

SALINITY-TEMPERATURE RELATIONS OF THE
AMPHIPOD COROPHIUM SALMONIS IN THE
COLUMBIA RIVER ESTUARY

SUBMITTED TO
U.S. ARMY CORPS OF ENGINEERS
PORTLAND DISTRICT

BY
ROBERT L. HOLTON, DUANE L HIGLEY
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OREGON STATE UNIVERSITY
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EXECUTIVE SUMMARY

The salinity-temperature relations of the amphipod Corophium salmonis in the Columbia River Estuary were investigated through a combination of field and laboratory studies. Corophium salmonis has great trophic importance in the estuary because of its wide distribution, high densities and strong contribution to the estuary's simple food chains, which involve several economically important fish species including juvenile salmonids.

Field studies were conducted in the summer and fall of 1983 on populations of C. salmonis existing along a seasonally temporary salinity gradient from upper Youngs Bay to outside the mouth of Youngs Bay. Mid-summer tidal exchanges produced observed salinity extremes of 1 to 17 parts per thousand (ppt) in the outer bay, while lower maxima occurred at most up-bay stations. By October, a mostly uniform water mass occupied the bay, so that tidal depth was the major cause of salinity differences among stations. C. salmonis populations exhibited mid-summer peaks and late summer, early fall declines to near zero densities at all stations. Declines proceeded most slowly at the intertidal stations, suggesting that mortality rates or migration patterns varied with salinity as influenced by tidal depth. These results support those of earlier studies by McConnell et al. (1978) and Wilson (1983) which documented a summer-peak pattern in the Youngs Bay region, and a winter-peak pattern in the Grays Bay region (the latter caused by immigration). The relative importance of movement across tidal depth vs. movement up and down the river in these populations is unresolved.

Laboratory studies found maximum survival rates near 10 ppt salinity. Death was rapid (< 1 day) at salinities >30 ppt, and was more rapid at 20 ppt than at 10 ppt. Survival rate declined with increasing temperature (7, 14 and 21 degrees C), and generally varied by sex according to the pattern juveniles>females>males. The addition of silt to treatment vessels significantly increased survival rate. No pattern of salinity preference was exhibited by C. salmonis within the 0 - 20 ppt range. This result agrees with a similarly wide salinity preferendum (10 - 30 ppt) found for the more marine oriented species C. volutator (McLusky 1970).

The present study combines with earlier studies to demonstrate that C. salmonis is adapted to moderate and low salinities, and that population dynamics and migration patterns may respond to local variations in salinity regime. Such responses could affect trophic relations within the Columbia River Estuary should channel depth be increased and allow a greater intrusion of marine water.

INTRODUCTION

Although many estuarine species are tolerant of fluctuating environmental conditions, seasonal changes in their distributional patterns often occur as conditions at the edges their distribution become unacceptable. A principal force behind such changes, of course, is seasonal fluctuations occurring in the upriver penetration of saline water and in the range of salinities produced at a given location through a tidal cycle.

In the Columbia River Estuary salinity fluctuations may be very large, owing to the river's immense freshwater flow that peaks with the spring snowmelt. Over most of the estuary, fluctuating brackish conditions combine with a sand-dominated substrate to produce a simplified infaunal community composed of a few amphipods, worms, insects and mollusks (Holton 1984). Principal among these species is the amphipod Corophium salmonis which builds its tubes in fine sediments over much of the estuary and upriver into totally freshwater habitats. This species has recently received much attention due to its frequent dominance of brackish-water infaunal communities in the Columbia River Estuary and in other Pacific Northwest estuaries, and because of its prevalence in the diets of juvenile salmonids and other economically important fish species (Durkin et al. 1979; Durkin, Lipovsky and McConnell 1979; Higley and Holton 1975). In this respect, the species is joined by the oft-studied C. voluator which occupies a central role in the food chains of several British estuaries (Green 1968).

Recent studies of the life history and distribution of C. salmonis in the Columbia River Estuary strongly suggest that the species undertakes seasonal movements which may be relatable to changing environmental conditions. The primary source of this information is the study by Wilson (1983) who followed life history events of C. salmonis on two fine-sand tidal flats in the estuary. At the most marine site, the species was present only in the spring-to-fall period, during which time it underwent a very strong density increase due to reproduction. In contrast, at the less marine site the summer pulse was much subdued but was followed by a winter increase created by the immigration of adults and subadults. Other seasonal studies conducted by Higley et al. (1982 a), Higley et al. (1982 b) and McConnell et al. (1978) found basically the same two patterns of density change in regions near Wilson's two study sites.

These decidedly different C. salmonis density patterns have strong implications to food chain processes within the Columbia River Estuary, both because the species figures so importantly in these processes and because the simple infaunal communities involved do not appear to offer suitable alternative prey species where C. salmonis populations are depleted or absent. The questions which require attention include: What are the patterns and distances of movements? What factors control the distribution and migrational

activities of the species? What conditions are optimal for growth and reproductive success, and which are marginal or unacceptable? What are the population dynamics in primary fish feeding areas such as Youngs Bay, and how susceptible are they to disruption by environmental changes?

Some of these questions were addressed in the present study, which was supported by the U.S. Army Corps of Engineers as part of an investigation to determine possible impacts of a plan to deepen the navigation channel in the Columbia River Estuary. The project would increase channel depth to provide access by deeper draft ships to ports.

Changes in channel depth would be expected to alter circulation patterns within the estuary and to allow a greater intrusion of saline water, with the result that sedimentation patterns and benthic habitats would likely be altered. These changes, combined with the direct effects of higher salinities on the biota, could change the simple food chains of the middle and upper estuary where C. salmonis is dominant.

The salinity requirements of members of the genus Corophium are known primarily through extensive studies conducted on C. volutator. This species does best in the 5-35 parts per thousand (ppt) salinity range, with an optimum near 20 ppt (McClusky 1967; Mills and Fish 1980). A co-occurring species, C. arenarium, requires slightly higher salinities and sandier substrates than C. volutator, so that while both species may be widely distributed within an estuary, distributional overlaps are restricted (Crawford 1937; Mills and Fish 1980; Watkin 1941). The habitat differences exhibited by these two species typify the variable requirements found among the some 45 known species of Corophium, which occupy marine, brackish and freshwater habitats and utilize mud, sand, rock and vegetative substrates.

The habitat requirements of C. salmonis are at present poorly studied, and may be only broadly deduced from distributional accounts. These accounts show C. salmonis to generally occupy fine sand and mud substrates in fresh and brackish water habitats (Albright and Armstrong 1982; Albright and Borithilette 1982; Higley and Holton 1975; Levings and Coustalin 1975). Salinities greater than about 25 ppt, and coarse sand or solid substrates appear to be little utilized. In the Columbia River Estuary, the species is common in many fine-sediment habitats from the Youngs Bay region (River Mile [RM] 12) to at least Portland (RM 95). Densities exceeding 20,000/m² have been found in Youngs Bay, Grays Bay, Cathlamet Bay and some mid-estuary sandy shoals (Higley et al. 1982a; Holton et al. 1984; Wilson 1983).

The present study was concerned with two aspects of C. salmonis distributional ecology: The varying patterns of seasonal density change exhibited by field populations along a salinity gradient, and the response of the species to experimentally manipulated salinity and temperature. It was hypothesized that population changes in the

highest salinities would approximate those of the Desdemona Sands population studied by Wilson (1983), while changes at the lowest salinities would be like those in her Grays Bay population. Confirmation of such patterns would lend support to the view that changing salinities induce population movements. The field studies were begun in July 1983. Funding allowed observations to be made only during the period July 12 through October 27, so that the potential density increases in the low salinity zone during the winter could not be documented.

Laboratory studies investigated the salinity-temperature conditions which produced maximum survival. In addition, animals were exposed to sudden changes in salinity or to a choice of salinities to determine if they would seek more favorable conditions. A wide salinity preferendum of 10 to 30 ppt has been documented for C. volutator (Meadows and Ruagh 1981). For C. salmonis it was expected that a lower range would be preferred based on the species' distributional characteristics.

In both tolerance and behavioral experiments, effort was concentrated on salinity-temperature combinations like those occurring within the species' distribution range. This meant for the most part that salinities of 0 to 30 ppt and temperatures 7 to 21 degrees C were utilized.

METHODS AND MATERIALS

Field Studies

Sampling stations were initially established at the Desdemona Sands intertidal sites (Station 11), and at six subtidal and intertidal sites in Youngs Bay and the Lewis and Clark River (Stations 12-17 and 19), as illustrated in Figure 1.

This sequence of locations provided the range of salinity regimes needed to investigate the responses of local populations to increased late summer and fall salinities. However, Stations 16 and 17 in the Lewis and Clark River proved to contain C. salmonis densities too low to allow study of population changes, and were abandoned. The problem appeared to be associated with disruptions due to log storage, which produced heavy bark and wood chip depositions and involved periodic dredging activity. A thorough investigation was made by boat of potential study sites in the lower several miles of the river (up to an impassable bridge), but no site was found that supported sufficient C. salmonis for the study's purposes. The freshest portion of the salinity gradient therefore was not be sampled.

Sediment texture was predominantly fine sands at Stations 11, 12, 13 and 19, and was muddy sand at Stations 14 and 15. Approximate water depth (relative to mean lower low water) was as follows: Station 11 (0 m), Station 12 (-2.5 m), Station 13 (-4 m), Station 14 (-2 m), Station 15 (0 m) and Station 19 (-3 m). Collection dates were July 12, July 26, August 10, August 23, September 8, September 21, and October 27. Exceptions were that Station 19 was omitted until August 23, and

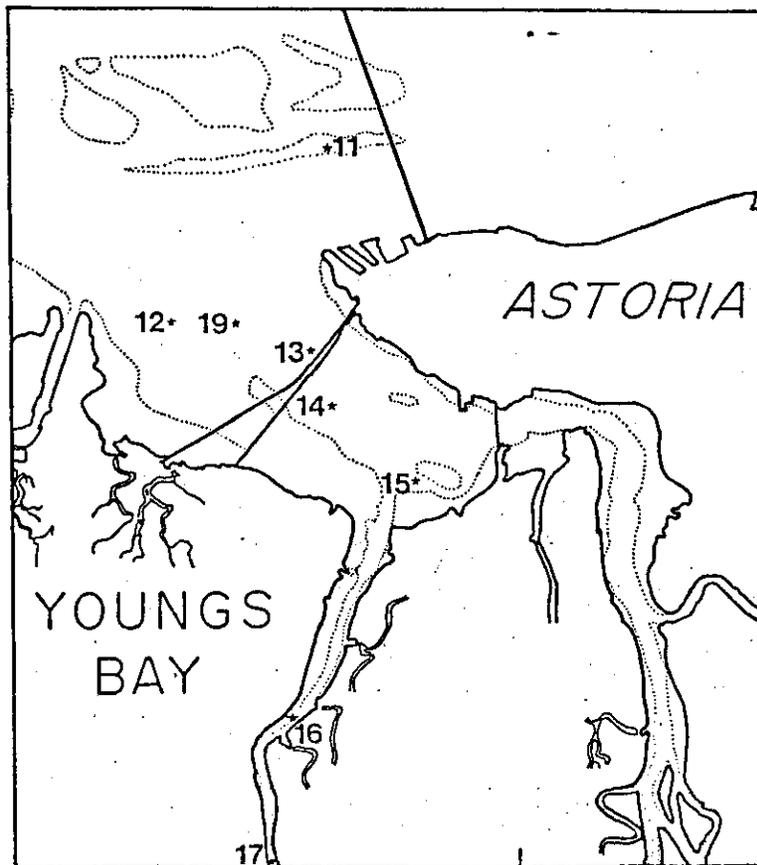
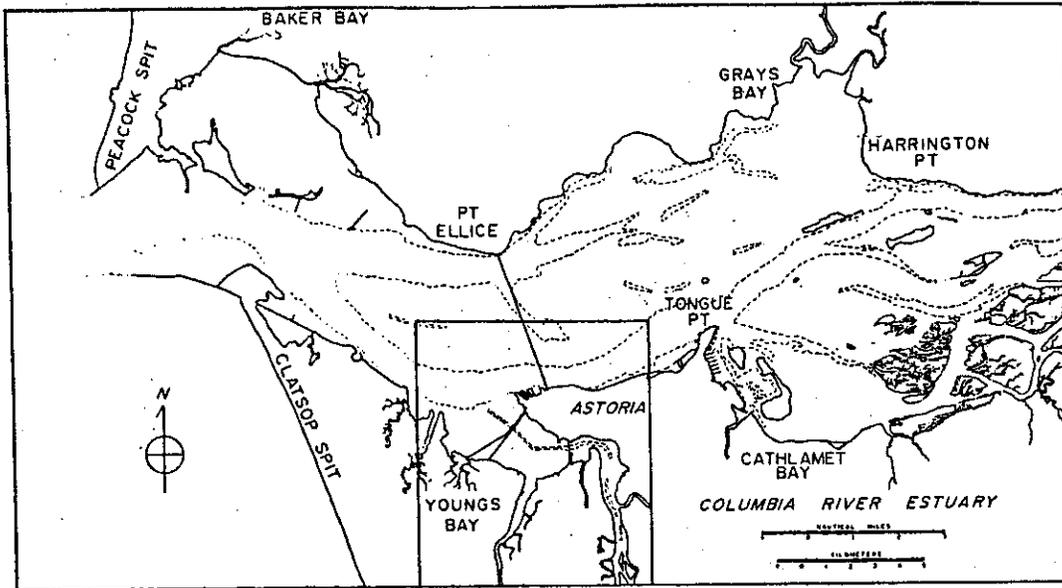


Figure 1. Location of field sampling Stations 11-15 and 19.

Station 11 was sampled on September 16 instead of September 21.

On each collection date, three samples per station were collected either from boat using a 0.05 m² Ponar grab sampler (Stations 12-15, 19) or on foot using a 10.2 cm diameter hand-held coring tube (Station 11). The grab sampler was deployed from a 24-foot (7.3-m) dory, which was positioned at each station by reference to nearby pilings or buoys. Station 11 was sampled during low tide within a 30 m x 100 m rectangular grid whose origin was marked by a metal stake. Sampling points were randomized within the grid. The Ponar grab usually sampled to a depth of about 5 cm (leaking samples or those with uneven jaw penetration were discarded), while the coring tube was pushed 10 cm into the sediment. The exception to the above collection methods occurred on the final collection trip (October 27, 1983), when unfavorable tides required that Station 11 be sampled by boat using the grab sampler rather than on foot.

Both grab and core samples were preserved using a 5-10% buffered aqueous formalin solution. After several days storage, the samples were sieved (aided by a mechanized agitator) on a 0.5 mm screen and the retained portion stored in a 70% aqueous solution of isopropanol. Rose bengal was added to this solution to stain the animals, which were then picked under 3-diopter magnifier and identified under a stereomicroscope. Only amphipods were picked and identified.

All members of the genus Corophium were separated from other amphipods, and a 50-member subsample removed to determine the relative proportions of C. salmonis and C. spinicorne, which are the only Corophium species which have been found in the sampling area. The proportions were used to calculate whole-sample C. salmonis counts, and these counts were converted to densities based on sampler size. The densities were transformed by $\log_{10}(X + 1)$, and means according to date and station computed and back transformed.

Tolerance Studies

Live C. salmonis were collected from the Columbia River Estuary on May 17, June 24, July 26, August 16, and August 22, 1983 (Table 1). Initial collections were from Grays Bay near Harrington Point, but on July 26 the collection site was moved to Desdemona Sands (Station 11 of the field studies, Figure 1) to reduce travel time. The surface 2-3 cm of sediment was gently scraped from the exposed tidal flat and stored in plastic buckets. The buckets were chilled (approximately 15 degrees C) in transit to the Marine Science Center. Aeration was included on warm days or when storage exceeded several hours. Rarely did aeration appear to be a problem, since only small amounts of sediment and a few centimeters of river water were added to each bucket. In a few instances extra layers of sediment were added to buckets, but this procedure increased mortality rates as well as laboratory sorting time, and was discontinued. Vibration during transport caused compaction of sediments (mostly silty fine sands) and this may have added stress to captured animals. The extent of this effect was not investigated since the laboratory populations provided large numbers of apparently healthy animals.

In the laboratory animals were maintained in the buckets, sediments, and water of their capture. Aeration was provided during culture, and temperature was controlled at 14 degrees + or - 1 degree C. By comparison, water temperatures at the collection sites exceeded 20 degrees C in mid-summer.

Culture and experimental containers were maintained at appropriate temperatures through a combination of water tables, chillers, thermostatically-controlled heaters, and a constant temperature room (set at 7 degrees C). Animals were separated from the sediment by gentle washing with water at ambient temperature and salinity on fine mesh screens (.125 - .250 mm). At low animal densities, soft camel hair brushes were used to transfer the animals from the screens to holding bowls, which contained short sections of capillary tubing (5 mm long x 1.8 mm internal diameter). At high densities, animals were decanted onto screens from the mud, and backwashed into bowls. After a few hours, most animals occupied the capillary tubes, and could be more easily studied and transferred to appropriate treatment vessels.

Two types of treatment vessels were employed in the salinity-temperature tolerance studies, depending on type of experiment and equipment availability. One method employed 200 ml finger bowls, which then received a treatment cohort of animals. The other method involved placing single animals in 8 dram shell vials which were stored in racks. Except as noted below for Experiment 7, the test vessels were barren of any substrate or food material. Test salinities were achieved by combining Marine Science Center supply water (from the lower Yaquina Bay) with fresh water from upper Yaquina Bay. Gentle heating of the lower bay water produced hyper-saline salinities. Water in the test vessels was normally changed every 1-2 weeks depending on experiment length.

Animals (in capillary tubes) were sorted by sex and size into appropriate treatment vessels. Three categories were recognized: males, females and juveniles. Juveniles were those animals less than 2.5 mm telson-to-rostrum length. No distinctions were made by size or maturity for adult animals, with the result that gravid and non-gravid females were mixed, but were in roughly equal proportions per treatment.

In the tolerance experiments, groups of 10 to 20 animals of each sex type (including juveniles) were exposed to each salinity level at a single temperature. In later experiments a factorial combination of temperatures and salinities was used. As indicated in Table 1, initial experiments (4 and 6) investigated tolerance within a wide salinity range while later experiments (7,9,10 and 11) focused on the 0-20 ppt range. Experiment 7 also investigated the effects of silt on survival: an eye-dropper full of interstitial (silty) water from native sediments collected from the field sites was added every other day to half of the bowls, representing each sex-salinity combination. The water was changed after one hour in both silt and non-silt vessels.

Table 1. Conditions of collection, maintenance and testing for Corophium salmonis utilized in salinity-temperature tolerance experiments.

	4		4		6		Experiment		9		10		11	
	(Group 1)		(Group 2)				7							
Collection site	GB*	GB	GB	GB	GB	GB	DS**	DS	DS	DS	DS	DS	DS	DS
Collection date	6/24	6/24	6/24	6/24	6/24	6/24	7/26	7/26	7/26	7/26	8/16	8/16	8/22	8/22
Maintenance (days)	7	13	13	13	24	24	10	6	6	3	3	3	11	11
Test vessel	bowls	bowls	bowls	bowls	bowls	bowls	bowls	vials	vials	vials	vials	vials	vials	vials
Test temperature (°C)	7	7	7	7	14	14	14	14	14	14	14	14	14	14
Test salinities (ppt)	0,10,20 30,40, 50,60	5,15,25	5,15,25	5,15,25	0,5,10, 15,20, 25,30	0,5,10, 15,20, 25,30	0,5,10, 15,20	0,5,10, 15,20	0,5,10, 15,20	5,10,20	5,10,20	5,10,20	5,10,20	5,10,20
Cohort size	10	10	10	10	10	10	20	16	16	16	16	16	16	16
Test length (days)	31	25	25	25	16	16	25	13	13	13	13	13	13	13

* Grays Bay

** Desdemona Sands

Exposure to test salinities were on an acute basis, except for Experiment 7. That is, animals were abruptly transferred from the culture to the test salinity without acclimation. For Experiment 7, animals were serially transferred across 5% salinity increments per day until the test salinity was achieved. Transition to different temperatures was not acute, in that test vessels (with animals) were placed in the temperature control apparatus and allowed to assume the test temperature.

Data analysis employed the methods of analysis of variance (ANOVA), followed by comparisons of means using the least significant difference (LSD) test ($p=.05$). The data analyzed was group survival rate (fraction alive after a certain number of days) transformed by the arcsine-square root function (Sokal and Rohlf 1981). Probit analysis was not employed since the data set was small and individual tests usually did not allow the computation of median lethal levels or times.

Behavioral Studies

Behavioral responses to salinity level were studied in two ways. In the first method (Experiment 5), surviving animals from Experiment 4 were abruptly exposed to a different salinity to determine if this would cause their exodus from the capillary tubes which had been their residence for 3 to 4 weeks. The second approach (Experiments 14-19), offered a choice of two salinities to test cohorts of 20 or 30 animals using a small partitioned chamber as described by McLusky (1970). The animals could move from one side of the chamber to the other (i.e., choose between test salinities) by crawling up a slope made of nitex netting which was stretched over the center partition. Minimum water depth (at the partition where the two water masses abutted) was 1.0 - 1.5 mm. Half of each test group was initially placed in each chamber half, and the number of animals in each half was counted at specified intervals. All preference experiments used animals collected on August 22 at the Desdemona Sands site. Preparatory to each experiment, the test animals were acclimated for 30 minutes at the average test salinity (e.g., 7.5 ppt for 5 vs. 10 ppt). The tests were conducted at 15 degrees C.

Experiment 14 investigated the effects of test chamber orientation to determine if this would affect animal distribution. Each chamber half was filled with 5 ppt salinity water and provided 10 test animals (mixed sexes). Counts were made after 40 minutes, when the box was rotated 180 degrees. A second count was made after another 40 minutes and a third after about 16 hours.

Experiment 15 investigated appropriate experiment length by assessing test animal distribution every 15 minutes for 1 hour. The test used salinities of 0 and 30 ppt, and 17 animals (mixed sexes).

In Experiment 16, test cohorts of 30 animals each were exposed to choices involving 0, 5, 10 and 20 ppt salinities. Counts were made at 30 minutes (when the boxes were rotated) and again at 1 hour. Separate tests were made for males and females. Experiments 17 and 18

replicated Experiment 16.

Analysis of the salinity choice data used G-tests with Williams' correction for small sample size, as described by Sokal and Rohlf (1981).

RESULTS

Field Studies

Diel salinity data were collected on three occasions at Station 11 (Figure 2). On August 23-24, bottom salinities ranged from lows of 1-4 ppt to highs of 8-12 ppt. During a short series collected on September 9, the range was 1-17 ppt, and during a complete diel series made September 14-15 the range was 2-8 ppt. Among the three series, highest observed bottom salinity (17.2 ppt) occurred during a spring tide when predicted tidal depths progressed from -.4 m (-1.2 ft) to 2.6 m (8.5 ft) to .2 m (.7 ft). In all three series, it may be seen that salinity highs and lows lagged times of predicted tidal highs and lows by 1-2 hours. It is also clear, especially as shown by the September 7-8 series, that salinity peaks could be very short-lived.

Maximum observed bottom salinity varied considerably among stations and by date (Table 2). The highest value was 19 ppt on October 27 at Station 13, although Station 12 more frequently had the highest value. Station 15, located at the mouth of the Lewis and Clark River, experienced the lowest salinities, the maxima there ranging from 1.8-6.5 ppt. This indicates that a salinity gradient existed from this inner bay station to the outer bay stations. This gradient is examined further in Figure 3, which shows vertical salinity profiles for August 10 and October 27. Salinities in the early profiles generally followed a horizontal gradient at all depths, with the exception of Station 12 where low surface salinities apparently resulted from Skipanon River outflows. On October 27, however, all of the profiles appeared similar, suggesting that a single water mass occupied all of the stations and that variations in bottom salinity were created only by differences in station depth. The result of these spatial and temporal patterns was that Station 15, located at a shallow tidal depth and in the most up-bay location, experienced the lowest salinities of all the stations. Salinities of 15 ppt and higher were recorded at all stations except Station 15, where the maximum was 6.5 ppt.

Measured high-tide temperatures ranged from 21.6 degrees C (surface temperature at Station 15, August 10) down to 11.8 degrees C (7 m depth at Station 13, October 27). Until October 27, temperatures rarely dropped below 16 degrees C, and generally exceeded 17 degrees C. This pattern is illustrated in Table 3, which shows temperature profiles for Station 13. During August 10 to September 16, temperatures declined slowly from the 17-19 degrees C range to the 16-17 degrees C range, but then declined more abruptly to 12-13 degrees C on October 27.

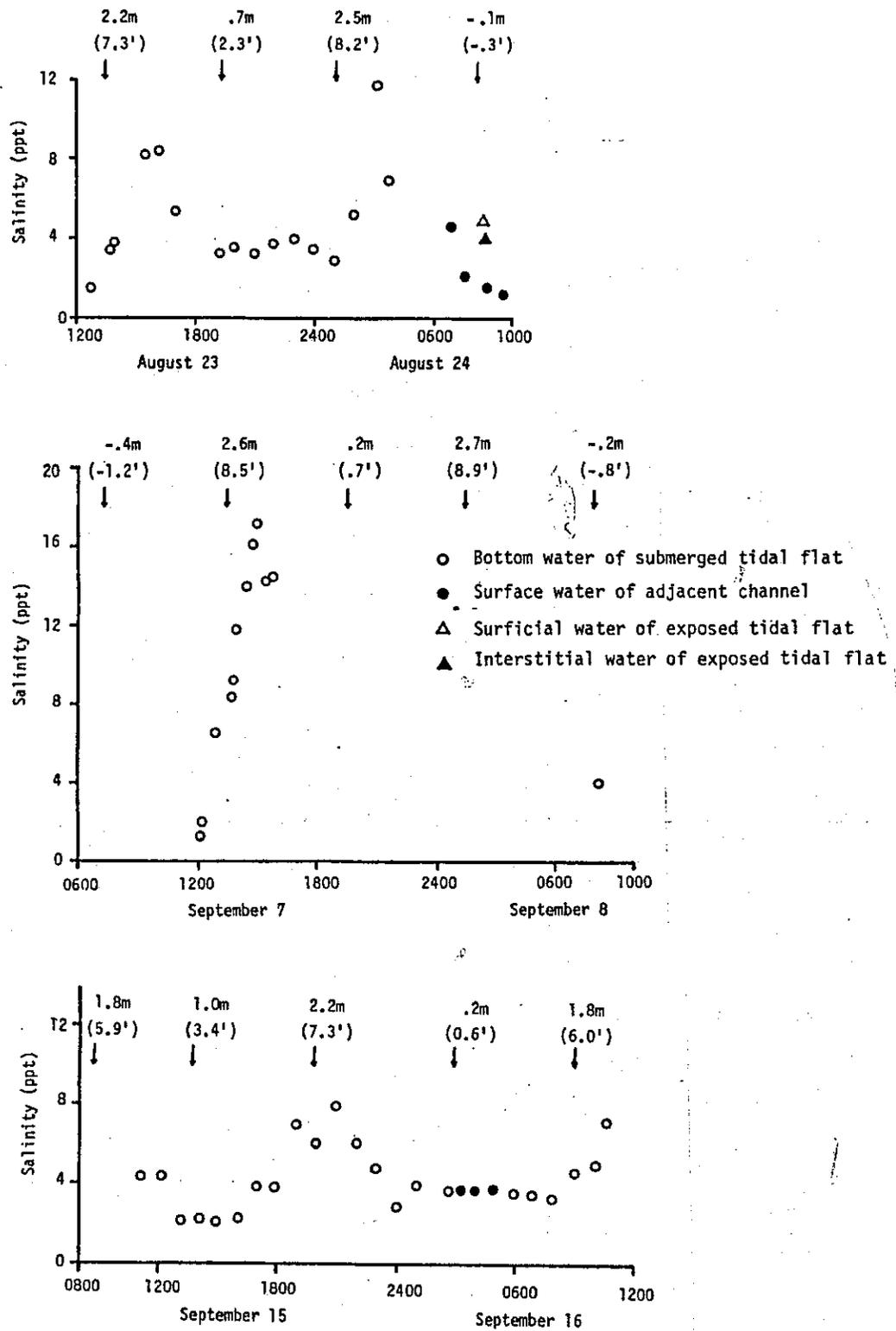


Figure 2. Diel changes in salinity at Station 11 on three dates in 1983.

Table 2. Bottom salinities at high tide. Time of observation, and time and height of high tide are shown.

Date	High Tide		Station 11		Station 12		Station 13		Station 14		Station 15		Station 19	
	Time (Hrs)	Height	Time	Sal (ppt)										
July 11	1424	2.3m (7.7')	--	---	--	---	--	---	1530	2.0	1520	0.5	--	---
July 26	1436	2.2m (7.2')	1635	5.0	1620	9.0	1610	8.0	1605	6.0	1550	5.0	--	---
August 10	1443	2.5m (8.3')	1530	10.0	1520	17.5	1550	13.7	1600	9.5	1615	1.8	--	---
August 23	1331	2.2m (7.3')	1608	8.5	1420	9.2	1440	8.0	--	---	--	---	1430	9.7
August 24	0106	2.5m(8.2')	0305	11.8	--	---	--	---	--	---	--	---	--	---
	1402	2.2m (7.4')	--	---	--	---	--	---	1445	8.5	1530	6.1	--	---
September 7	1329	2.6m (8.5')	1500	17.2	1221	9.7	1235	8.7	--	---	--	---	1229	9.9
September 15	0823	1.8m (5.8')	1202	4.4	--	---	--	---	--	---	--	---	--	---
	1947	2.2m (7.3')	2100	8.0	--	---	--	---	--	---	--	---	--	---
September 16	0929	1.8m (6.0')	1027	6.5	1047	8.0	1107	12.3	1121	11.0	1145	7.5	1100	12.4
October 27	1720	2.4m (7.9')	1711	13.0	1737	15.7	1750	19.0	1755	15.0	1804	6.5	1742	17.4

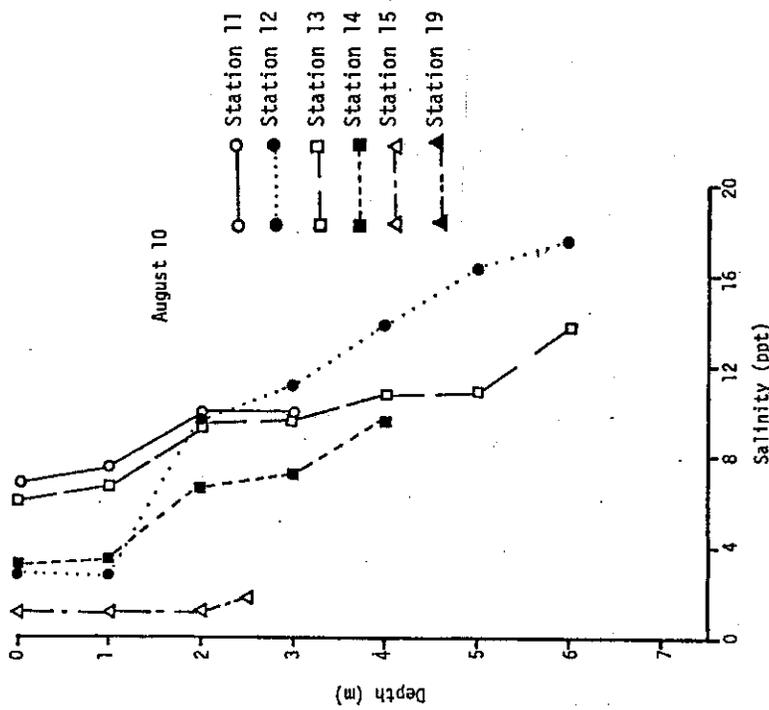
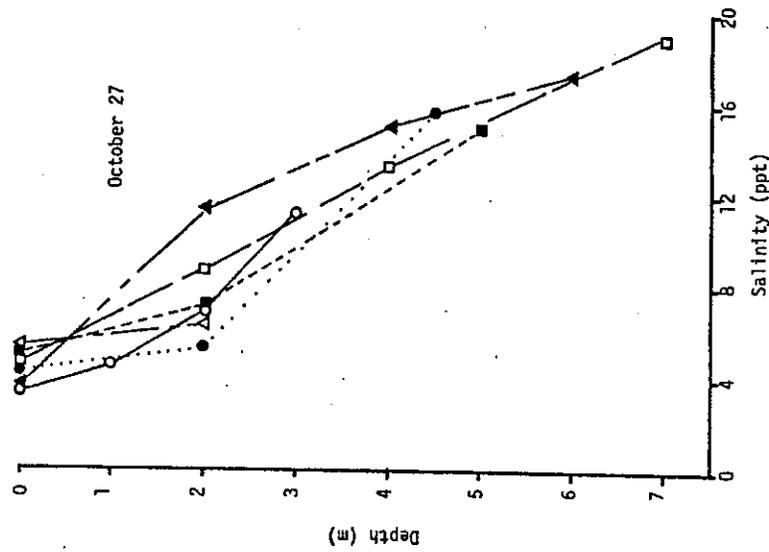


Figure 3. High-tide salinity profiles for Stations 11-15 and 19 on two dates in 1983.

Table 3. High-tide temperatures ($^{\circ}\text{C}$) according to depth at Station 13.

<u>Date</u>	<u>0</u>	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>	<u>7</u>
August 10	19.3	19.8	18.2	18.2	17.9	17.8	17.2*	----
August 23	18.7	18.5	18.4	18.4	18.1	18.2*	----	----
September 7	17.6	17.6	----	17.6	----	17.6	----	17.5*
September 16	17.4	17.3	16.7	16.5	16.2*	----	----	----
October 27	13.1	----	12.9	----	12.3	----	----	11.8*

*bottom

With minor exceptions, Corophium salmonis was the dominant Corophium species at all stations. Generally, this species comprised 95% or more of the individuals identified to species (about 50 per sample, where available), the remaining individuals being C. spinicorne. C. spinicorne occurred in greatest, and sometimes dominant, numbers at Station 15.

F.W. Station had fewer C. salmonis

At Station 11, C. salmonis densities fluctuated between 36,000 and 53,000/m² from July 12 through September 8 (Table 4). These were the highest densities of any of the stations. By September 21, the density had dropped to about 8,000/m² and by October 27 to 14/m². This pattern of mid-summer highs followed by drastic declines occurred at all of the stations, although with variation in density level and timing.

At Stations 12 and 13, initial densities varied between 11,000 and 24,000/m², and began declining in late August. At Station 14, initial densities were about 10,000/m² and also declined in late August.

Initial densities at Station 15 were lower at about 2,000 to 10,000/m² than at the other stations, but the densities declined more slowly. The low C. salmonis July 26 density of 1,633/m² at Station 15 co-occurred with a relatively high C. spinicorne density (about 6,000/m²). C. spinicorne commonly contributed about 20 % of the Corophium count at this station, but in the July 26 collection comprised nearly all of one sample and most of a second sample. Probably, colonies of both species were patchily distributed at this station due to habitat variation created by the proximity of the channel leading into the Lewis and Clark River.

Station 19 was not sampled until August 23, but exhibited the same rapid population decline after this date found at Stations 12 and 13.

Tolerance Studies

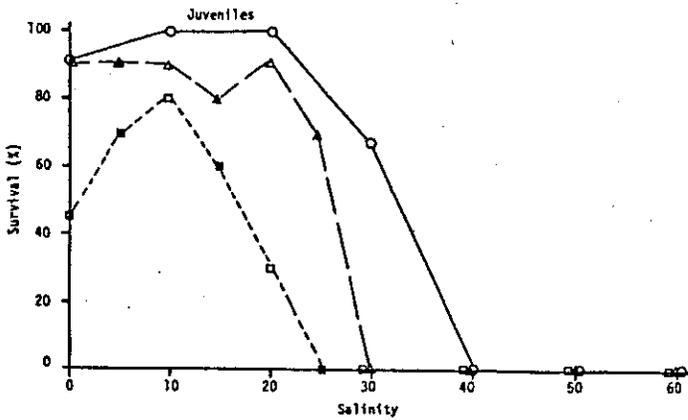
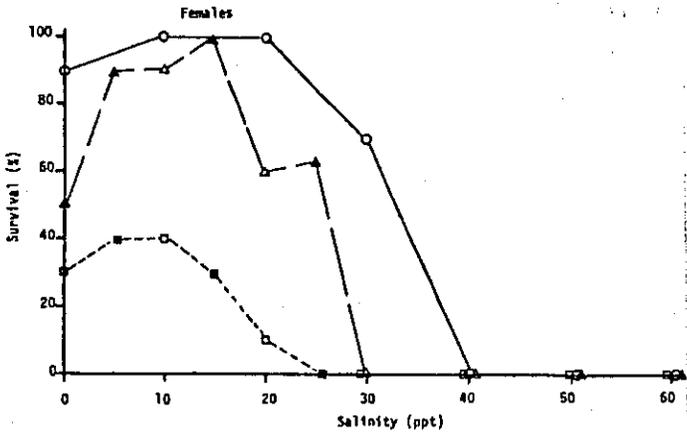
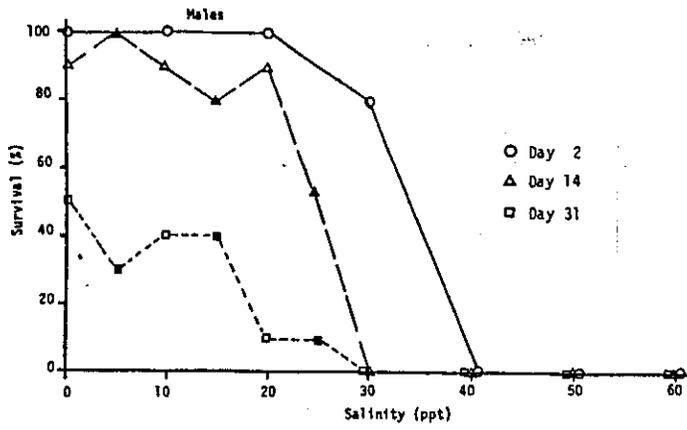
In both Experiment 4 and Experiment 6, C. salmonis was exposed to a wide range of salinities at a single temperature.

Experiment 4, conducted at 7 degrees C, initially included salinities of 0, 10, 20, 30, 40, 50 and 60 ppt. However, at day 7 additional treatments of 5, 15 and 25 ppt were added. Inspection of the survivorship results indicated that the closest similarity between results of the two treatment groups was obtained when the second group (5, 15 and 25 ppt) was assumed to have started at the same time as the first group. This is apparent in Figure 4, which shows 2-day, 14-day, and 31-day survivorship patterns based on this earlier starting date. Note that the 2-day survivorships include only the first treatment group because of this assumption for starting date. Rapid mortalities occurred in Experiment 4 at salinities of 40-60 ppt, where all animals died within one day. At lower salinities, survivorship in males, females and juveniles all tended to be moderate near 0 ppt, peaked near 5-10 ppt, and dropped sharply toward 30 ppt.

Table 4. Corophium salmonis densities (number per m²) at Stations 11-15 and 19, July 12 to October 27, 1983.

<u>Date</u>	<u>11</u>	<u>12</u>	<u>13</u>	<u>14</u>	<u>15</u>	<u>19</u>
July 12	48,378	23,062	23,858	10,525	4,572	--
July 26	36,007	19,212	11,098	10,671	1,633	--
August 10	52,950	17,914	16,174	10,167	10,638	--
August 23	40,937	8,773	8,109	503	6,790	10,220
September 8	45,797	408	24	26	3,971	178
September 21	8,385	23	9	56	1,019	14
October 27	14	33	16	20	0	23

Experiment 4



Experiment 6

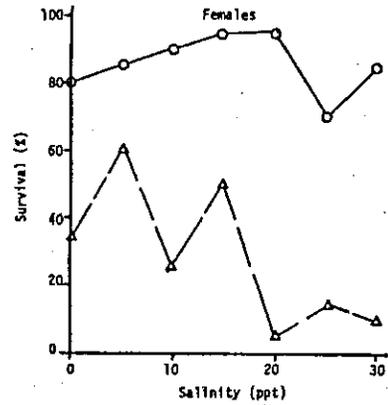
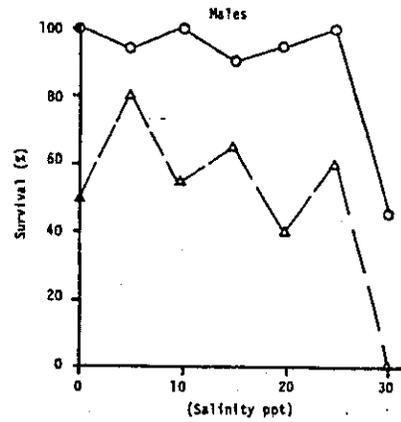


Figure 4. Survival of *Corophium salmonis* according to salinity in Experiment 4 (conducted at 7°C) and in Experiment 6 (conducted at 14°C).

Table 7. Factor level means and associated statistics for Experiments 9, 10 and 11, based on transformed 13-day survival rates. All pairwise comparisons were significant except the 5 ppt vs. 20 ppt salinity comparison.

Factor	Means			ANOVA (p)	Stand Error	LSD (.05)
	Male	Female	Juvenile			
Sex:						
	.6177 (33.5)*	.7966 (51.1)	.9304 (64.3)	<.0001	.0253	.0719
Temperature (°C):	7	14	21			
	.9487 (66.0)	.8284 (54.3)	.5676 (28.9)	<.0001	.0253	.0719
Salinity (ppt):	5	10	20			
	.7612 (47.6)	.8675 (58.2)	.7161 (43.1)	<.001	.0253	.0719

*Equivalent percentage values in parentheses.

(without further rotation) it was 6-14. Since these results did not clearly exclude the possibility that animals favored one side, ensuing choice tests (Experiments 16-18) included distributional counts at 30 minutes when the boxes were rotated, and again at 60 minutes.

Experiment 15 employed a 0 vs. 30 ppt salinity choice to establish a suitable experiment length. The 0-30 ppt counts at 15 minute intervals were 14-3, 15-2, 14-3, 14-3. On this basis, a half hour duration was deemed adequate, although Experiments 16-18 were run longer to accommodate the rotation factor.

One-hour distributional counts from the multiple salinity preference tests conducted as Experiments 16-18 are summarized in Figure 5. Part A of Figure 5 represents the frequency with which each test salinity (0, 5, 10 and 20 ppt) was chosen in all the individual salinity-pair tests. These sums range from 224 animals (21%) for 5 ppt to 308 animals (28%) for 0 ppt, and show that none of the four salinities was strongly favored.

Part B of Figure 5 breaks these results down according to sex for each salinity test pair. The results are equally ambiguous in this form, since according to G-tests only 4 of the 12 tests produced distributions which significantly differed from the 1:1 distributional ratio established at the beginning of each test. The four salinity tests producing significant results showed 0 ppt > 5 ppt and 20 ppt > 10 ppt for females, and 10 ppt > 5 ppt and 0 ppt > 10 ppt for males. Neither these four test results nor a combination of significant and non-significant results provide a clear picture of salinity preference within the 0 to 20 ppt salinity range tested. The results do not appear to have been influenced by box rotation. Analysis of animal distribution before and after rotation showed that the left-oriented chamber lost animals in 17 incidences (55 animals) and gained animals in 13 incidences (36 animals) after rotation.

The half-hour (pre-rotation) distributional patterns provided no insights into salinity preference beyond the one-hour results presented and therefore are not included.

DISCUSSION

Population declines began at some stations in late August. By this time, at least one station had experienced salinity >17 ppt (Station 12 on August 10; Table 2). Due to increasing uniformity of the water mass occupying Youngs Bay, other stations of similar depth must also have encountered salinities in this range, although they were likely of short duration and were not recorded. Thus, the population declines may have been a response to high-tide salinity excursions.

Population declines at the several stations did not follow the same time pattern. Stations 12, 13, 14 and 19 exhibited pronounced declines in late August or early September while populations at Stations 11 and 15 declined more slowly, with densities still

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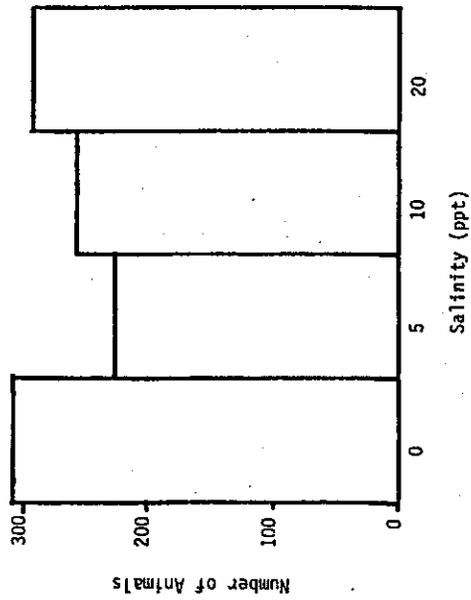
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A



B

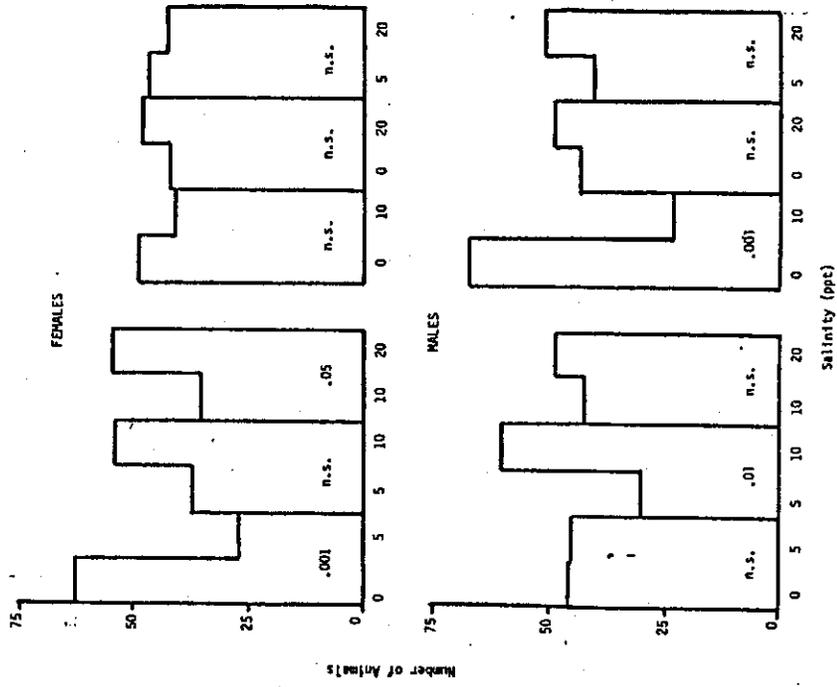


Figure 5. Results of salinity choice Experiments 16-18, based on one-hour distribution counts. A. Cumulative choice, expressed as the sum of all animals (over experiments and sex) choosing each of the four test salinities. B. Choice according to each pair of test salinities (animals summed over replicate experiments.) Probability value is provided within each histogram (n.s. = non-significant at .05 level).

>1,000/m² on September 21 (Table 4). This pattern of declines seems more relatable to tidal level (Stations 12, 13, 14 and 19 were subtidal and Stations 11 and 15 were intertidal) than to geographic location in the estuary. It is possible that emigration or death was more rapid at deeper stations due to their higher salinities, or that a late summer subtidal-intertidal migration occurred independent of salinity changes.

Temperature as the immediate cause of the population declines does not seem likely, since the declines began while temperatures were still high (>17 degrees C) (Table 3). This view is supported by the findings of Davis (1978) and Wilson (1983) that populations in the Youngs Bay area contained juveniles and mature females through September. Thus, temperature related reproductive turn-down is unlikely to have caused the population declines.

Population changes in intertidal areas of the upper estuary contrast with the patterns documented here for the Youngs Bay area. In a Grays Bay intertidal population studied by Wilson (1983), density stayed near 10,000/m² from August to November, and then steadily increased to a high of 30,000 in February, to be followed by a steady decline into the next summer (Figure 6). Data provided by McConnell et al. (1978) show that several intertidal populations of Miller Sands followed a similar summer-low, winter-high pattern (Figure 7). Based on Wilson's population size-structure analysis, these winter increases were created by immigration and not by reproduction. Winter data are not available from the present study for the Youngs Bay populations, but the summer and fall data suggest that populations at all of the stations followed the same summer-high, winter-low pattern earlier documented by Wilson (1983) for her Desdemona Sands station (the same as Station 11) (Figure 6). Support for this conclusion is provided by seasonal benthic studies conducted by Higley et al. (1982 a and b) at several intertidal, shallow subtidal, and deep channel stations near the mouth of Youngs Bay. C. salmonis populations at all 10 stations followed the summer-high, winter-low pattern.

The tolerance and behavioral response experiments conducted on Corophium salmonis employed animals collected at Grays Bays and Desdemona Sands of the Columbia River Estuary. All animals were maintained in static cultures (with aeration) utilizing sediments and water obtained at the collection site. While vigorous test animals were extracted from these cultures for up to 3 weeks after collection, the longevity and nutritional condition of the animals under these conditions were not determined. It was observed in Experiment 4 that survival patterns among animals which were introduced to experimental conditions on different dates (that is, groups 1 and 2) were more consistent when the starting dates of the two groups were assumed to have been the same. That is, the second group died faster than the first group. In part, this may have resulted, from a longer exposure of the second group to the 15 degree C culture temperature (Experiment 4 was conducted at 7 degrees C). However, it also seems probably that the cumulative stresses of culture in the buckets without replenished food resources combined with the animal's short life span (on the order of a few months) to predispose longer-cultured animals to

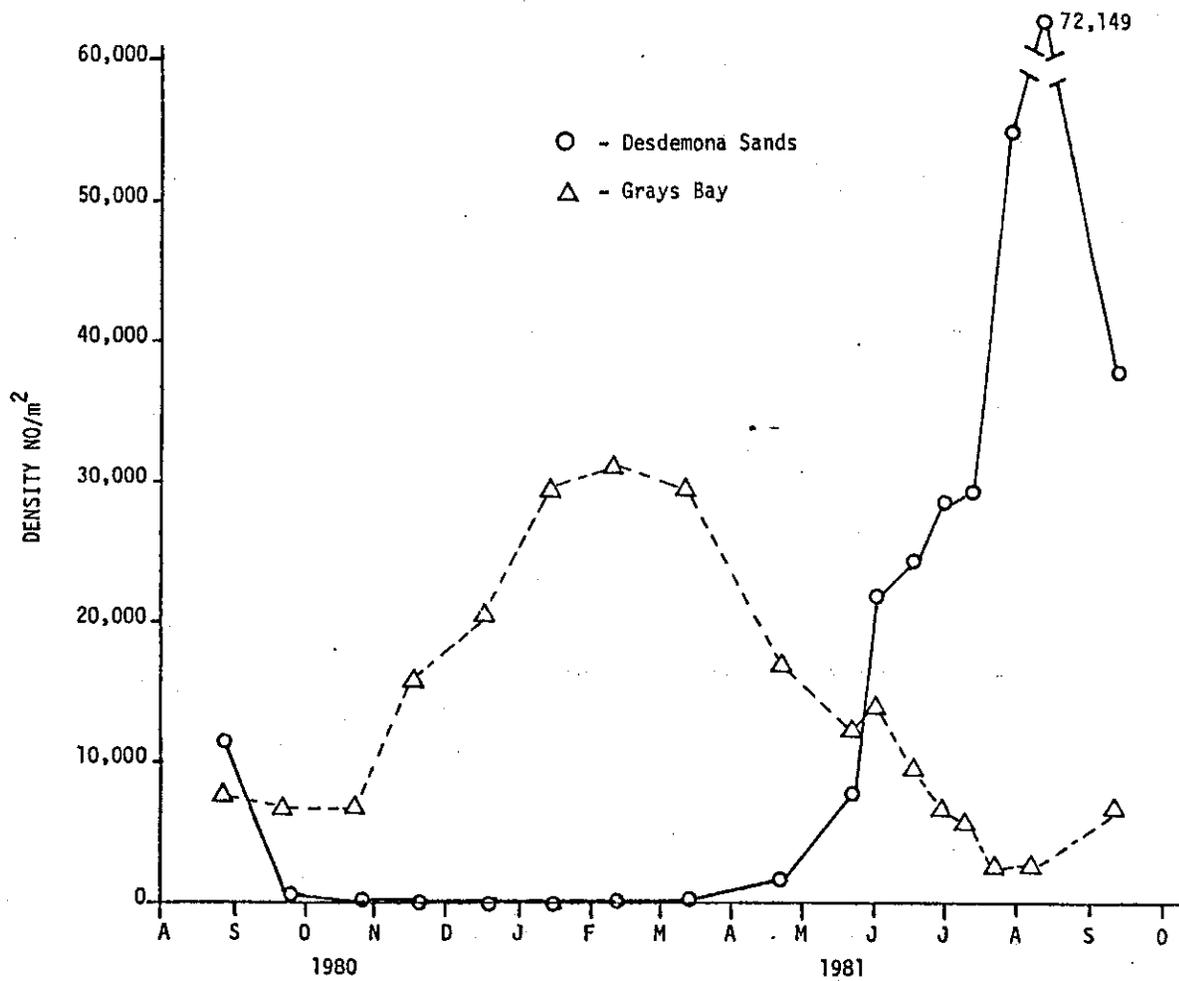


Figure 6. Changes in Corophium salmonis density at the Grays Bay and Desdemona Sands stations studied by Wilson (1983).

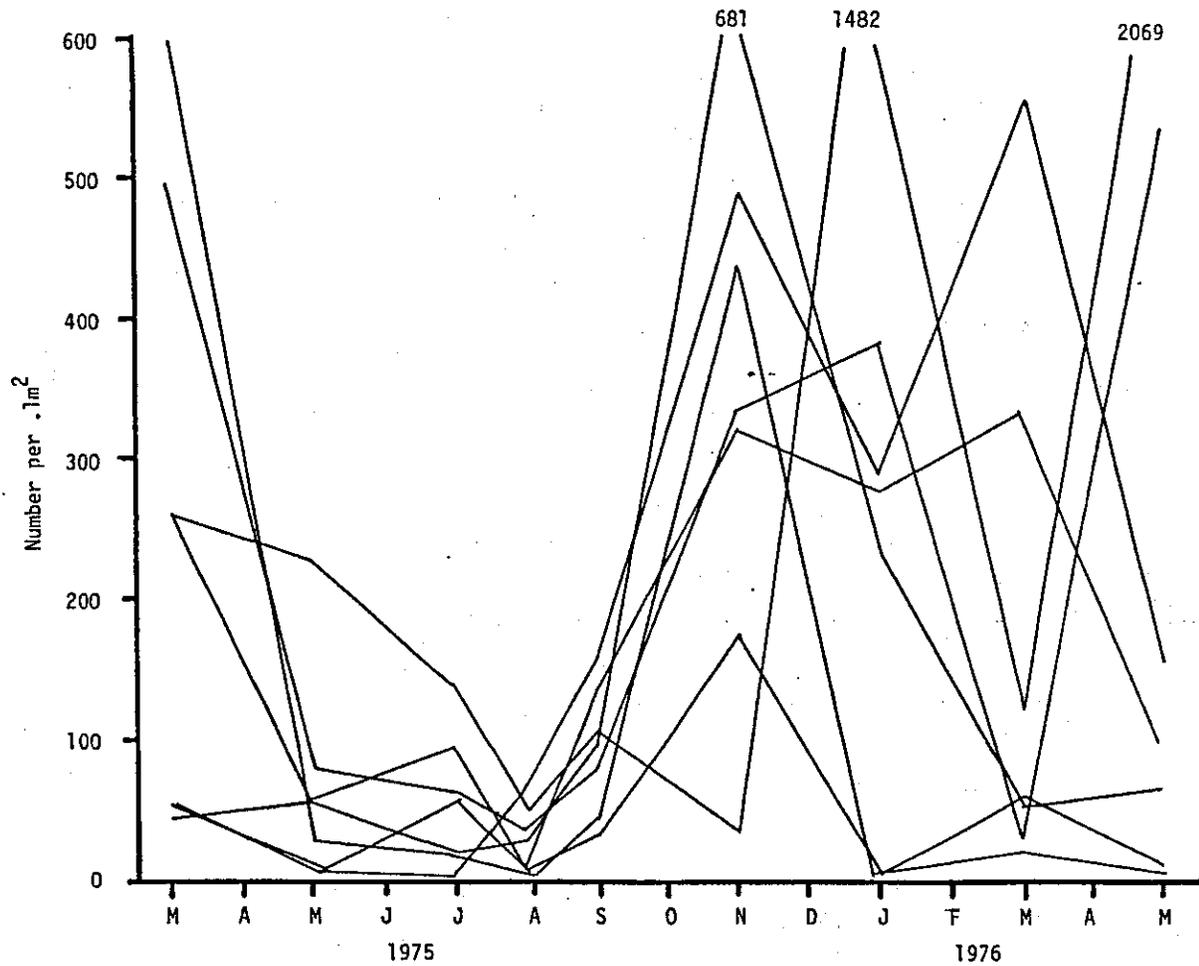


Figure 7. Changes in *Corophium salmonis* density at seven Miller Sands stations studied by McConnell et al. (1978).

earlier deaths. Because of these influences and because the field populations underwent continuous changes in size structure and animal maturity, the results were examined to determine patterns of survival across test conditions rather than to establish absolute survival rates according to exposure time, which would vary with test conditions and test animals. In analysis of the survival data, variance due to differences in test conditions (e.g., test vessel or temperature) or animals (e.g., collection date, culture length) was isolated by blocking the data according to experiment where appropriate. For Experiments 9, 10 and 11, and less so for Experiments 4 and 6, variance due to experiments formed a considerable portion of the total variance in the analysis of variance.

In none of these data tests subjected to ANOVA were there significant interactions among the factors tested (temperature, salinity, sex and availability of silt). It was thus possible to summarize animal responses according to the separate factors.

Temperature responses were tested only in Experiments 9, 10, and 11 where the results were clear in showing that survival decreased with increasing temperature (7, 14, and 21 degrees C) irrespective of both salinity (5, 10 and 20 ppt) and sex (males, females and juveniles). Such results would be expected on metabolic considerations, especially where food was denied, as was the case here. Under normal conditions, 7 to 21 degrees C is the temperature range which Columbia River populations would experience through a yearly cycle. However, during the winter intertidal populations might be exposed to near freezing temperatures at low tide, and such conditions might reduce survival rates as compared to the 7 degree C temperature tested.

Salinity responses were defined in all three data groups analyzed. Experiments 4 and 6 demonstrated that rapid and complete mortalities occur at salinities of 40 ppt and higher at both 7 and 14 degrees C experimental temperatures. Continued exposure (to 14 days) insured the deaths of nearly all animals exposed to 30 ppt. Below this salinity, the pattern of survival appeared to favor salinities in the 5-10 ppt range. An equation expressing the relation of salinity to survival based on Experiments 4 and 6 predicted maximum survival at 7.8 ppt. In comparison, a similar equation developed for the data of Experiment 7 predicted maximum survival at 10 ppt; and the replicate tests of 5, 10 and 20 ppt provided by Experiments 9, 10 and 11 found survival at 10 ppt to significantly exceed those at both 5 and 20 ppt.

These results indicate that optimal conditions for survival were near 10 ppt for Corophium salmonis collected in the brackish water zones of the Columbia River Estuary. It is possible, of course, that animals collected in different salinity regimes would express differing optima. In the present tests, culture water was 2 to 5 ppt, while salinities at the sites probably varied from 1 to 17 ppt at Desdemona Sands and 1 to 6 ppt at Grays Bay, based both on salinity measurements made in the present study and by Wilson (1983), and on model predictions provided by Jay (1984). Assuming acclimation to field conditions, a slightly higher optimum might be expected from the

Desdemona Sands population than from the Grays Bay population. This in fact occurred, although the difference (7.8 vs. 10 ppt) was minor. Comparisons among more widely separated populations, especially including animals from totally freshwater habitats, would help assess the euryhalinity of the species.

The demonstration that salinities near 10 ppt provided for optimal survival rate by C. salmonis is consistent with its brackish to freshwater distribution in the Columbia River Estuary, and places it with several other Corophium species which favor the fresh end of the salinity gradient. Among these species are C. spinicorne (also a resident of the Columbia River Estuary), C. lacustre and C. riplateense (Crawford 1937; Shoemaker 1949). Most Corophium species appear to favor higher salinities, although the genus as a whole is euryhaline, based on Crawford's (1937) review.

In some instances, as in the case of C. volutator and C. arenarium, differing substrate and salinity affinities create an at least partial ecological separation of co-existing species. Meadows (1964) demonstrated that C. arenarium preferred sandier soils than C. volutator, and Mills and Fish (1980) showed that in terms of molting, egg laying and hatching, and survival, C. arenarium was more successful than C. volutator at high salinities (>45 ppt) but was less successful at low salinities (<10 ppt). These authors conjectured that the higher salinity tolerance of C. arenarium would help insure its survival in sandy substrates where evaporation at low tide elevated interstitial salinities.

In the Columbia River Estuary, C. salmonis and C. spinicorne have mostly been found in different substrates but in similar salinity zones. C. salmonis strongly dominates soft sediment habitats, while C. spinicorne dominates rock, piling, vegetation and the other hard surface habitats (Higley and Holton 1975). C. spinicorne, however, is not restricted to such habitats, as demonstrated by its sporadic abundance at Station 15 in the present study, and by such studies as Smith (1953), Felice (1958) and Eriksen (1968) who found the species on sand and rubble bottoms. Comparative studies of C. salmonis and C. spinicorne substrate and salinity relations would help interpretation of the distributions and interactions of these two trophically important species.

In testing the salinity tolerance of C. salmonis, animals were transferred directly from the culture medium to the experimental salinity, except in Experiment 7. This acute exposure of Corophium specimens to the test salinities was used also by Mills and Fish (1980), McLusky (1967) and Shyamasundari (1976), and does not account for changes in tolerance which might accrue through the period of steadily increasing or decreasing salinities of a tidal exchange. It is possible then that mortalities among C. salmonis would be less dramatic at salinities >30 ppt or that the optimum would shift, should test conditions simulate tidal rates of salinity change. That the optimum remained at 10 ppt in Experiment 7 where salinity increments were 5 ppt per day is evidence of a stable response. Whether it is or not, however, it seems evident from both laboratory and field work

that C. salmonis responds best to moderate and low salinities.

Survival rate by sex did not present a consistent pattern across the several experiments. In Experiments 4 and 6, the relation was males>females>juveniles, but the differences were non-significant. This is explained by the fact that the relation differed between the two experiments: in Experiment 4 juveniles>males>females, and in Experiment 6 males>females>juveniles (Appendix 1). The results in Experiment 7 were females>males>juveniles, with males and females significantly greater than juveniles, and in Experiments 9, 10 and 11 were juveniles>females>males. All differences were significant in Experiments 9, 10 and 11, and the relation was the same in all three experiments.

In most instances, then, juveniles had the highest survival rates, a result predictable on the basis of the species' short life span. The anomalous results of Experiment 7 where juvenile survival was relatively short has no obvious explanation in experimental conditions or material. The relation of females>males>juveniles did not vary with availability of silt, although it is possible that the acclimation procedure favored adult animals.

In the work of Mills and Fish (1980) tolerance to salinity at high temperature by C. volutator and C. arenarium followed the relation gravid females>non-gravid adult females>adult males. The present results generally conform to this order in that females>males (gravid and non-gravid females being grouped together) in terms of survival rates under experimental conditions. The implication of these results is that determination of the acceptable salinity range for the species must take into account different survivability according to sex, maturity state and individual size. For C. salmonis, adult males would appear to limit species distribution. However, other life history events than adult survival must also be considered. These include molting, egg laying and hatching, embryonic growth and survival, and individual growth, any of which might limit population viability. Mills and Fish (1980) determined that for both C. volutator and C. arenarium breeding and molting were more sensitive to low salinities than was embryonic development. Careful study of reproductive and growth characteristics according to salinity is needed to determine the acceptable salinity range for viable C. salmonis colonies, as opposed to transient or non-reproductive colonies.

The remaining factor influencing survival which was investigated was food availability, as represented by the regular addition of silt to some test groups in Experiment 7. Animals receiving silt could be seen filling their guts, and survival overall was significantly higher (31 vs. 19%) among fed animals through the 19-day test period. Since the water was changed after 1 hour, the effect was not likely to have been caused by substrate buildup. It may be presumed then that mortality rates in other experiments were increased by the effects of starvation. Were food to have been provided at high salinities (30 ppt and higher), however, mortality would most probably have still been high, since the deaths at these salinities occurred very

quickly.

A diffuse pattern of responses by C. salmonis was observed in the replicated testing of salinity choice which composed experiments 16-18. No salinity preferendum could be established within the 0-20 ppt range tested.

McLusky (1970) demonstrated a salinity preferendum of 10-30 ppt for C. volutator, which has a more marine distribution than C. salmonis. In McLusky's study, which used essentially the same procedures and apparatus as the present study, C. volutator preferred higher salinities when offered salinity pairs in the 0 to 10 ppt range, and preferred lower salinities when offered salinities of 30 to 40 ppt. In the 10 to 30 ppt range, no preference was evident. In an earlier study, McLusky (1967) determined that optional survival for starved animals occurred at 20 ppt, although animals provided mud survived at similar rates through a 5 to 45 ppt salinity range. Many animals survived at 2 ppt, but successful molting required at least 5 ppt. Blood ionic concentration varied with ambient salinity in the 20 to 50 ppt salinity range, but exhibited hyperosmotic regulation below 20 ppt.

The distributional, physiological and behavioral attributes of C. volutator present a consistent picture of a euryhaline species adapted to the more saline portions of the salinity gradient. In comparison, C. salmonis appears to occupy a fresher portion of the salinity spectrum, but is also euryhaline in its behavioral responses, since no choice pattern could be demonstrated in the 0 to 20 ppt range. It seems likely that this range holds the same relation to C. salmonis as the 10 to 30 ppt does to C. volutator: a wide salinity preferendum which centers near a demonstrable survival optimum. Choice experiments involving salinities higher than 20 ppt would probably demonstrate the species' preference for lower salinities. Such preference is suggested by the results of Experiment 15 in which 0 ppt was preferred to 30 ppt, but confirmation is needed.

Sudden salinity increases or decreases as provided in Experiment 5, evoked essentially no response by animals which had been long-term residents of capillary tubes. This would seem to suggest that animal migration in the field is not stimulated by salinity elevations. However, several factors restrict this conclusion:

1. The test animals had had a long laboratory exposure and may have been unfit;
2. The capillary tubes and other test conditions may have poorly simulated natural field conditions; and
3. Higher salinities than those tested may produce a response.

In support of the first point, freshly collected animals were observed to regularly exit capillary tubes during water changes involving salinity changes for culture or acclimation purposes.

Response to salinity change is therefore not yet adequately studied with respect to the possibility that migration may be stimulated by salinity excursions.

McLusky (1968) established a probable pattern of salinity stimulated migration by C. volutator in the Ythan Estuary (Scotland). The species had low densities in regions having interstitial salinities below 5 ppt, and was absent below 2 ppt. He suggested that the species was able to colonize an area where salinities exceeded 2 ppt, but required higher salinities (>7.5 ppt) for successful breeding.

In contrast to C. volutator which is limited upstream by low salinities, C. salmonis is limited downstream by high salinities. The mechanisms of these responses appear different. For C. volutator, critical low salinities are created at low tide by river water, or by rainfall on exposed tidal flats. For C. salmonis, critical high salinities are created by flood-tide inflows of marine water. McLusky (1968) felt that interstitial water represented the immediate environment of C. volutator and thus determined distribution. However, Corophium species are tube dwellers and would be more affected by overlying water which they circulate through their tubes than by interstitial water (Sanders, Mangelsdorf and Hampson, 1965). Therefore, the distribution of both Corophium species is most likely to be determined by salinity extremes in the over-flowing water rather than by the less changeable salinities of interstitial water.

McLusky's (1968) study provided no indication as to the fate of animals which emigrated from areas of decreasing salinities. In the Columbia River Estuary, the present study and the studies by Wilson (1983) and McConnell et al. (1978) suggest that C. salmonis may move upriver and/or into shallower habitats in response to increasing salinity or to changes in some other environmental factor.

Population movements by C. salmonis may have strong trophic impacts, since depopulated areas offer few alternative infaunal prey species to fish feeding in the Youngs Bay area. It appears from the present study and from Higley et al. (1982 a and b) that C. salmonis populations may essentially disappear from this area in the August and September, which includes a substantial portion of the warm weather feeding period. On the other hand, upriver C. salmonis populations (in the intertidal zone, at least) increase during the winter and may provide spring-time colonists for the downriver area.

Based on existing distributional and salinity-tolerance data, there remains reason to be concerned that salinity increases in the Columbia River Estuary could cause an upriver shift in the distribution of C. salmonis, such that Youngs Bay populations would no longer provide a substantial summer-time food base. Similarly, sufficient salinity increases could cause upriver fine-sediment habitats, as in Cathlamet Bay, to support only transient C. salmonis populations like those presently found in Youngs Bay. Other more marine-tolerant infaunal species may invade upriver, but their trophic contribution is

uncertain.

FURTHER RESEARCH NEEDS

The following list summarizes several areas of investigation which would clarify the response of Corophium salmonis to changes of habitat conditions in the Columbia River Estuary:

1. Better definition of habitat use (by tidal depth, salinity zone and sediment type) according to season.
2. Patterns of movement, and the causes of migration (e.g., crowding, food availability, temperature, salinity, day length).
3. The relation of size and maturity to movement.
4. The location and relative size of winter-time high-density areas, and their role in seeding transient colonies.
5. The roles of die-off (senescence), predation and emigration in rapid population declines.
6. More precise determination of temperature-salinity tolerance attributes, especially sublethal effects (e.g., reproductive success, and behavioral response to tidal rates of salinity change).
7. Definition of the physiological mechanisms underlying the tolerance and behavioral responses (e.g., changes in blood ion concentrations).

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Appendix 1. Treatment level means according to experiment in Corophium salmonis salinity-temperature tolerance studies.

Experiment	Test Day	SEX		TEMPERATURE				SALINITY (PPT)				SILT					
		Level	n	Survivorship %	Level	n	Survivorship %	Level	n	Survivorship %	Level	n	Survivorship %	Survivorship Transf			
4	31***	M	7	.4825	21.5	7	0	3	.7001	41.5	0	3	.7001	41.5			
		F	7	.4072	15.7	5	3	.7518	46.6	10	3	.8255	54.0				
		J	7	.6142	33.2	15	3	.7168	43.2	20	3	.4077	15.7				
						25	3	.1072	1.1	30*	3	0	0	0			
										0	3	.7001	41.5	0	3	.7001	41.5
										5	3	.7518	46.6	10	3	.8255	54.0
										15	3	.7168	43.2	20	3	.4077	15.7
4**	31***	M	5	.6112	33.0	7	0	3	.7001	41.5	0	3	.7001	41.5			
		F	5	.5701	29.1	5	3	.7518	46.6	10	3	.8255	54.0				
		J	5	.8598	57.4	15	3	.7168	43.2	20	3	.4077	15.7				
										0	3	.7001	41.5	0	3	.7001	41.5
										5	3	.7518	46.6	10	3	.8255	54.0
										15	3	.7168	43.2	20	3	.4077	15.7
										20	3	.4077	15.7	0	3	0	0
6	14	M	7	.7480	46.3	14	0	3	.6274	34.5	0	3	.6274	34.5			
		F	7	.5390	26.3	5	3	.9095	62.3	10	3	.7148	43.0				
		J	7	.4567	19.4	15	3	.7289	44.4	20	3	.4779	21.2				
										25	3	.4279	17.2	30	3	.1824	3.3
										0	3	.6274	34.5	0	3	.6274	34.5
										5	3	.9095	62.3	10	3	.7148	43.0
										15	3	.7289	44.4	20	3	.4779	21.2
6**	14	M	5	.8701	58.4	14	0	3	.6274	34.5	0	3	.6274	34.5			
		F	5	.6107	32.9	5	3	.9095	62.3	10	3	.7148	43.0				
		J	5	.5943	31.3	15	3	.7289	44.4	20	3	.4779	21.2				
										0	3	.6274	34.5	0	3	.6274	34.5
										5	3	.9095	62.3	10	3	.7148	43.0
										15	3	.7289	44.4	20	3	.4779	21.2
										20*	3	.4779	21.2	0	3	0	0
7	19	M	10	.5828	30.2	14	0	6	.4179	16.5	0	6	.4179	16.5			
		F	10	.6281	34.5	5	6	.4885	21.4	10	6	.6395	35.6				
		J	10	.3476	11.6	15	6	.5793	30.0	20	6	.4805	21.4				
										0	6	.4179	16.5	5	6	.4885	21.4
										5	6	.4885	21.4	10	6	.6395	35.6
										15	6	.5793	30.0	20	6	.4805	21.4
										20	6	.4805	21.4	0	6	0	0
9	13	M	9	.8078	52.2	7	9	1.1033	79.7	5	9	.9556	66.7				
		F	9	.9587	69.5	14	9	1.0091	71.6	10	9	1.0100	71.7				
		J	9	1.1104	80.3	21	9	.7644	47.9	20	9	.9114	62.5				
										0	6	.4179	16.5	5	6	.4885	21.4
										5	6	.4885	21.4	10	6	.6395	35.6
										15	6	.5793	30.0	20	6	.4805	21.4
										20	6	.4805	21.4	0	6	0	0
10	13	M	9	.7749	48.9	7	9	1.0044	71.2	5	9	.8343	54.9				
		F	9	.8650	57.9	14	9	.9125	62.6	10	9	.9857	69.5				
		J	9	1.0203	72.6	21	9	.7035	41.8	20	9	.8403	54.5				
										0	6	.4179	16.5	5	6	.4885	21.4
										5	6	.4885	21.4	10	6	.6395	35.6
										15	6	.5793	30.0	20	6	.4805	21.4
										20	6	.4805	21.4	0	6	0	0
11	13	M	9	.2705	7.1	7	9	.6984	41.3	5	9	.4937	22.4				
		F	9	.5660	28.8	14	9	.5637	28.5	10	9	.6069	32.5				
		J	9	.6605	37.6	21	9	.2349	5.4	20	9	.3965	14.9				
										0	6	.4179	16.5	5	6	.4885	21.4
										5	6	.4885	21.4	10	6	.6395	35.6
										15	6	.5793	30.0	20	6	.4805	21.4
										20	6	.4805	21.4	0	6	0	0

* 40, 50 and 60 ppt salinities caused 100% mortalities at 1-day and were omitted.

** 0-20 ppt salinities version of data which was analyzed by ANOVA.

*** Except for 5, 15 and 25 ppt salinities, which are 25-day results.