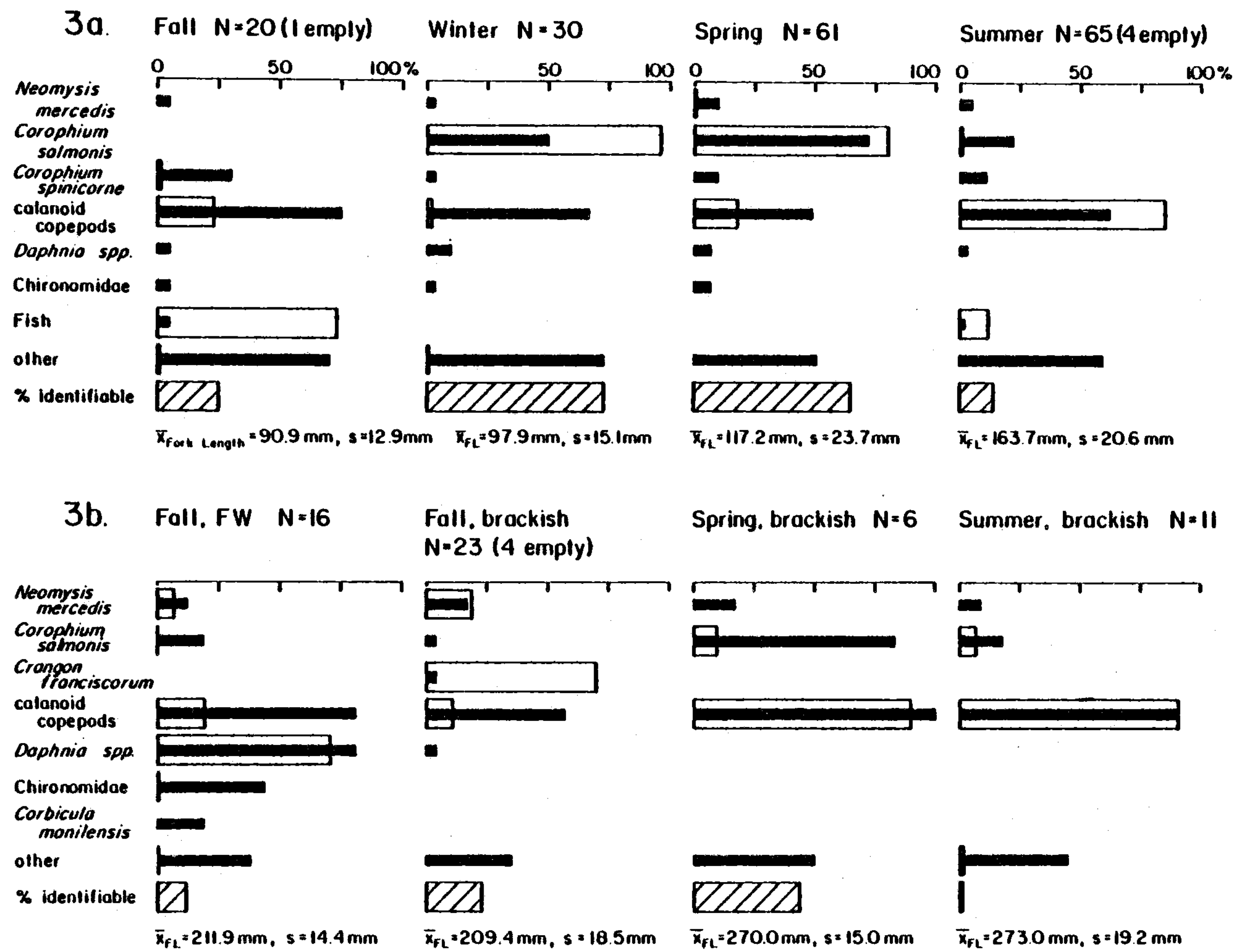

Figure 3, A and B

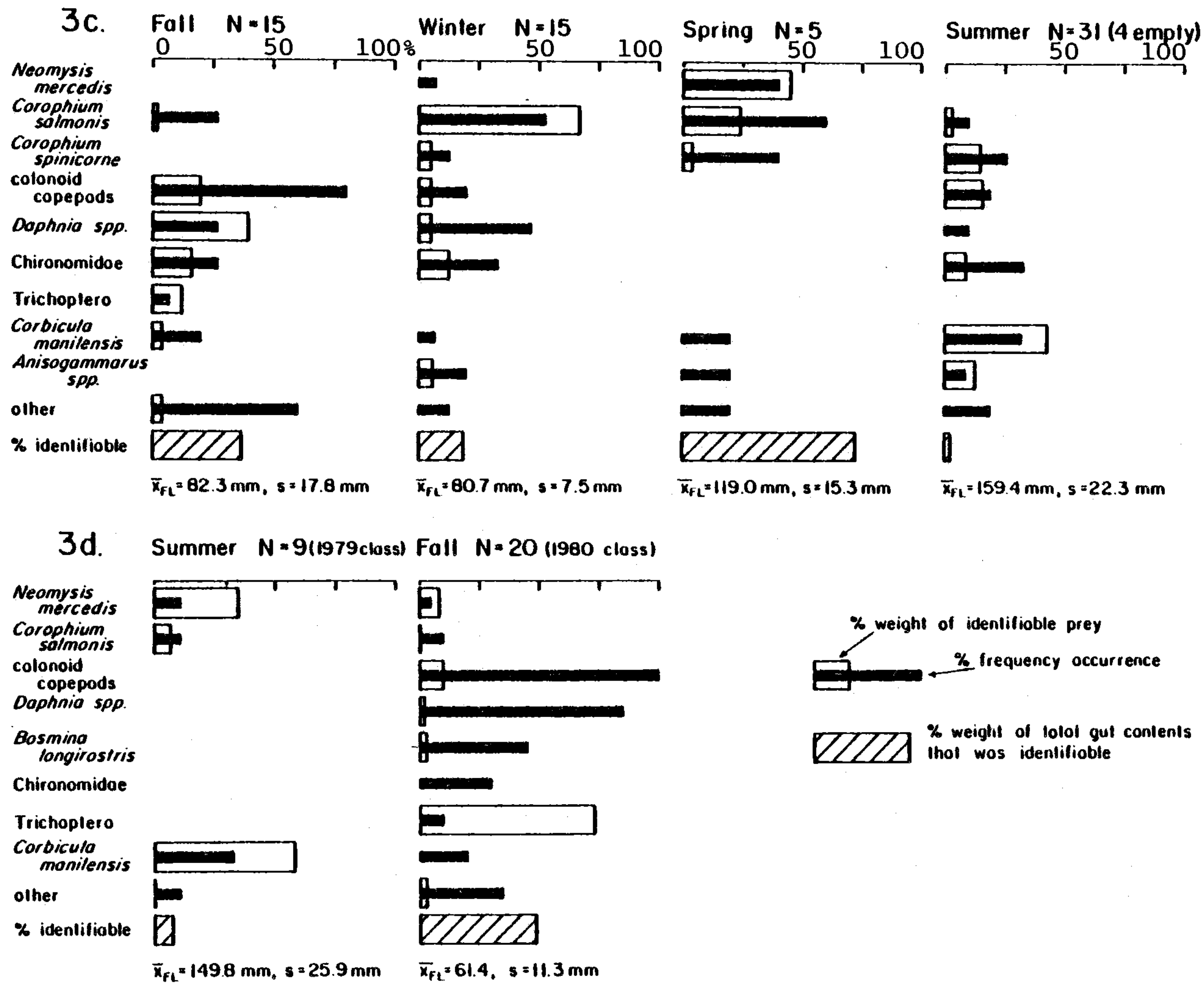

Figure 3, C and D

prey biomass, but occurred in only one of the 23 stomachs in the sample, again biasing the data. In the spring of 1980, yearling shad fed on calanoid copepods and Corophium salmonis, but during the summer, Corophium was consumed by 65% fewer shad. Nevertheless, calanoid copepods still represented 90% of the identifiable prey biomass.

Subyearling shad in fresh water (Figure 3c) fed on Daphnia spp., calanoid copepods, Chrinomidae larvae and pupae, and Trichoptera (Insecta) adults during fall 1980. In the winter (1980), few shad were caught in freshwater areas of the estuary (Figure 2), but those subyearlings caught there fed mostly on Corophium salmonis. In the spring, Neomysis mercedis and Corophium salmonis were important prey species. No calanoid copepods were found in the stomachs of these shad. Most of the stomach contents examined during the summer of 1980 were unidentifiable. Remnants of juvenile Corbicula manilensis, Corophium spp., calanoid copepods, and Daphnia spp. were, however, identified. Thirty percent fewer shad preyed on Corophium salmonis than had during the spring, and that species contributed only 3% to the weight of the identifiable prey. Corophium spinicorne was consumed more during summer than it had been in previous seasons.

B. Beach Seine

The stomach contents of yearling shad (Figure 3d) were in an advanced state of digestion, but Corbicula manilensis juveniles, Neomysis mercedis, and Corophium salmonis were identified. Subyearling shad fed on Trichoptera adults, calanoid copepods, and cladocerans. Although Trichoptera adults represented 73% of the identifiable prey biomass, calanoid copepods and cladocerans were consumed by a much larger percentage of the shad in the group (Figure 3d).

C. Otter Trawl

In marine water (Figure 4a), subyearling shad fed mostly on calanoid copepods, fish larvae, and *Neomysis mercedis* during fall 1980. In the winter, calanoid copepods were heavily preyed on although *Neomysis rayii* (found in only one shad stomach) composed 45% of the prey weight. During spring (1980), *Corophium salmonis* made up the bulk of the identifiable prey biomass. Calanoid copepods were also important.

In brackish water (Figure 4b) subyearling shad fed mostly on calanoid copepods during fall and winter. During spring, a greater percentage of the stomach content weight was identifiable; the bulk of it consisted of *Neomysis mercedis*, *Aniosgammarus* spp. (Amphipoda, Gammaridae), and calanoid copepods.

In fresh water (Figure 4c), during fall 1980, *Neomysis mercedis* was again the dominant prey species. *Corophium salmonis*, calanoid copepods, and *Daphnia* spp. were also important. In winter, fish larvae composed 50% of the identifiable prey biomass. *Corophium* was consumed by every fish in the sample, although it only represented 12% of the prey biomass. During spring, *Neomysis mercedis* was by far the most important prey species making up 90% of the identifiable prey biomass.

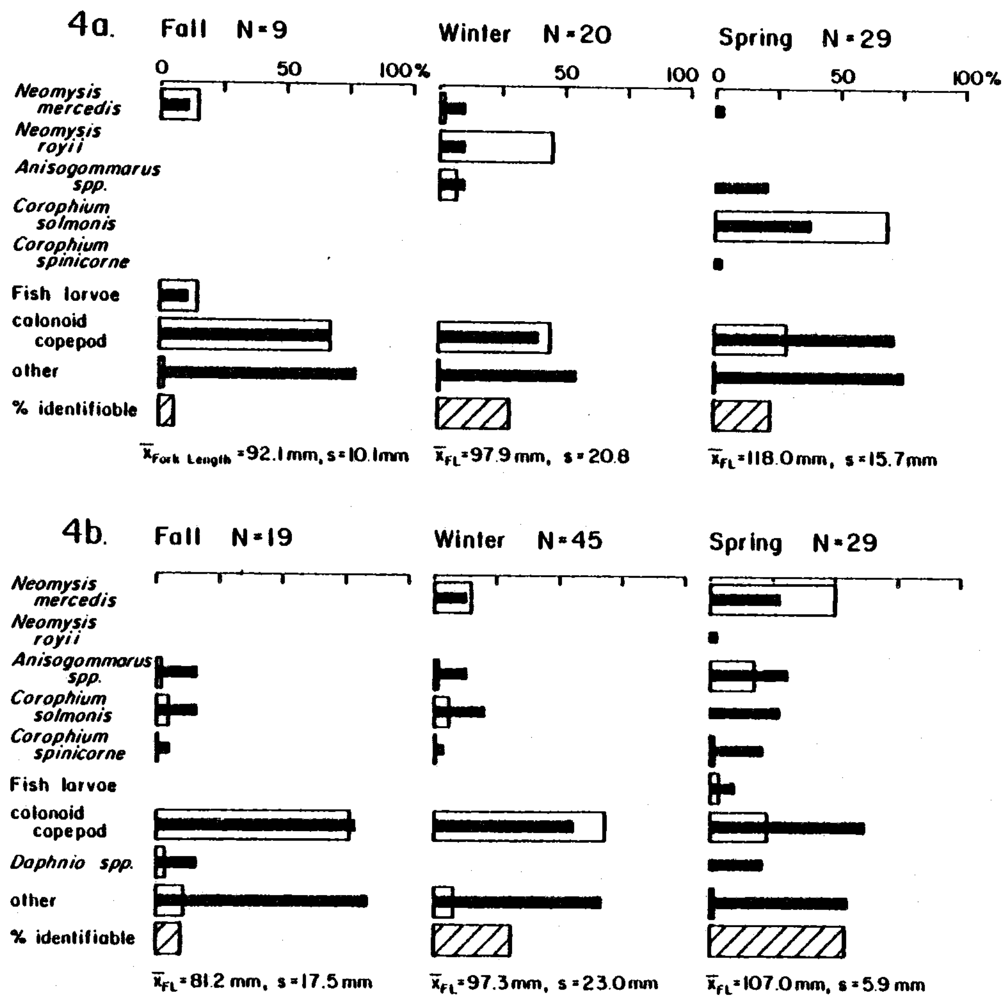

Figure 4. Stomach contents of shad caught in the otter trawl.

A. Marine water

B. Brackish water

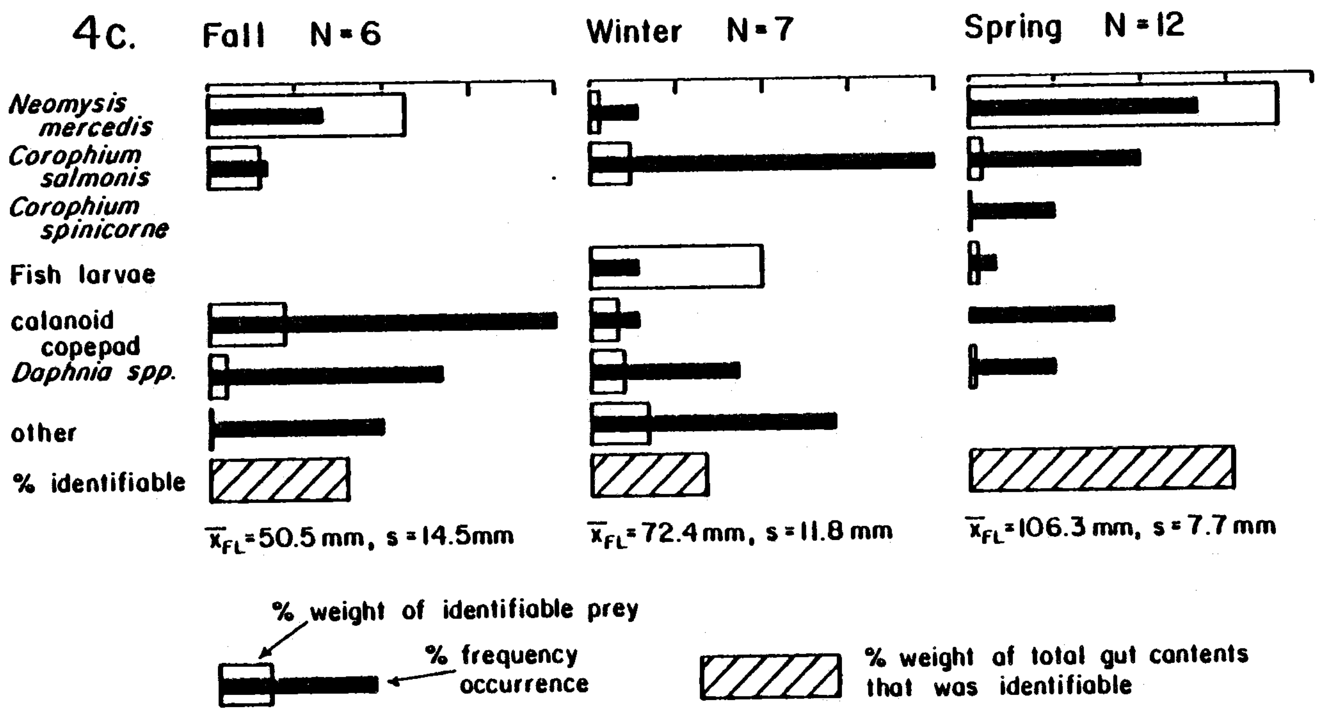

Figure 4. Stomach contents of shad caught in the otter trawl.

C. Fresh water.

D. Diel Study

In April 1980, small numbers of shad were caught at night in the purse seine, and periodically throughout the sampling period in the otter trawl. Shad were not caught in the otter trawl during the diel studies of May, June, and July. In May and June, however, shad were caught around the clock in the purse seine (Figure 5). In July, incidental (fewer than ten) catches of shad occurred periodically.

There was no apparent diel change in feeding during the May and June diel samplings. April and July catches were too small and patchy to allow for comparison, so they were not analyzed. Calanoid copepods composed nearly 100% of the identifiable prey biomass in every shad taken for stomach analysis during the May diel study (N=48). In June the prey biomass was not quantified, but again, no change was observed (N=68). There was also no diel change observed in the relative stomach fullness during May (Figure 6) and June (Figure 7) (see appendix I for methods of investigating relative stomach fullness).

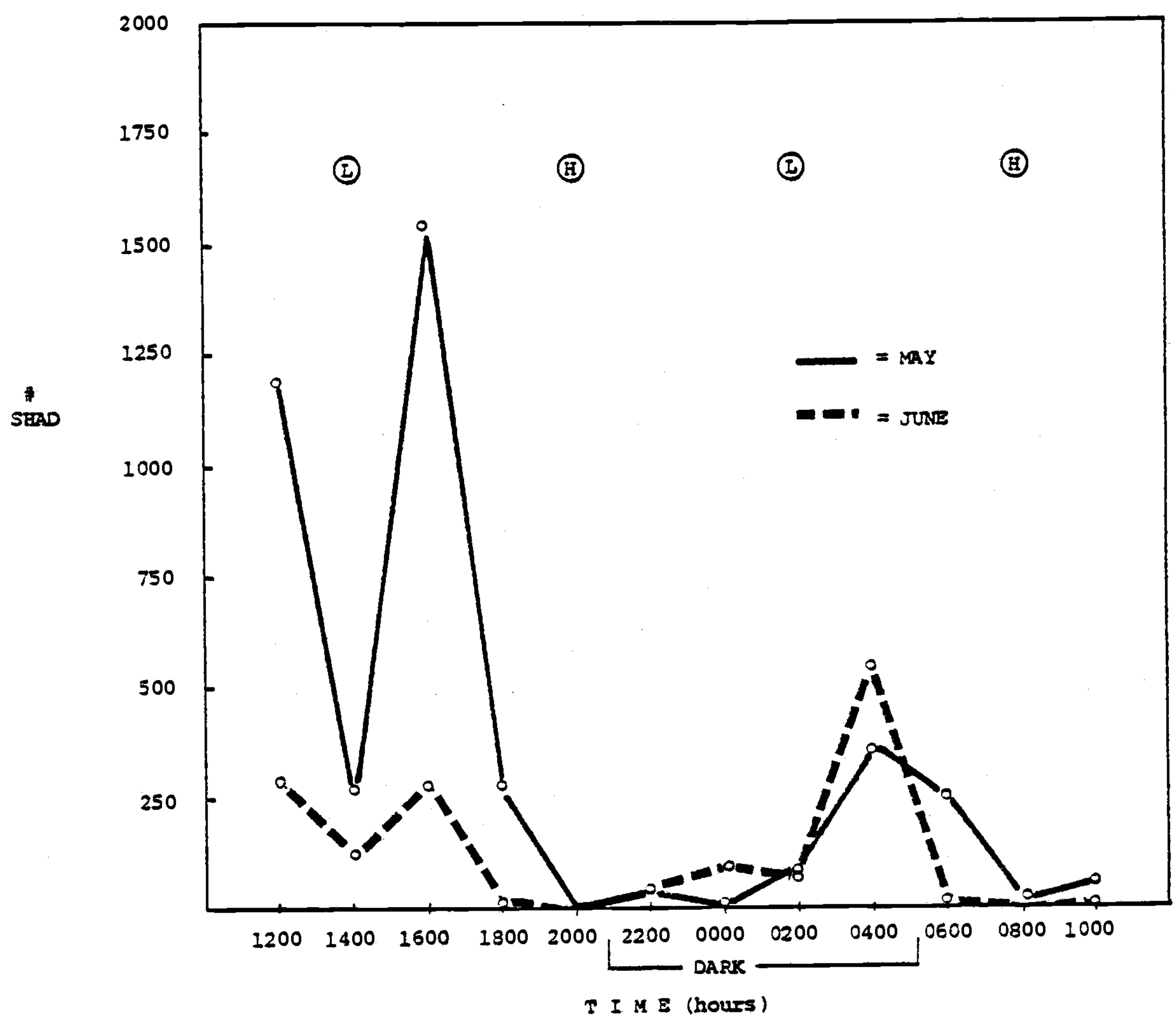

Figure 5. Total shad catches per time during May and June diel studies. (L = low tide; H = high tide).

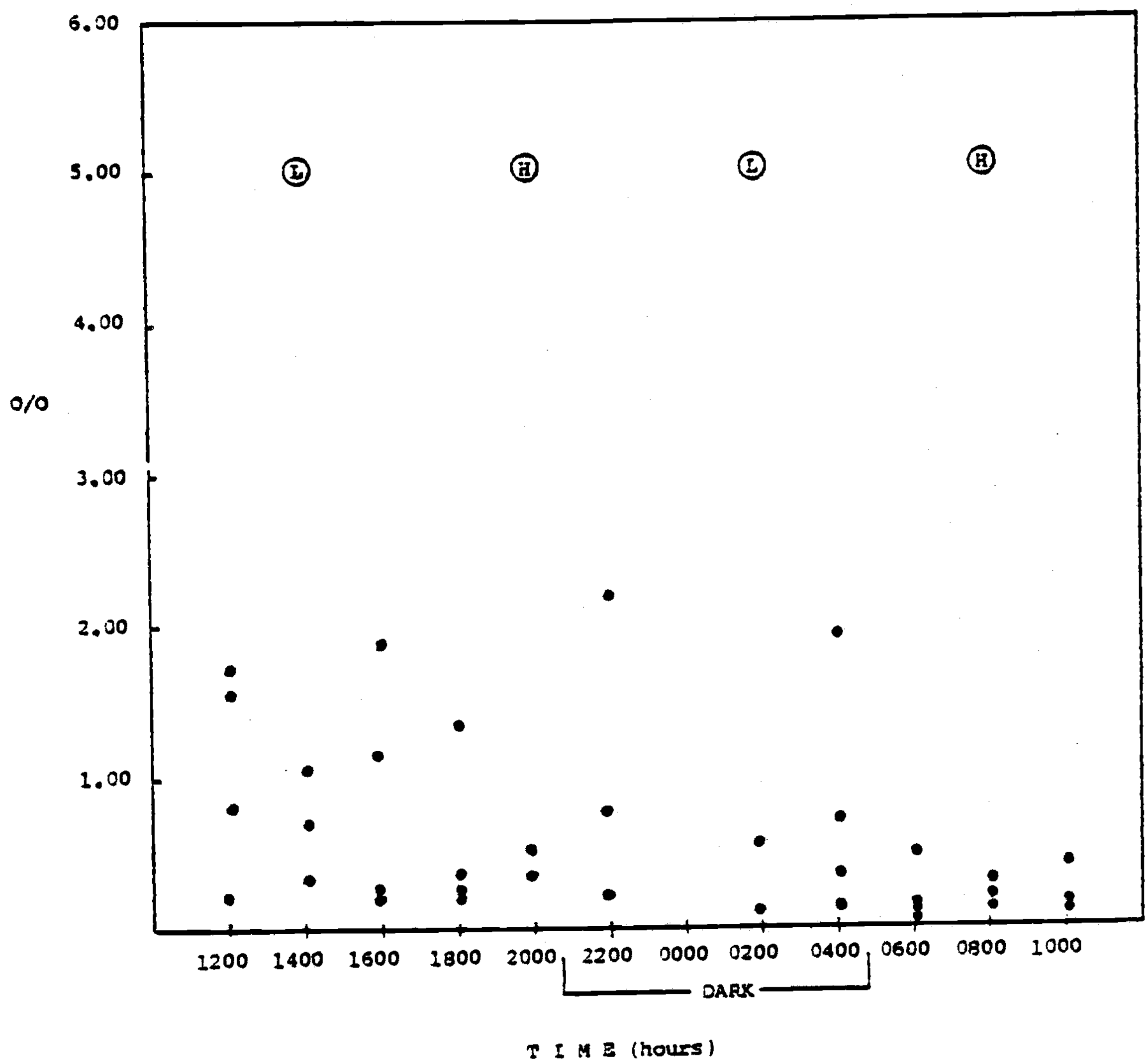

Figure 6. Relative stomach fullness (% fish body weight represented by stomach content weight) for feeding samples taken during the May diel study; N=48.

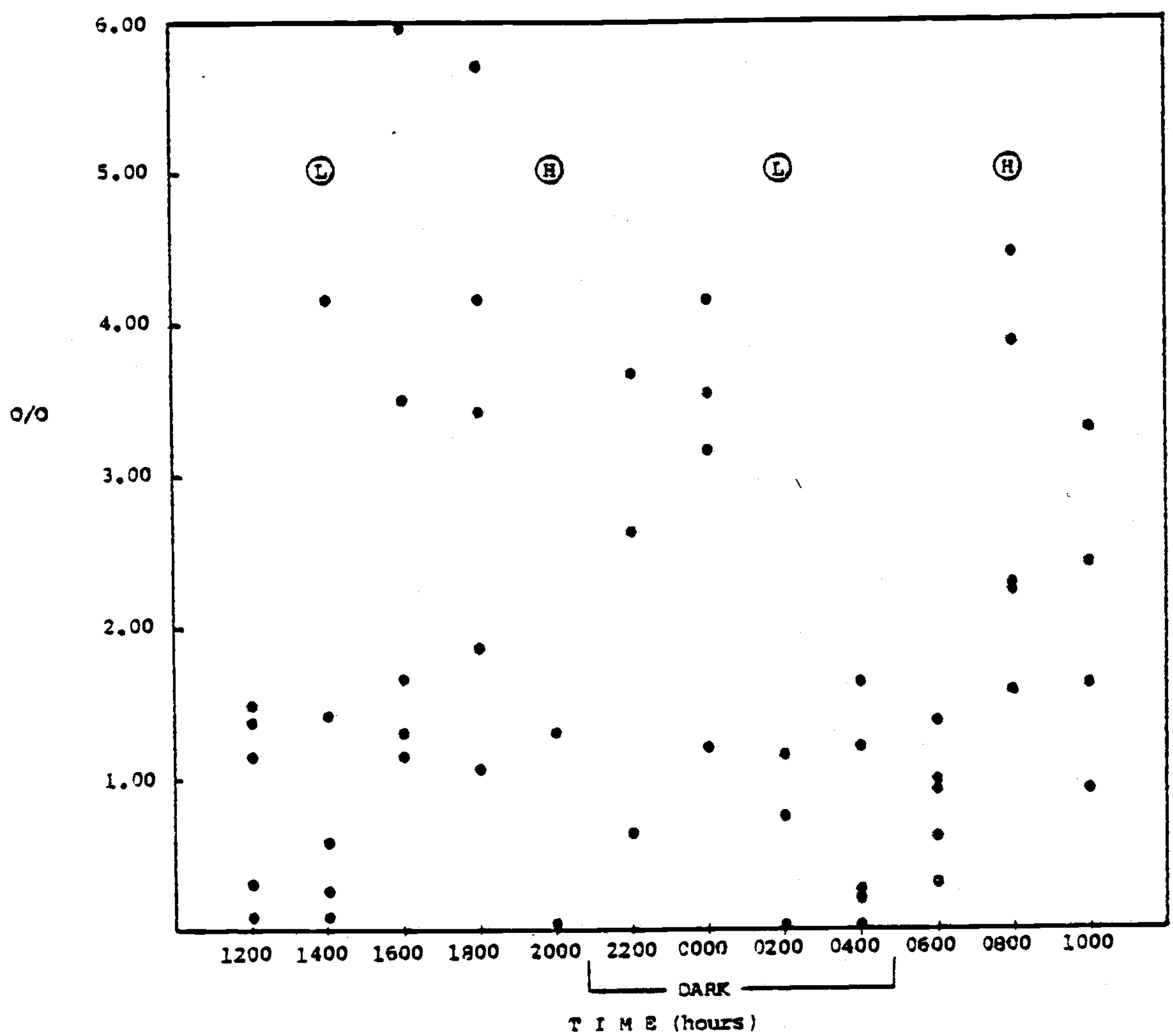

Figure 7. Relative stomach fullness (% fish body weight represented by stomach content weight) for feeding samples taken during the June diel study; (N=68).

V. DISCUSSION

Water temperature is very important in the life history of American shad (Leim, 1924; Chittenden, 1969; Leggett and Whitney, 1972), and may influence their horizontal and vertical location in the estuary. The capacity of shad to evade the nets may also be affected by temperature. Chittenden (1972) found that juvenile shad, undergoing slow temperature decreases, would avoid temperature below about 8°C, and noted strong avoidance at temperatures below 5°C. He found, furthermore, sublethal effects from exposure to low temperatures; i.e. sluggishness, difficulties maintaining equilibrium, and decreased sensitivity to visual stimuli.

Catches of shad in the purse seine were smallest during February through April 1980 (Figure 2), and were almost entirely in brackish water areas. The surface temperature at this time averaged 3.5° to 8.0°C, while the temperature in the salt wedge was between 8.0° and 10.0°C. Because the shad presumably avoided the surface waters and occupied the warmer brackish waters of the salt wedge, fewer were available to be captured in the purse seine. The purse seine fished to 10 m in depth, thus some shad were likely captured from the salt wedge.

Although fewer shad were available to be captured in the purse seine, more were probably available to the otter trawl, a factor which may explain, in part, the larger catches in the otter trawl during February and March 1980. Sublethal effects from exposure to low temperatures may have also contributed to these larger catches. In May, with surface temperatures over 13°C, young shad were likely higher in the water column where they would be more available to capture in the purse seine than in the otter trawl. Furthermore, in these warmer temperatures, shad were probably better able to avoid the otter trawl than they were in previous months.

During November and December 1980, huge numbers of young-of-the-year shad were caught throughout the estuary. The water temperature at that time was below 15°C, thus supporting the findings of Leggett and Whitney (1972) that the downstream migration of juvenile shad began when the temperture was lower than 15.5°C. As the catches in January 1981 were much lower than in December 1980, most of the young-of-the-year shad had probably migrated to the ocean. Furthermore, the apparent "no-growth" (Table I) of age group 0 shad from October through December 1980 may be explained by an out-migration of shad through the estuary at a similar size over several months. A similar pattern was observed in the Umpqua River in Oregon (Mullen, 1977) and in the Connecticut River (Watson, 1968). Some shad remained in the estuary, however, and presumably occupied the salt wedge, as was previously discussed.

Small numbers of adult shad on their spawning migration were first caught in May 1980. Because adult shad are very efficient in avoiding nets (Leggett and Jones, 1971), our catches of large shad probably do not truly reflect their abundance. Leggett and Jones (1971), using ultrasonic tracking, found adult shad typically to approach commercial monofilament drift gillnets to within 1 to 2 m, turn, and swim along the net. When they could swim around it, they would continue their upstream migration. This behavior was noted even in turbid water. Our small-mesh purse seine would surely be easily detected, and being fished open, would allow adults to escape. Nevertheless, the presence of adults in the catches from May through December 1980 does correspond to when they have been reported in the system. As spawning occurs through mid-September (Coutant and Becker, 1968), it is not surprising that adults were caught in October.

Differences in feeding were found among seasons, salinity zones, and gear types. The only clear difference found among age groups is that adults did not appear to feed. Yearling shad caught in the purse seine during fall (brackish water) consumed *Neomysis mercedis* while subyearlings did not. Subyearlings did, however, consume *Neomysis* during spring (fresh water). There was no apparent difference in the sizes of *Neomysis* between those consumed in the fall and those consumed during the spring, thus the apparent difference in diet cannot be explained by changes in feeding structure due to fish growth, for example gape size. Unfortunately, no data on prey availability is available to compare with the observed diet of shad. Studies have shown however, that shad feed opportunistically on the most abundant prey organisms (Domermuth and Reed, 1980; Walburg, 1956; Levesque and Reed, 1972). This would explain many of the observed changes in diet.

The dominant prey species were very similar to those reported in other estuaries, on both the Pacific and Atlantic coasts. Calanoid copepods were important throughout the year, while *Corophium salmonis* and *Neomysis mercedis* were important during fall, winter, and spring. During summer and fall, freshwater prey were consumed in addition to those prey species consumed in brackish and marine areas. The most important freshwater prey were *Daphnia* spp. and Chironomidae larvae and pupae. For those shad feeding in shallow water near beaches, adult Trichoptera were important. In addition to prey, plant fragments often occurred in the stomachs, probably accidentally swallowed while filtering the water for prey. This phenomenon was also found for shad feeding in Virginia rivers (Massmann, 1963).

Occasionally Corbicula manilensis juveniles were present in the stomachs. Those consumed were less than 2 mm in length and would have been easily suspended in the water column by currents, as was the case for many benthic animals found in the stomachs of shad feeding in Scotman Bay, Bay of Fundy (Leim, 1924). That Corbicula represents large percentages of the identifiable prey weight in two sample groups can be explained by remembering that in all feeding analyses the differential digestion of different prey species potentially can bias the results. The greater the degree of digestion, the greater is the bias toward slower-digesting organisms (i.e. those with more hard parts, shells, etc.). Those two sample groups, both composed of shad caught in the summer, were in an advanced state of digestion, but the bivalves were in relatively good condition. Thus, bivalves would appear more important than they probably were. The warmer waters of summer would increase the digestion rate resulting in the observed increase in the degree of digestion.

The epibenthic amphipod Corophium salmonis was utilized to a much greater extent by shad caught in the purse seine than by those caught in the otter trawl, during winter and spring. David (1979) found that in Youngs Bay (Columbia River Estuary) Corophium salmonis would migrate vertically at night. This migration would place these small amphipods up in the water column where they would be affected by the water currents, and thus more available to shad feeding in the water column than those feeding above the bottom.

During summer 1980, the consumption of *Corophium salmonis* was much less than it was during winter and spring. This may have been due to a seasonal factor that changed *Corophium*'s availability to shad, but during the stomach analyses, an abrupt change in *Corophium* consumption between May and June was noted. This suggests the presence of some factor having a more rapid influence than most seasonal changes. On 18 May 1980, the eruption of Mount St. Helens sent tremendous amounts of suspended material down into the Columbia River, reaching the estuary 21 May 1980 and greatly increasing its turbidity. This may have contributed to the natural seasonal variation in *Corophium*'s availability to shad by affecting shad, *Corophium*, or both. For example, the occurrence of large prey such as mysids, *Crangon* shrimp, and fish in shad's diet suggests that particulate feeding may be utilized in addition to the more common filter feeding. Vision is vital to particulate feeding fishes, and may also be important in the identification of dense plankton patches in which to filter (Durbin, 1979). Gardner (1981) found that increased turbidity significantly reduced the feeding rates of bluegills; particulate plankton feeders. Therefore, the increased turbidity may have decreased shad's ability to locate and capture *Corophium*. Furthermore, there was a significant decrease in the relative stomach fullness of shad caught during summer (Appendix III) indicating that total feeding efficiency may have been affected as well. *Neomysis mercedis* also disappeared from the diet of purse seine caught shad in the summer for perhaps the same reasons. Increased turbidity, however, may have also affected *Corophium*'s diel vertical migrations, which were found to be stimulated by light (Davis, 1979).

Adult shad do not appear to feed while on their upstream migration in the Columbia River. In another Columbia River study, adult females were found with stomachs nearly empty (Hasselman, 1966). In the freshwater areas of the Delaware River, adult shad appeared to feed rarely, and to die of starvation (Chittenden, 1976b). Atkinson (1951), however, reported that adult shad in a freshwater pond fed actively on a diet of ground fish or a live-fish meal mix. He suggested that the reason adult shad in fresh water are found with empty stomachs is that the available food is too small to be retained by their gill-rakers. In support of Atkinson (1951), Chittenden (1969) found an occasional adult shad to forage on adult insects during a hatch, or on dying young shad that were under the influence of rotenone, but that usually, there was no suitable plankton food for foraging adult shad in the freshwater Delaware River. Preliminary results from a study of the developmental morphology of shad's filtering apparatus cause me to believe that the gill-rakers of adult shad are of sufficient design to retain zooplankton of sizes similar to those consumed by juvenile shad in the Columbia River Estuary. Therefore, adult shad apparently do not actively filter feed while on their spawning migration, but occasionally feed selectively on prey large enough to present sufficient visual stimuli.

VI. SUMMARY

1. Adult shad and age group I and II juveniles entered the estuary from the ocean beginning in May 1980.
2. Young-of-the-year shad first reached the estuary during their seaward migration in September 1980. A large surge of these juveniles passed through the estuary toward the ocean during November and December 1980.
3. During winter, juvenile shad avoided the cold surface waters of the estuary and occupied the warmer waters of the salt wedge.
4. Adult shad did not appear to filter feed during their upstream migration, but may have occasionally fed selectively on prey large enough to present sufficient visual stimuli.
5. Dominant prey species for juvenile shad were calanoid copepods, *Corophium salmonis*, *Neomysis mercedis*, and in fresh water, *Daphnia* spp. and insects.
6. No clear differences in feeding were found among the juvenile age groups.
7. The epibenthic amphipod *Corophium salmonis* was consumed more by shad caught in the water column than by those caught near the bottom, presumably due to the vertical migrations of these amphipods.
8. It is suggested that the increased turbidity in the estuary following the eruption of Mount St. Helens may have affected the feeding efficiency of shad by decreasing their ability to visually locate and capture prey.
9. Except for those migrating, American shad were caught principally in marine and brackish areas of the Columbia River Estuary.

10. During the May and June diel studies, no diel difference in feeding was found. Calanoid copepods were consumed around the clock, and there was no difference in the relative stomach fullness.

VII. NEEDED RESEARCH

There still remains many questions concerning the American shad population in the Columbia River Estuary. Cleaver (1951) and Coutant and Becker (1968) have suggested that the lower river below Bonneville dam including the estuary may be the major spawning grounds. Investigation of this possibility is very important, as is the exact identification of the chief spawning areas. Furthermore, knowledge of the proportion of the population that utilizes the downstream areas for spawning is needed.

Although the dam counts give an indication of the size of the upstream spawning population, they give no information concerning the numbers of shad spawning below the dams. Thus, in addition to a more accurate population estimate for the upstream population, an equally accurate estimate is needed for the downstream population.

Another important question with management implications is whether or not the estuary and lower river is reaching its carrying capacity for shad, or if this capacity is changing. If so, is this a limiting factor to population growth, or are shad being "forced" to utilize increasingly further upstream areas as spawning grounds?

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APPENDICES

APPENDIX I. Methods for Investigating Relative Stomach Fullness.

Relative stomach fullness was calculated as the percentage of the fish's total body weight represented by stomach content weight (i.e. stomach content weight ÷ fish weight X 100). Empty stomachs were not included in the calculation. In the analysis of these data the standard deviation varied directly with the mean of relative stomach fullnesses, so the logarithmic transformation was used to stabilize the variance (Snedecor and Cochran, 1967). Differences between various groups were tested for by the Bonferroni Multiple Comparison Method (Neter and Wasserman, 1974), and are presented in appendices III and IV. The mean log relative stomach fullnesses were transformed back by taking the anti-log. These geometric means (Snedecor and Cochran, 1967) are presented in appendix II.

APPENDIX II. Geometric mean Relative Stomach Fullness for Feeding Groups (anti-log of mean log % of total fish body weight represented by stomach content weight).†

Season and Age	PURSE SEINE (C.V.=3.66%;d.f.=273)		OTTER TRAWL (C.V.=250%;d.f.=167)		
	Brackish	Fresh	Marine	Brackish	Fresh
Fall '80					
'S'	0.12	0.17	0.09	0.14	0.25
'Y'	0.05	0.04	....	....	....
Winter '80 & '81					
'S'	0.14	0.06	0.07	0.13	0.23
'Y'	....	....	....	....	....
Spring '80					
'S'	0.43	0.62	0.33	0.33	0.20
'Y'	0.23	....	....	....	....
Summer '80					
'S'	0.10	0.06	....	....	....
'Y'	0.20	....	....	....	....

† Calculation not including empty stomachs.

APPENDIX III. Bonferroni multiple comparison statistics[1] for comparisons between purse seine feeding groups.

(MSE-0.4471; S=12; d.f.=273; C.V.=366%; Bonferroni family confidence coefficient = 0.9979 [p=0.05]; critical t=3.0368).

Comparison	$\overline{X}$ (log units)	N	't'	significant?
Fall, Brackish, 'S'	-0.9054	19	2.3331	no
Fall, Brackish, 'Y'	-1.2633	19		
Fall, Brackish, 'S'	-0.9054	19	0.6265	no
Fall, Fresh, 'S'	-0.7607	15		
Fall, Brackish, 'Y'	-1.2633	19	0.6924	no
Fall, Fresh, 'Y'	-1.4204	16		
Winter, Brackish, 'S'	-0.8475	30	1.7281	no
Winter, Fresh, 'S'	-1.2111	15		
Spring, Brackish, 'S'	-0.3678	61	0.9386	no
Spring, Brackish, 'Y'	-0.6364	6		
Summer, Brackish, 'S'	-0.9876	61	1.3386	no
Summer, Fresh, 'S'	-1.1945	27		
Summer, Brackish, 'S'	-0.9876	61	1.3026	no
Summer, Brackish, 'Y'	-0.7023	11		
Fall, Fresh, 'S'	-0.7607	15	2.7452	no
Fall, Fresh, 'Y'	-1.4204	16		
Spring, Brackish, 'S'	-0.3678	61	0.5115	no
Spring, Fresh, 'S'	-0.2087	5		
Fall, Brackish, 'S'	-0.9054	19	0.3045	no
Winter, Brackish, 'S'	-0.8457	30		
Winter, Brackish, 'S'	-0.8457	30	3.2051	yes
Spring, Brackish, 'S'	-0.3678	61		
Spring, Brackish, 'S'	-0.3678	61	5.1192	yes
Summer, Brackish, 'S'	-0.9876	61		
Spring, Brackish, 'S'	-0.3678	61	3.0602	yes
Fall, Brackish, 'S'	-0.9054	19		
Fall, Brackish, 'S'	-0.9054	19	0.4679	no
Summer, Brackish, 'S'	-0.9876	61		

APPENDIX III (continued)

Comparison		$\overline{X}$ (log units)	N	't'	significant?
Summer, Brackish,	'S'	-0.9876	61	0.9517	no
Winter, Brackish,	'S'	-0.8457	30		
Fall, Fresh,	'S'	-0.7607	15	1.8447	no
Winter, Fresh,	'S'	-1.2111	15		
Winter, Fresh,	'S'	-1.2111	15	2.9030	no
Spring, Fresh,	'S'	-0.2087	5		
Spring, Fresh,	'S'	-0.2087	5	3.0282	no
Summer, Fresh,	'S'	-1.1945	27		
Summer, Fresh,	'S'	-1.1945	27	2.0146	no
Fall, Fresh,	'S'	-0.7607	15		
Summer, Fresh,	'S'	-1.1945	27	0.0771	no
Winter, Fresh	'S'	-1.2111	15		
Fall, Fresh,	'S'	-0.7607	15	1.5986	no
Spring, Fresh,	'S'	-0.2087	5		

[1] See Appendix I.

APPENDIX IV. Bonferroni multiple comparison statistics[1] for comparisons between otter trawl feeding groups. (age 'S')

(MSE-0.2954; S=9; d.f.=167; C.V.=250%; Bonferroni family confidence coefficient = 0.9971 [p=0.05]; critical t=2.9291)

Comparison	$\bar{X}$ (log units)	N	't'	significant?
Fall, Marine	-1.0378	9	0.8775	no
Fall, Brackish	-0.8448	19		
Fall, Brackish	-0.8448	19	0.9646	no
Fall, Fresh	-0.5993	6		
Fall, Marine	-1.0378	9	1.5308	no
Fall, Fresh	-0.5993	6		
Winter, Marine	-1.1826	20	2.0471	no
Winter, Brackish	-0.8836	45		
Winter, Brackish	-0.8836	45	1.1457	no
Winter, Fresh	-0.6306	7		
Winter, Marine	-1.1826	20	2.3127	no
Winter, Fresh	-0.6306	7		
Spring, Marine	-0.4804	29	0.0532	no
Spring, Fresh	-0.4880	29		
Spring, Brackish	-0.4880	29	1.1401	no
Spring, Fresh	-0.7007	12		
Spring, Marine	-0.4804	29	1.1809	no
Spring, Fresh	-0.7007	12		
Fall, Marine	-1.0378	9	0.6637	no
Winter, Marine	-1.1826	20		
Winter, Marine	-1.1826	20	4.4450	yes
Spring, Marine	-0.4804	29		
Fall, Marine	-1.0378	9	2.6878	no
Spring, Marine	-0.4804	29		
Fall, Brackish	-0.8448	19	0.2609	no
Winter, Brackish	-0.8836	45		
Winter, Brackish	-0.8836	45	3.0566	yes
Spring, Brackish	-0.4880	29		

APPENDIX IV (continued)

Comparison	$\bar{X}$ (log units)	N	't'	significant?
Fall, Brackish	-0.8448	19	2.2242	no
Spring, Brackish	-0.4880	29		
Fall, Fresh	-0.5993	6	0.1035	no
Winter, Fresh	-0.6306	7		
Winter, Fresh	-0.6306	7	0.2712	no
Spring, Fresh	-0.7007	12		
Fall, Fresh	-0.5993	6	0.1947	no
Spring, Fresh	-0.7007	12		

[1] See Appendix I.

APPENDIX V. Comparison of mean fork lengths between subsamples selected for stomach analysis and total measured catches.

Month	Sta.	N	$\overline{X}$	SD	't'	df	't_c'
FEBRUARY	8						
subsample		5	97.6	12.5	1.723	53	2.006
total		50	106.5	10.9			
MARCH	9						
subsample		5	115.8	21.3	0.4577	28	2.048
total		25	112.8	11.8			
APRIL	8						
subsample		5	108.8	32.7	0.0660	48	2.010
total		45	108.3	14.9			
MAY *	8						
subsample		5	135.6	23.1	1.1099	106	1.981
total		103	143.7	15.7			
JUNE	8						
subsample		5	153.0	14.6	0.4489	53	2.006
total		50	150.5	11.6			
JULY	8						
subsample		5	192.4	19.8	0.6109	30	2.042
total		50	202.4	10.6			
SEPTEMBER	12						
subsample		4	73.3	4.5	1.2606	17	2.110
total		15	78.7	8.3			
subsample		1	207.0	...	0.3878	34	2.032
total		35	212.0	12.6			
OCTOBER	12						
subsample		5	88.2	9.8	0.0686	53	2.006
total		50	88.9	21.2			
NOVEMBER	8						
subsample		5	81.6	3.8	1.5544	53	2.006
total		50	85.6	5.6			
DECEMBER	9						
subsample		5	74.4	3.8	0.4530	53	2.006
total		50	75.6	5.9			

APPENDIX V. (continued)

Month	Sta.	N	$\bar{X}$	SD	't'	df	't_c'
JANUARY	8						
subsample		4	97.0	11.0	1.5335	46	2.013
total		44	86.8	12.9			
subsample		1	243.0	....	0.1207	2	4.303
total		3	240.0	19.1			

* Total catch was measured.