

AN ABSTRACT OF THE THESIS OF

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Title: The Life History of Corophium salmonis in the Columbia  
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The benthic amphipod Corophium salmonis was sampled seasonally from two sites (Desdemona Sands and Grays Bay) in the Columbia River estuary. Populations of C. salmonis at both sites were found to have a two generation per year life cycle, a spring generation and a fall generation. The spring generation juveniles were produced in May 1981. These juveniles then grew throughout the summer and produced the fall generation in July and August. The fall juveniles were the overwintering population which would then produce the next spring generation. Brood sizes and mature female lengths were both found to be larger for the spring broods than for the fall broods.

The population of C. salmonis on Desdemona Sands disappeared from the site in September 1980 and reappeared in April 1981. These events coincided with density fluctuations at the Grays Bay site. It was also observed that salinity at the Desdemona Sands site varied more than salinities at the Grays Bay site especially during the winter. Higher salinities at the Desdemona Sands site may have been responsible for the migration of C. salmonis in and out of the Desdemona Sands habitat.

The Life History of Corophium salmonis  
in the Columbia River Estuary

by

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THE LIFE HISTORY OF COROPHIUM SALMONIS  
IN THE COLUMBIA RIVER ESUTARY

I. INTRODUCTION

The amphipod (Phylum Arthropoda, Class Crustacea) genus Corophium was described in 1806 by Latreille with a single specimen of Corophium longicorne (Crawford, 1937). It has since been expanded to contain approximately 45 species located throughout the world in a wide range of salinities (Greene, 1975). Most species in the genus inhabit marine and brackish waters but a few are fresh-water forms (Greene, 1975).

Corophium species are characteristic of harbors and estuaries and frequently inhabit intertidal muddy shores (Crawford, 1937; Meadows and Reid, 1966). Crawford observed that all known species of the genus formed tubes of mud or muddy sand, either in the substratum or attached to solid substrates. Corophium are capable of swimming and C. volutator has been observed walking over the surface of the mud, both when the tide was in and when it had just ebbed (Greene, 1975).

Hart (1930) described C. volutator as a true deposit feeder which was also capable of filter feeding. Particles of food, organic detritus and its associated micro-organisms are sorted out from the substratum by the gnathopods and passed to the mouthparts. Substrate is raked in the burrow by the second antennae while the animal is partly or wholly out of its burrow (Greene, 1975). Filter feeding occurs when the animal is in the burrow. It creates a respiratory current flowing through the U-shaped burrow from which

food particles are filtered (Greene, 1975). Meadows and Reid (1966) observed, however, that filter feeding was not occurring because the burrow openings were raised above the sediment surface allowing only the finest particles to enter the burrow, which would be missed by the filter setae. It also appeared that the Corophium were not feeding while on the sediment surface but when they were in their burrow.

In most species of the genus both sexes exist (Crawford, 1937). The exception is the British species C. bonelli which is parthenogenic with only females observed (Moore, 1980). In British species where both sexes are present, Crawford (1937) observed that females were usually more abundant than males. The young of the Corophium remain in a maternal brood pouch until they are juveniles. They are released from the brood pouch while in the burrow (Greene, 1975).

Fourteen species of Corophium have been described from the west coast of America. Barnard (1954) described four species from Oregon which were collected from Coos Bay; C. acherusicum, C. brevis, C. salmonis and C. spinicorne. Of these species, three have been observed regularly in the Columbia River estuary (Figure 1).

Corophium brevis, primarily a marine species has been captured sporadically in the lower estuary (Davis, 1978). This tube dwelling species is mainly distributed in the more saline water downstream of Youngs Bay (Higley and Holton, 1978) but was captured by Davis (1978) in Youngs Bay and was probably swept into the bay with the salinity intrusion. C. spinicorne, a fairly abundant species in the estuary, attaches its mucous tubes to algae, rocks and pilings along the shoreline of Youngs Bay and sporadically downstream and

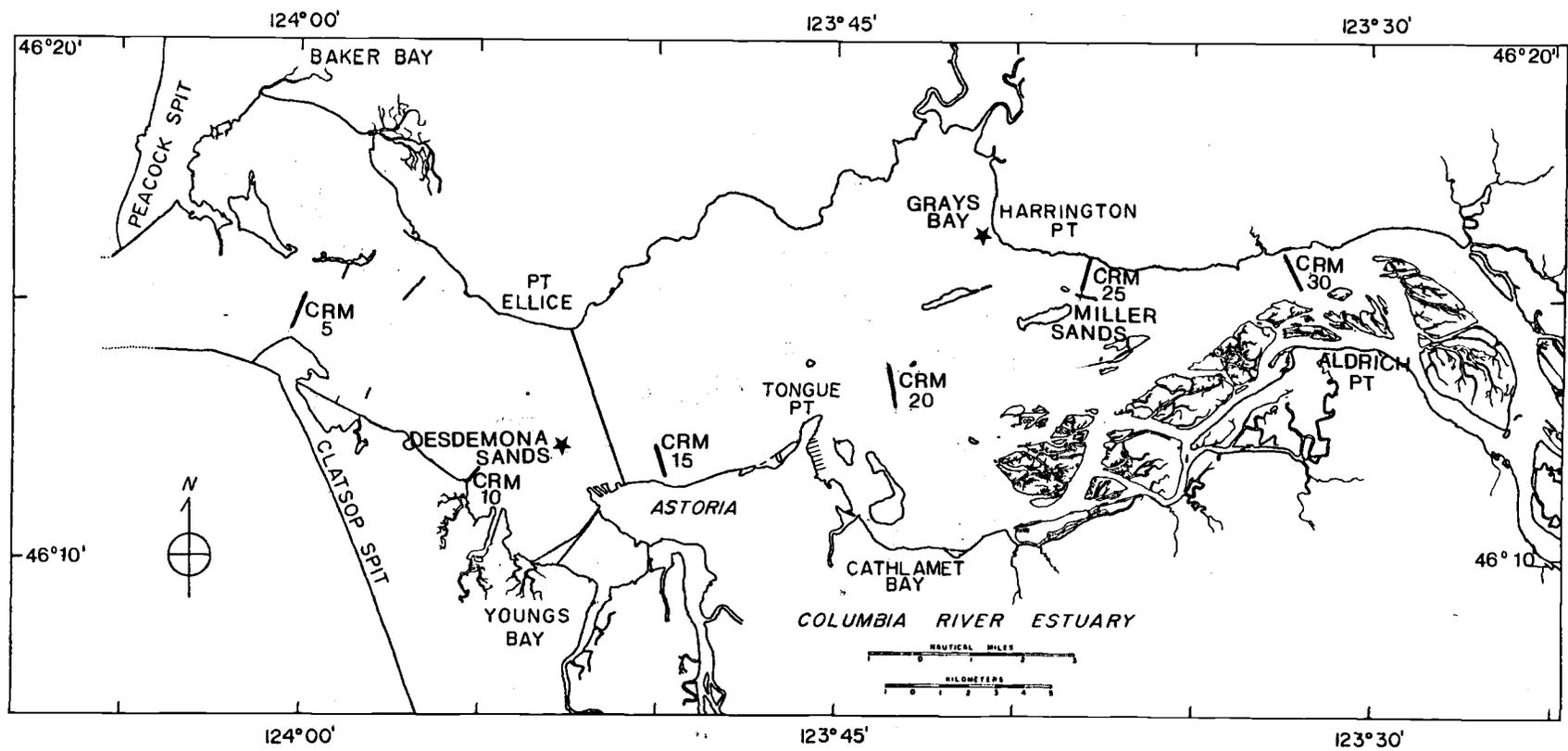


Figure 1. Location of the two sampling sites in the Columbia River estuary. Stars indicate sample site locations.

possibly upstream (Davis, 1978). It is considered a broadly euryhaline species and may occur in waters ranging from fresh to marine (Hazel and Kelly, 1966; Aldrich, 1961). The most abundant species of Corophium in the Columbia River estuary is C. salmonis, a major member of the freshwater and brackish water infauna of the estuary. One specimen of C. insidiosum was captured by Davis (1978) but its regular occurrence in the estuary has not been established. C. insidiosum builds tubes of mud on algae and hydroids (Sheader, 1978) and is found in shallow brackish inshore areas and estuaries with a high degree of turbidity (Nair and Anger, 1979).

Corophium salmonis is an important species in the Columbia River estuary because of its frequent high abundance and heavy utilization as prey by other organisms in the estuary. It inhabits sandy mud deposits in the estuary, extending from and into Youngs Bay, upstream at least to Portland (Higley and Holton, 1978; Davis, 1978). It is also found in isolated portions of Baker Bay. Densities commonly exceed  $10,000/m^2$  and may reach as high as  $40,000/m^2$  (Higley and Holton, 1975). The higher densities were encountered where sandy mud sediments accumulated in quiet portions of Youngs Bay.

Corophium salmonis typically builds mucus and mud U-shaped tubes in sand, either intertidally or subtidally. It feeds mainly as a selective deposit feeder, using its second antennae to scrape surface deposits and detritus near its burrow (Eckman, 1979). It may also filter feed utilizing the respiratory current generated through its tube. C. salmonis may be observed at low tide either crawling on the substratum surface or swimming in pools of water remaining

after the ebb tide.

Corophium salmonis is a major prey item of many estuarine fish including juvenile chinook salmon (Oncorhynchus tshawytscha), chum and coho salmon (O. keta and O. kisutch), starry flounder (Platichthys stellatus), pacific staghorn and prickly sculpins (Leptocottus armatus and Cottus asper), shiner perch (Cymatogaster aggregata), longfin smelt (Spirinchus thaleichthys), pacific tomcod (Microgadus proximus) and American shad (Alosa sapidissima) (Clairain et al., 1978; Haertel and Osterberg, 1967; Higley and Holton, 1975; Hammann, 1982). It is also eaten by larger benthic invertebrates including polychaetes and nemerteans, as well as by shorebirds, wading birds, gulls and waterfowl (Hart, 1930). The heavy utilization of Corophium salmonis as prey in the estuary makes knowledge of its life history patterns and production characteristics important. At present, there is no published information on C. salmonis life history except that of Davis (1978) who studied Corophium salmonis in Youngs Bay with regard to diel migration, coloration and life history. He reported that the life cycle of Corophium salmonis was similar to that of C. volutator, having two generations per year. Because of their widespread distribution throughout the estuary, the present study was undertaken to examine potential variations in the life history of C. salmonis in habitats with different salinity and energy regimes.

Corophium salmonis populations from two different habitats in the Columbia River estuary were selected for intense examination of life history characteristics including reproductive season, seasonal density, sex ratio, size at sexual maturity and brood size.

This work was done as part of the Columbia River Estuary Data Development Program (CREDDP). The purpose of the study is to increase understanding of the Columbia River estuary as a system and to structure the information gathered for use in making land/water management decisions.

## II. METHODS AND MATERIALS

### Study Area

The Columbia River flows 1,210 miles from its origin in Columbia Lake, B.C., Canada and has a combined drainage area of 259,000 mi.<sup>2</sup> (Neal, 1972). It has played a major role in the development of the Pacific northwest, serving as a route for commercial traffic, supplying water for irrigation, municipalities and hydroelectric generation, providing a recreational resource and acting as a waste disposal medium for municipalities.

Maximum flow in the river occurs in May, June and July from the melting of the winter snowpack in the headwater regions. Minimum flows are from September to March although high water can occur in the winter due to heavy winter rains in the coastal regions (Neal, 1972).

The lower Columbia River divides into two distinct parts. The upper portion from Aldrich Point (Columbia River Mile (CRM) 31) to Longview consists of one channel bordered by steep valley walls (Hubbell and Glenn, 1973). Below Aldrich Point is a coastal plain estuary (Lutz et al., 1975) where the water spreads the entire width of the estuary at high tide (Hubbell and Glenn, 1973). This results in sand deposition in the central region of the river forming vast shallow flats and shoals. The surrounding lands are drained by four large shallow embayments located at the lower end of the estuary.

Maximum seawater intrusion usually extends to CRM 23 in late summer just above Harrington Point during high tide when river flow

is lowest. During high river flow the seawater intrusion may extend less than 5 miles upriver (Neal, 1972). The Columbia River estuary is characterized mainly as a partially mixed estuary and can be divided into three sections. From the mouth to about CRM 7 it is basically marine. Upstream of CRM 23 the environment is fluvial (fresh water) while the section between is transitional (mixing) (Hubbell and Glenn, 1973).

Two sites previously established during preliminary surveys as supporting Corophium salmonis populations were selected for study. One site was in Grays Bay, a large protected embayment on the north side of the estuary on the edge between the mixing and the fresh water zone (Figure 1). The second site was located on Desdemona Sands, a midriver sand shoal situated in the mixing salinity zone which differs from Grays Bay in both tidal energy and salinity.

The eruption of Mt. St. Helens in May of 1980 sent large quantities of ash through the Columbia River estuary. Although a thin layer of ash was visible in Grays Bay directly following the eruption, by August 1980 when the study was initiated there were only scattered traces of ash observable. Thus the sites chosen for the study were considered unaffected by the eruption of Mt. St. Helens.

### Sampling

In August 1980 a grid 100 meters (alongshore) x 30 meters (perpendicular to shore) was established at each site at low tide at approximately the +1.0 foot tidal level. Five randomly placed samples were collected from each grid monthly until June 1981. Sampling frequency was then increased to twice monthly until

August 1981 as summer was suspected to be the period of reproductive activity. Sampling ended in September 1981.

Samples were collected in August and September 1980 with a 10.16 cm diameter hand corer to a depth of 10 cm. In October, a related vertical distribution study at the Grays Bay site (Jones et al., 1982) indicated that while sampling to a 10 cm depth captured 93% of the Corophium present, an additional 5 cm depth brought the percent captured to 99%. Accordingly, a 7.62 cm diameter corer to a 15 cm depth was used for the remainder of the study. The diameter of the corer was reduced in order to keep the sample size within acceptable processing levels. All infaunal samples were preserved with 5% buffered formalin.

Water temperature was measured on each sampling date and a water sample collected for salinity analysis at each site. Samples and measurements were taken at low tide and were obtained from the nearby river channel, which provided the nearest water to the exposed grid. Salinity was measured to the nearest 0.1‰ by hydrometer (G. M. Manufacturing Company) in the lab.

One sediment sample was collected from each site on each sampling date with a 3.5 cm diameter x 15 cm deep coring tube. Samples were frozen for later textural analysis as a part of the CREDDP study using standard methods of sieving and pipette analysis. A sediment stake was also established at each site on the first sampling date. Sediment level relative to the stake was observed during each sampling.

### Sample Analysis

In the lab the samples were sieved on three stacked screens having mesh openings of 0.5 mm, 0.25 mm and 0.125 mm. The use of several screens aided in the sorting process. The fine mesh screens were used to insure retention of juveniles. Fractions retained on the 0.25 mm and 0.125 mm screens contained large amounts of sand and were elutriated prior to sorting. The elutriation process involved agitation of small portions of the sample within a water-filled jar and decanting off the fluid and suspended animals after the sand had settled. The animals sorted from both the 0.5 mm fraction and the elutriate fractions were sorted under a three diopter magnifier.

The Corophium salmonis from each sample fraction were counted and individual length measured as the distance from the front of the rostrum to the tip of the telson. Each animal was classified according to its sexual development in a scheme modified from Davis (1978):

1. unsexable juvenile: all have female type antennae and lack other sexual characteristics (genital papillae or oostegites)
2. immature males: incomplete development of the male type spines on the second antennae
3. mature males: fully developed hook and male type spines on second antennae and complete development of the gonads
4. immature females: nonbreeding females; oostegites present but not full sized and lacking marginal setae

5. mature females: breeding females; oostegites fully enlarged and bearing marginal setae.

Mature females were further classified as gravid (brood pouch containing eggs or embryos) or nongravid (either before deposition of eggs into the brood pouch or after release of the brood). When gravid females had intact broods (those that did not appear damaged or partially released) the number of eggs or embryos was counted.

### III. RESULTS

#### Site Description

Water temperature at low tide at the two sites was very similar throughout the year (Figure 2). Temperatures were lowest during the winter at 6.5°C for Grays Bay in December 1980 and 5.0°C for Desdemona Sands in February 1981. The peak temperature was 19.0°C at both sites occurring in June 1981 at Grays Bay and in August 1981 at Desdemona Sands.

Salinity varied more than temperature at low tide between the two sites (Figure 2). Salinity at Desdemona Sands was higher than at Grays Bay during the winter of 1980-1981. Peak salinities at Grays Bay were 5.2‰ and 6.9‰ occurring in October and November 1980. For the rest of the study the salinity at Grays Bay ranged from 2.1‰ to 4.2‰. Desdemona Sands salinities peaked in the winter at 10.5 in December 1980. Salinities at Desdemona Sands dropped in February 1981 to 3.0‰ and remained below 5‰ until July 1981 when they again began to increase. The salinity and temperature measurements were made at low tide from the nearest river channel. They do not reflect the total salinity and temperature regimes experienced by the animals at the sites but are an indication of seasonal changes experienced by the fauna.

Sediment texture data indicates that the two study sites had a similar sediment structure that was fairly homogeneous over the study period. Median particle size measured in phi units,  $\phi$ , ranged from 2.48 $\phi$  to 2.89 $\phi$  at Grays Bay and from 2.25 $\phi$  to 2.50 $\phi$  at Desdemona Sands (Figure 3). Percent silt and clay at Desdemona Sands was

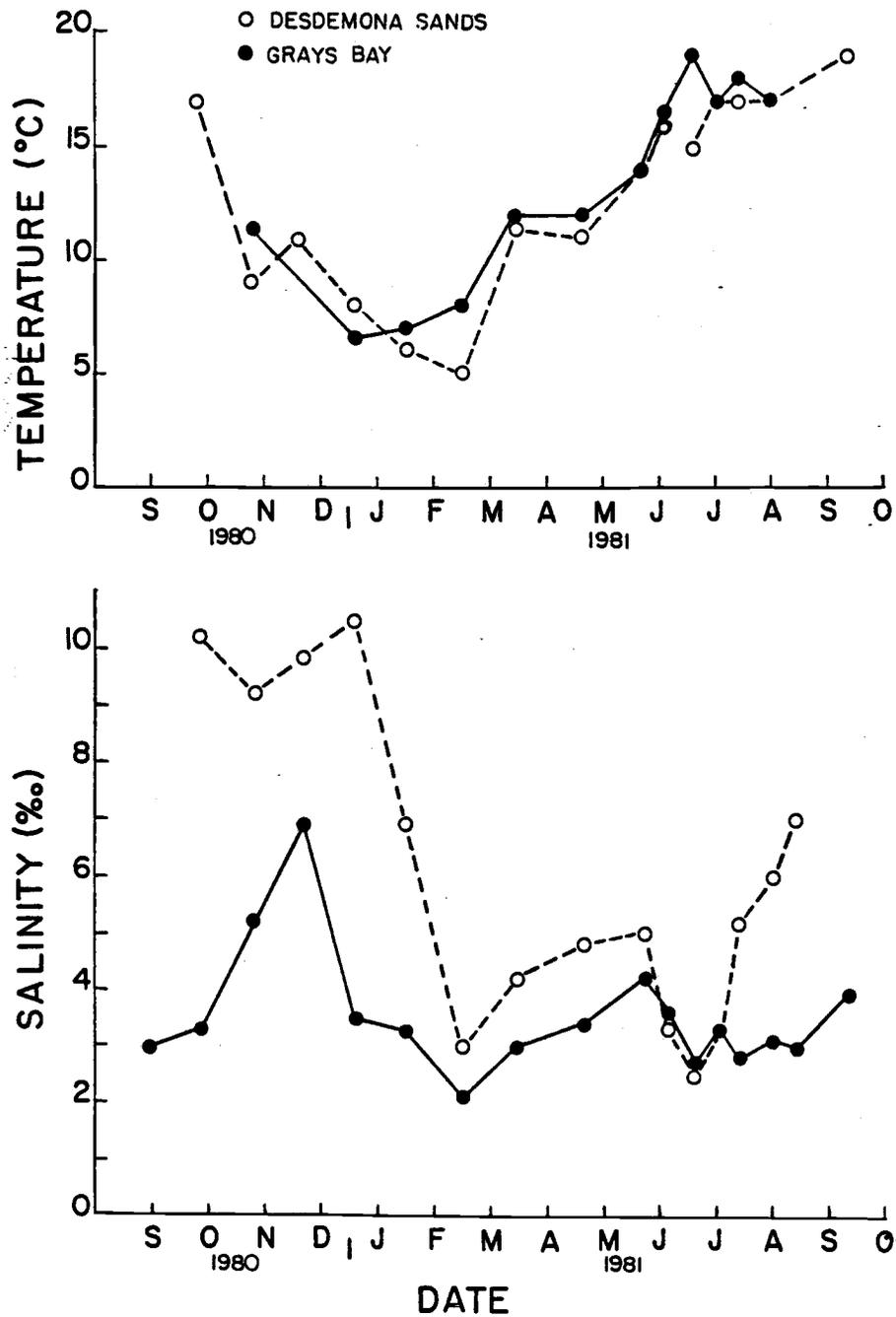


Figure 2. Monthly temperature and salinity at Desdemona Sands and Grays Bay.

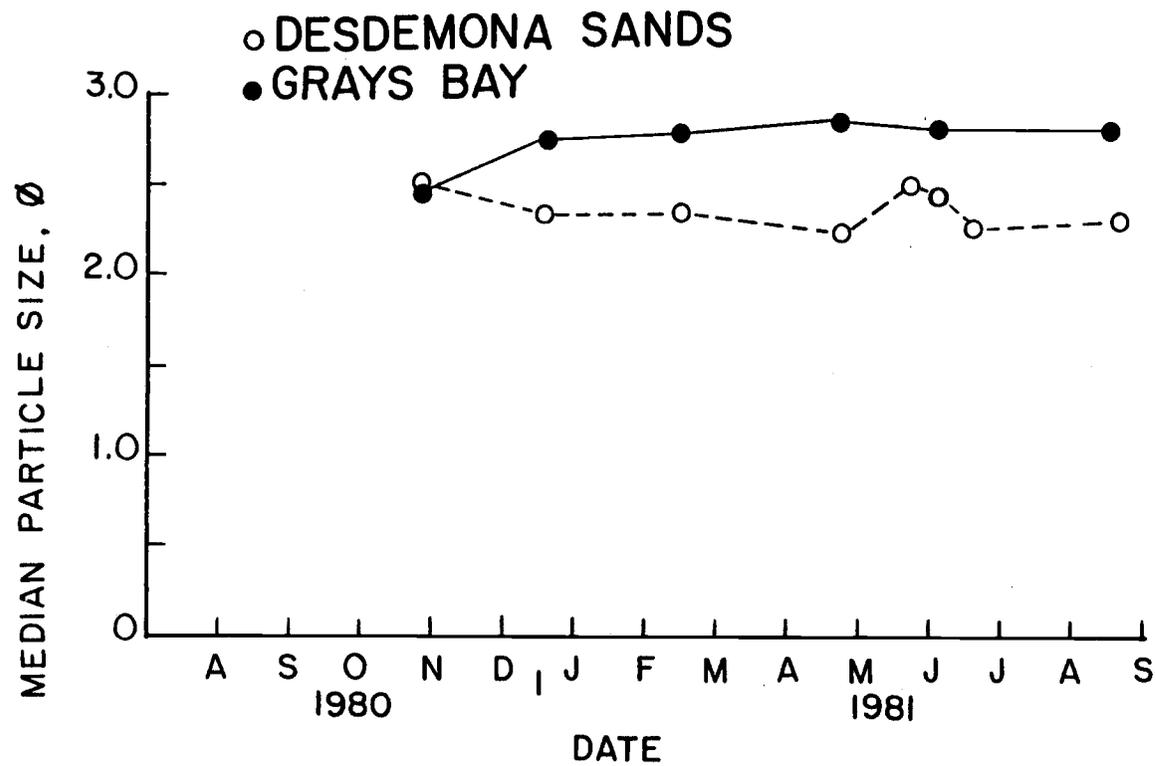


Figure 3. Median particle size at Desdemona Sands and Grays Bay.

consistently low throughout the study with a range of 3.42% to 5.80% (Figure 4). However, at Grays Bay percent silt and clay rose dramatically in April 1981 from December 1980 values of 4.96% to a high of 21.79%. The lowest value in Grays Bay was 3.00% in October 1980. No differences in sediment level could be determined at the sediment stakes established at the beginning of the study at the two sites. No major erosional or depositional events occurred at the study sites.

#### Population Structure of *Corophium salmonis*

Length-frequency histograms were constructed for both sites on each sampling date to examine seasonal population size structure patterns (Figures 5 and 6). The length-frequency histograms for Grays Bay indicate that the population was producing young when sampling began in August 1980 and continued to produce juveniles through November 1980 (Figure 5). By November, breeding females observed in the previous three months had disappeared leaving a population dominated by juveniles, immatures and mature males. From December 1980 until April 1981 juveniles produced the previous fall grew and matured until those released in early fall became adults and those in late fall became immatures. At this time, the population was dominated by early adults and later stage immatures.

In May 1981 a second pulse of juveniles, the spring generation appeared resulting in a population with two distinguishable cohorts, juveniles and adults, with some late stage immatures also present. As indicated by Figure 5, the juveniles increased in length throughout the summer and matured to adults by August. The appearance of

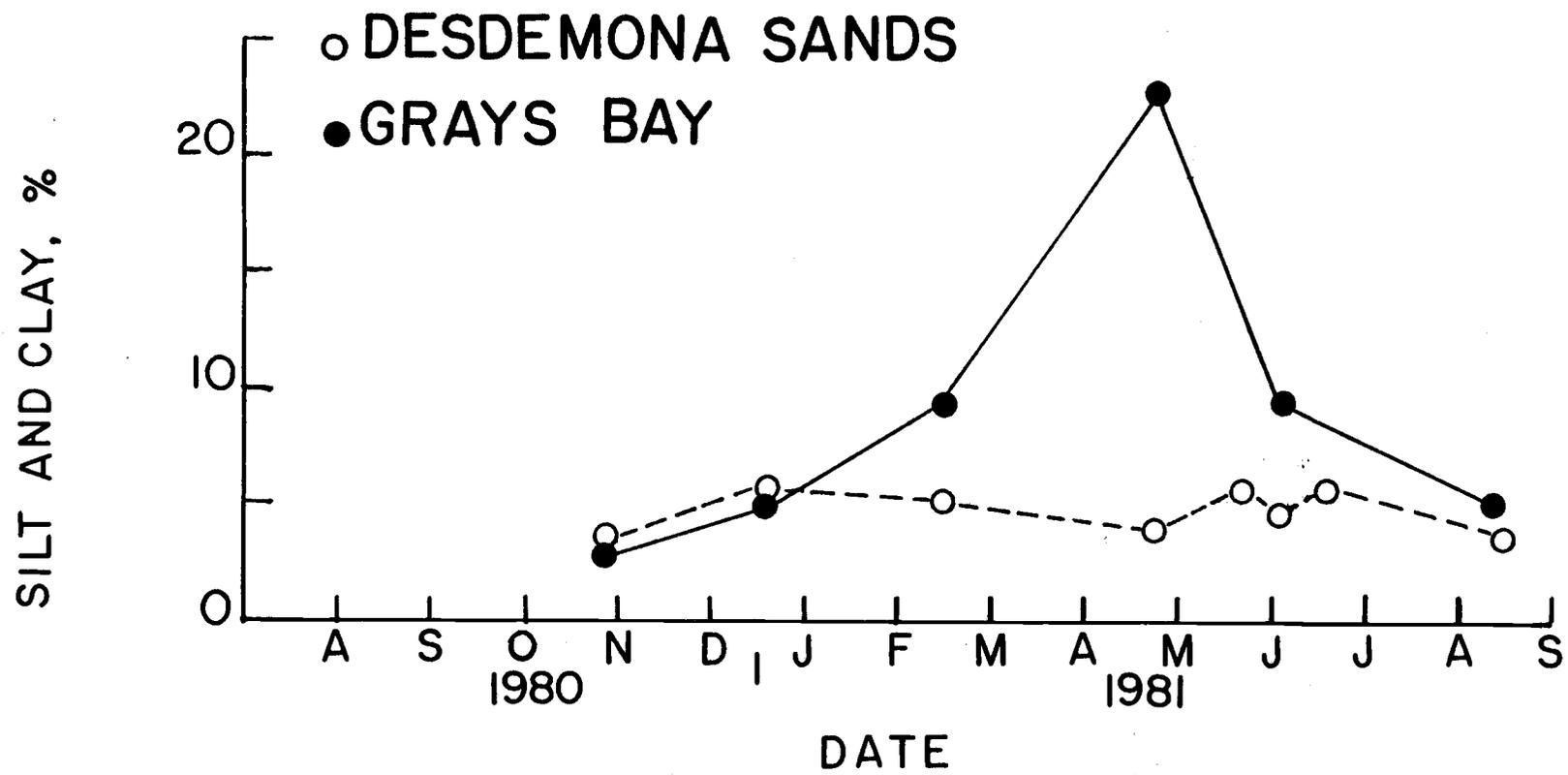


Figure 4. Percent silt and clay at Desdemona Sands and Grays Bay.

Figure 5. The percentage size distribution of Corophium salmonis collected from Grays Bay.

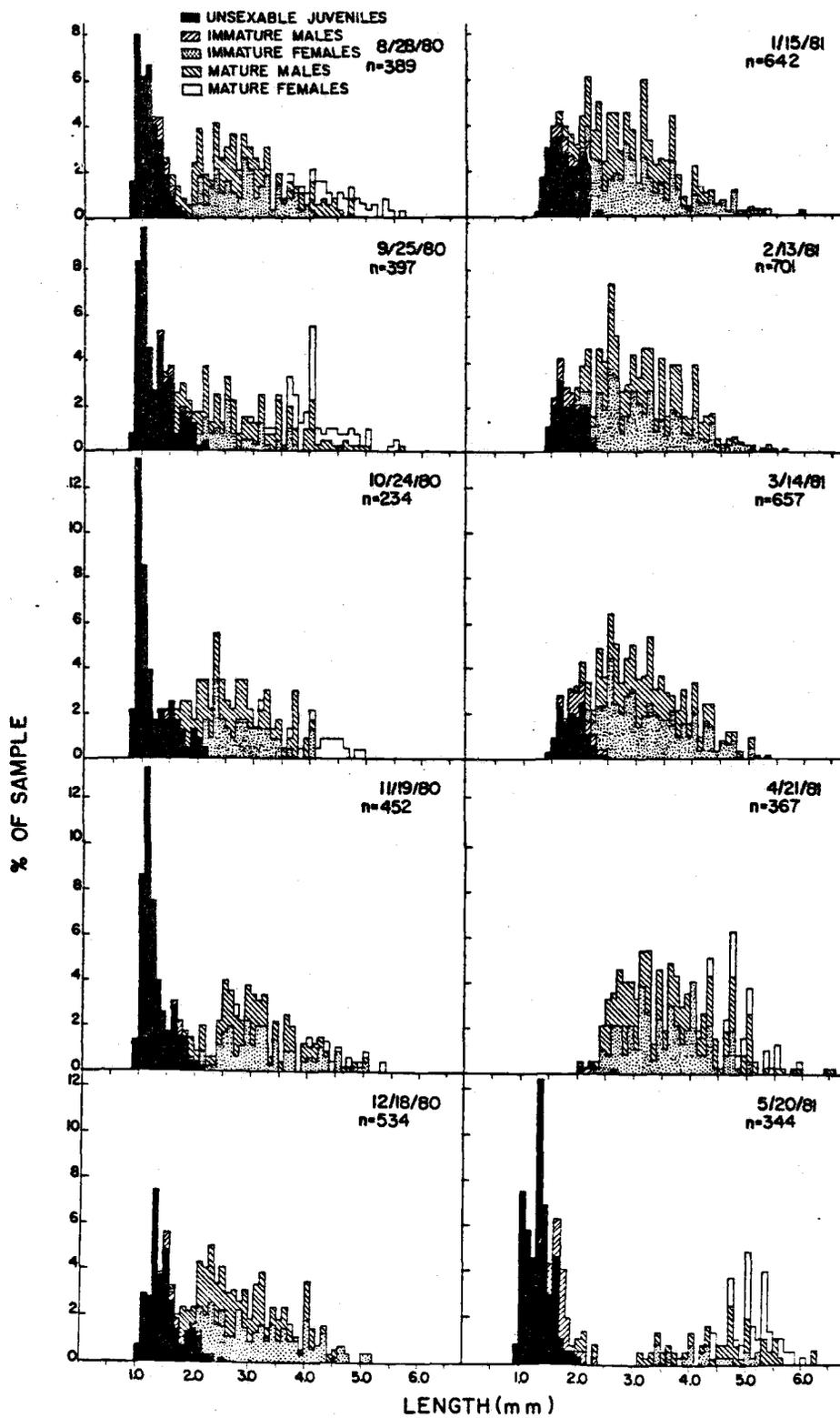


Figure 5

Figure 5. (Continued)

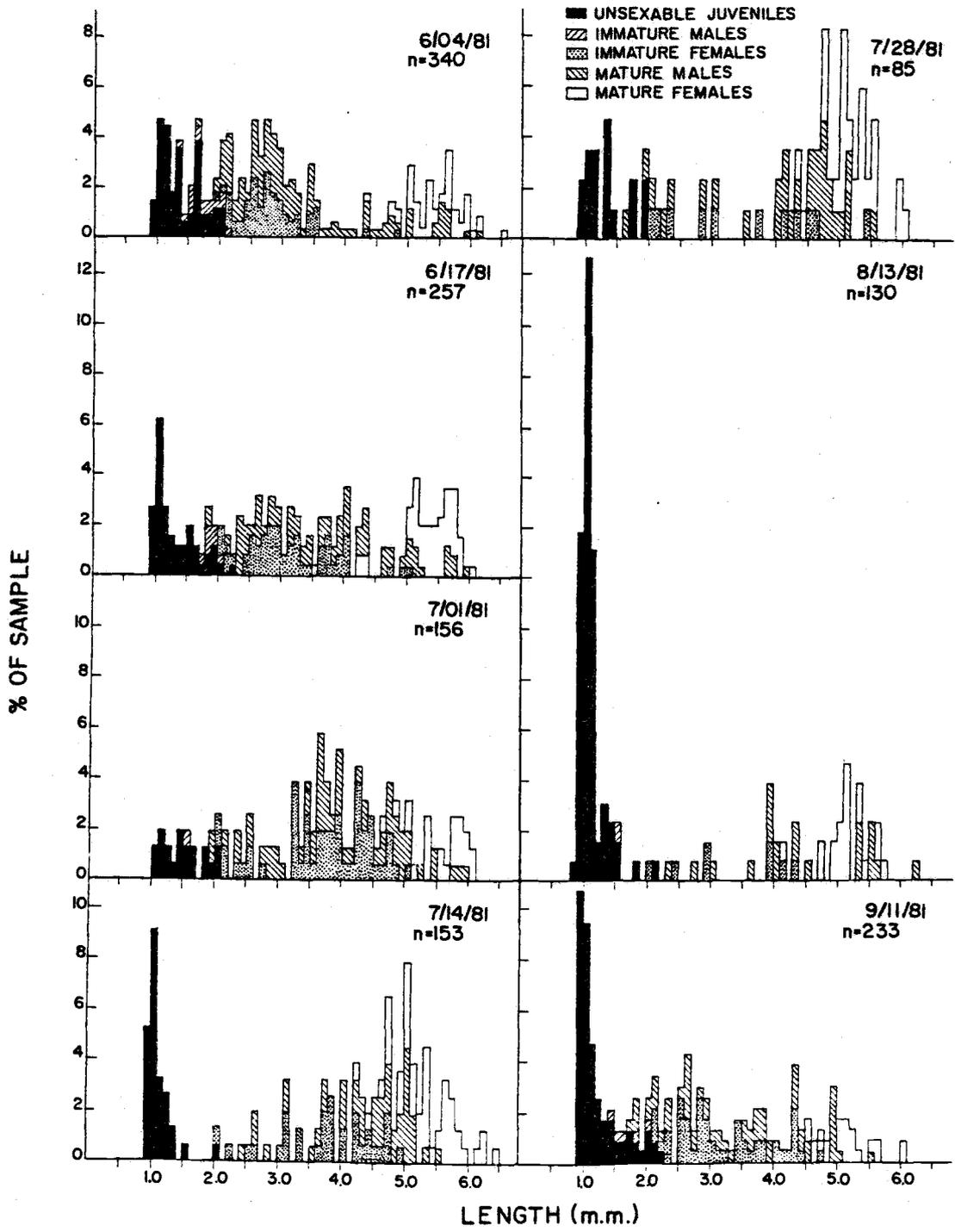


Figure 5

Figure 6. The percentage size distribution of Corophium salmonis collected from Desdemona Sands.

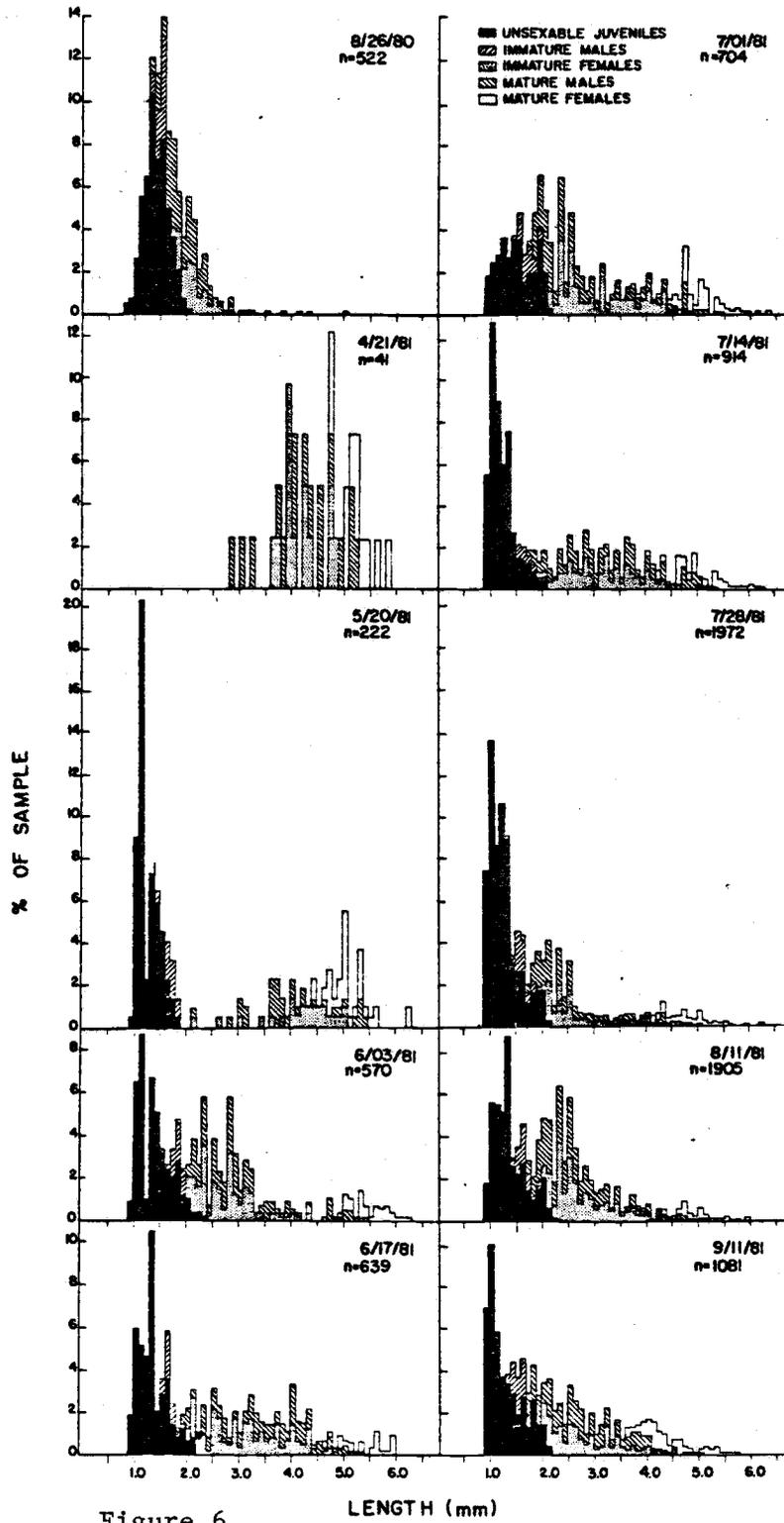


Figure 6

LENGTH (mm)

juveniles tapered off in June 1981 and was low until August when another pulse of juveniles appeared to form the 1981 fall brood. The juveniles produced between the spring and fall generation were presumably offspring of late maturing adults from the previous year's late fall brood. These data, therefore, indicate that the Corophium salmonis at Grays Bay produce two main generations per year, one in the spring and the other in the fall.

The length-frequency histograms for Desdemona Sands (Figure 6) document the same two generation per year reproductive cycle found at Grays Bay. However, the pattern of animal residence was very different from that of Grays Bay. A fall brood began appearing in August 1980 as at Grays Bay but instead of continuing into the fall the entire Desdemona Sands population disappeared in September 1980. In August the population consisted mainly of juveniles, early immatures and a few small adult males. No animals were captured on any of the seven sampling tries from October 1980 to April 1981. The population reappeared in April 1981 and was composed entirely of adults and older immatures, a structure similar to that in Grays Bay. Also similar to Grays Bay, reproduction began again in May 1981 with a large pulse of juveniles. Juveniles of the spring cohort increased in length throughout the summer becoming the breeding adults in July. The breeding females produced a fall brood in late July and continued reproduction until sampling ended in September 1981.

Examination of the graph for percent gravid females of total females for Grays Bay shows that the population contained a greater percentage of breeding females in May and August 1981 corresponding to the spring and fall reproductive seasons (Figure 7). The percent

Figure 7. The number of gravid females as a percentage of the total female population at Grays Bay and Desdemona Sands.

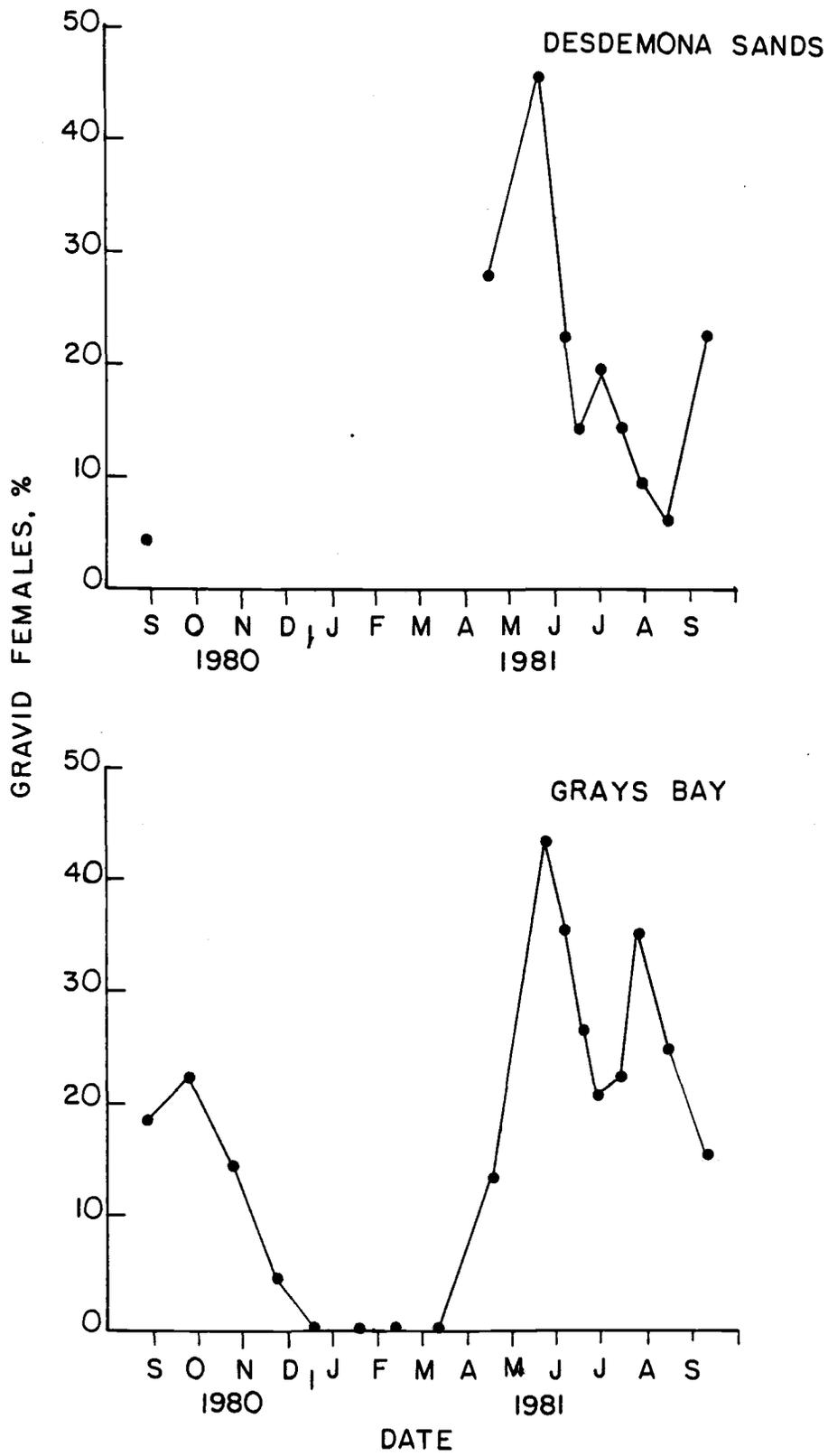


Figure 7

gravid females of total females at Desdemona Sands also peaked during the spring and fall indicating two reproductive seasons.

Throughout the study the average size of males was smaller than the females at both sites. The maximum size of males at Desdemona Sands was 5.4 mm and at Grays bay, 6.2 mm. The maximum female size at Desdemona Sands was 6.6 mm and 6.5 mm at Grays Bay. Males tended to be sexable at a smaller size than females. Corophium salmonis juveniles are produced such that all have female type second antennae (Davis, 1978). Females are identified when oostegites are formed while males are identified when the spines on the second antennae begin to form the characteristic male hook. As a result, males are identifiable at a much smaller size than females, approximately 1.5-2.0 mm, as compared to 2.0-2.5 mm for immature females. Some juveniles were captured with a length as small as 0.8 mm but most were 1.0 mm or greater in length.

#### Density of *Corophium salmonis*

Mean densities were calculated for each sample at both sites (Figures 8 and 9). Density at Grays Bay increased steadily from 9,741/m<sup>2</sup> in August 1980 through the winter of 1980-1981 to a high of 31,754/m<sup>2</sup> in February 1981. Densities declined through the spring and summer to a low of 4,122/m<sup>2</sup> on July 28, 1981. The subsequent increase the following fall follows the pattern exhibited the previous year. Length-frequency histograms, calculated with absolute numbers of animals (Figure 10) indicate that the increase in density which began in December 1980 and continued through the winter was not due to recruitment of juveniles, but was due to an immigration

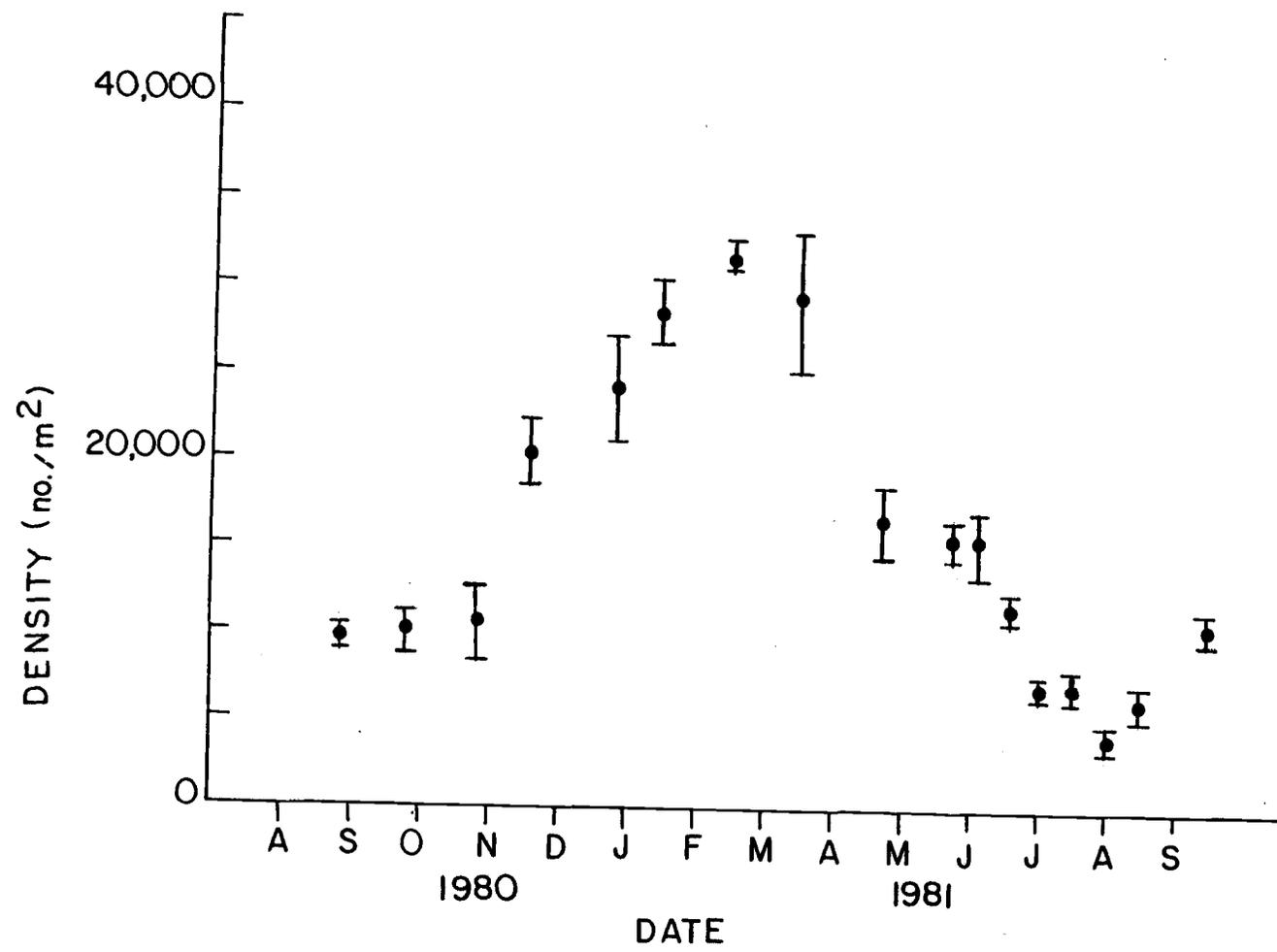


Figure 8. Density of *Corophium salmonis* collected from Grays Bay. Brackets indicate standard error.

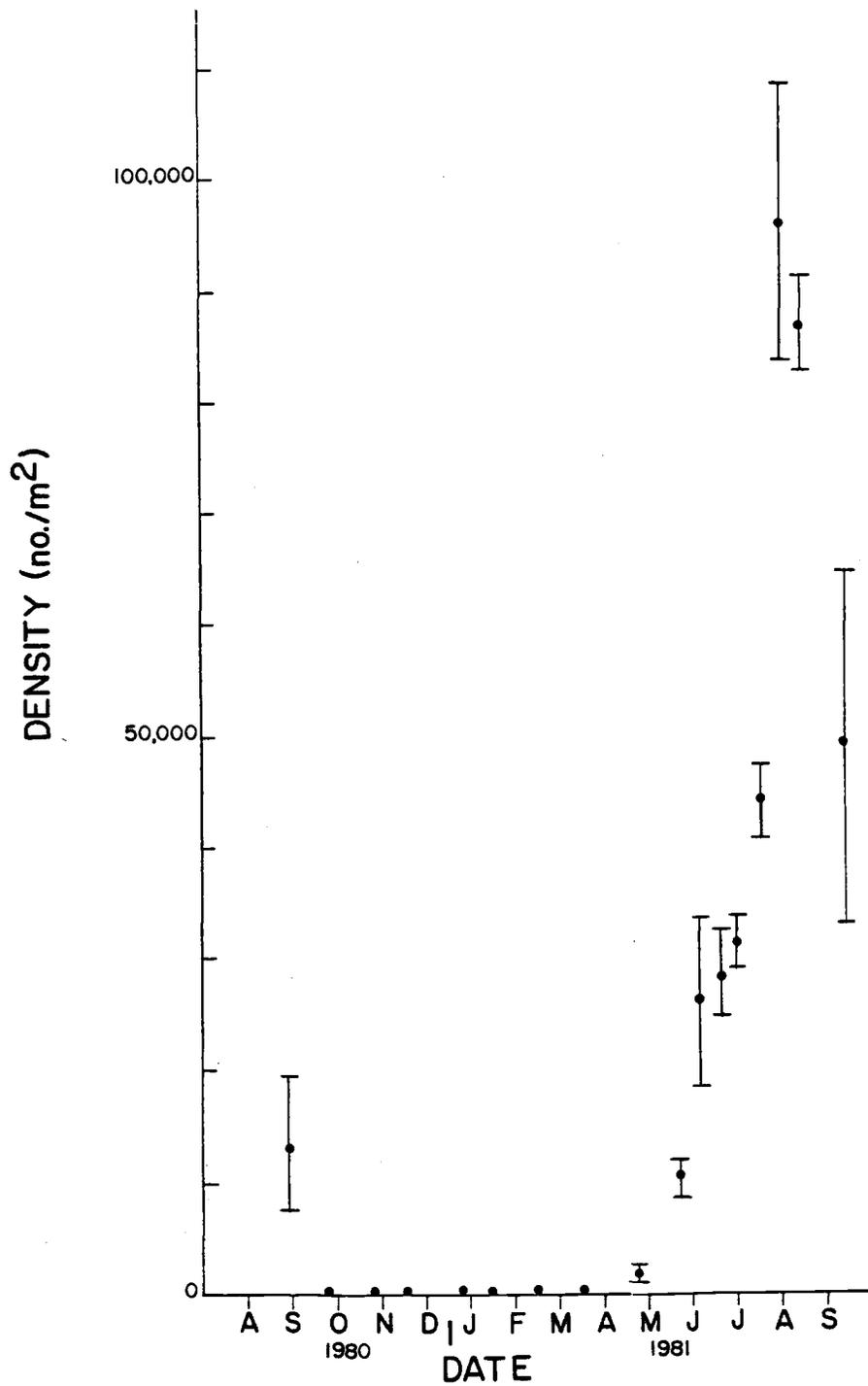


Figure 9. Density of Corophium salmonis collected from Desdemona Sands. Brackets indicate standard error.

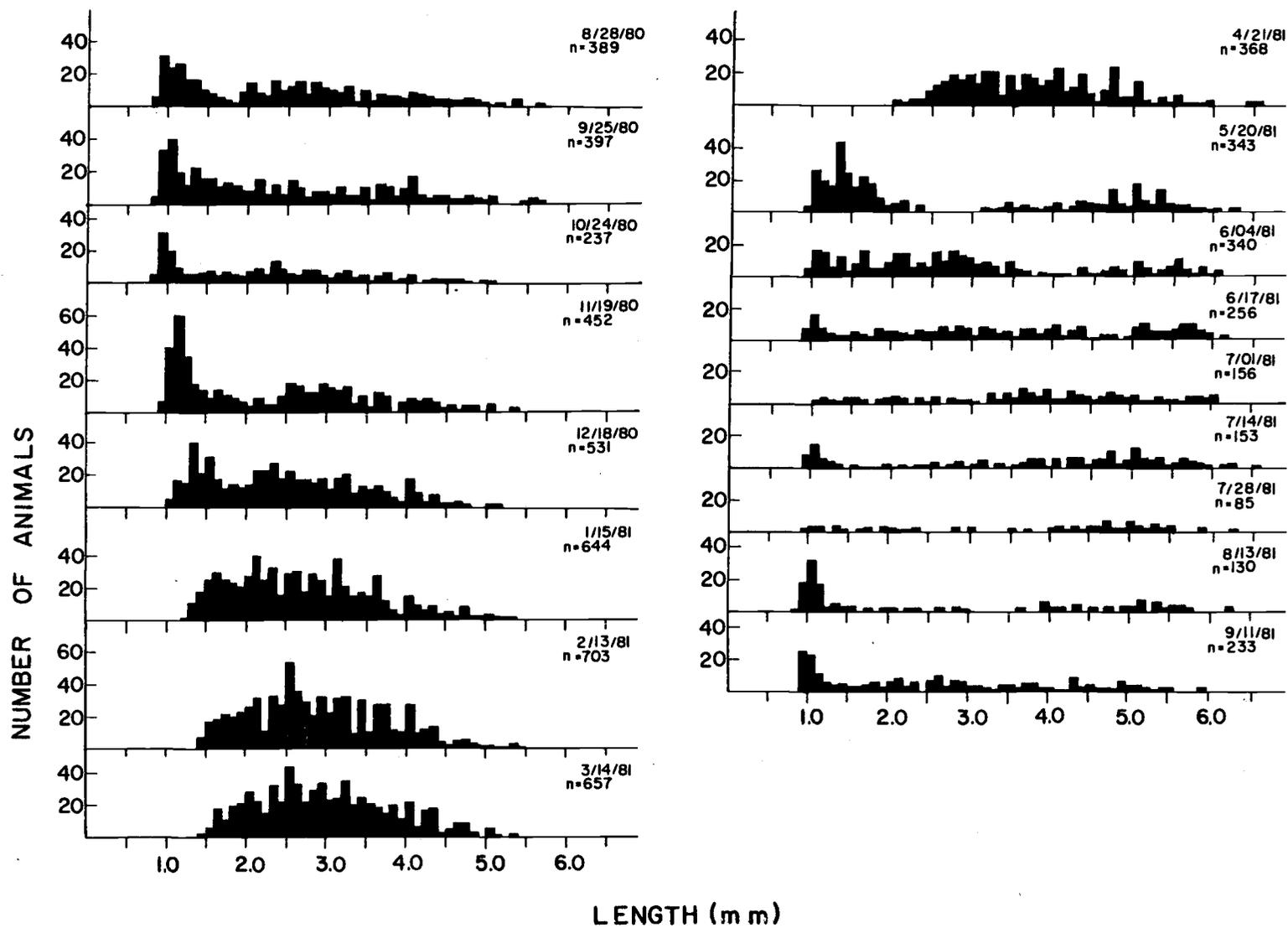


Figure 10. The absolute number size distribution of *Corophium salmonis* collected from Grays Bay.

of adults or immatures into the population.

Densities decreased in March and April 1981 during a period of no reproduction. This strongly suggests a disappearance of adults and immatures. In contrast, during the spring reproductive period, density neither decreased nor increased significantly. Since juveniles appeared during this season without a corresponding increase in total density, it may be assumed that a loss of adults or immatures from the population occurred. The rise in density observed in August and September 1981 appears to have been due to the production of the fall generation of juveniles, which apparently exceeded the loss of older animals.

The seasonal density pattern at Desdemona Sands differs from that at Grays Bay. The Desdemona Sands population (Figure 11) disappeared in September 1980 and reappeared in April 1981. Densities increased throughout the summer until a peak density of  $96,096/m^2$ , the highest observed in the study, was reached in August 1981. When Corophium salmonis reappeared in April, the population was composed of adults and late stage immatures. The increase in density through the summer appears to have been due mainly to recruitment of juveniles into the population from both the spring and the fall generation. The decline in density that occurred in September 1981 resulted from a loss of immatures or adults from the population. Non-quantitative field observations conducted in October 1981 indicated that the population had again disappeared as during the previous fall.

A one way analysis of variance was conducted for time on the density at both Grays Bay and Desdemona Sands, using sampling date to represent time. The seasonal effect was found to be highly

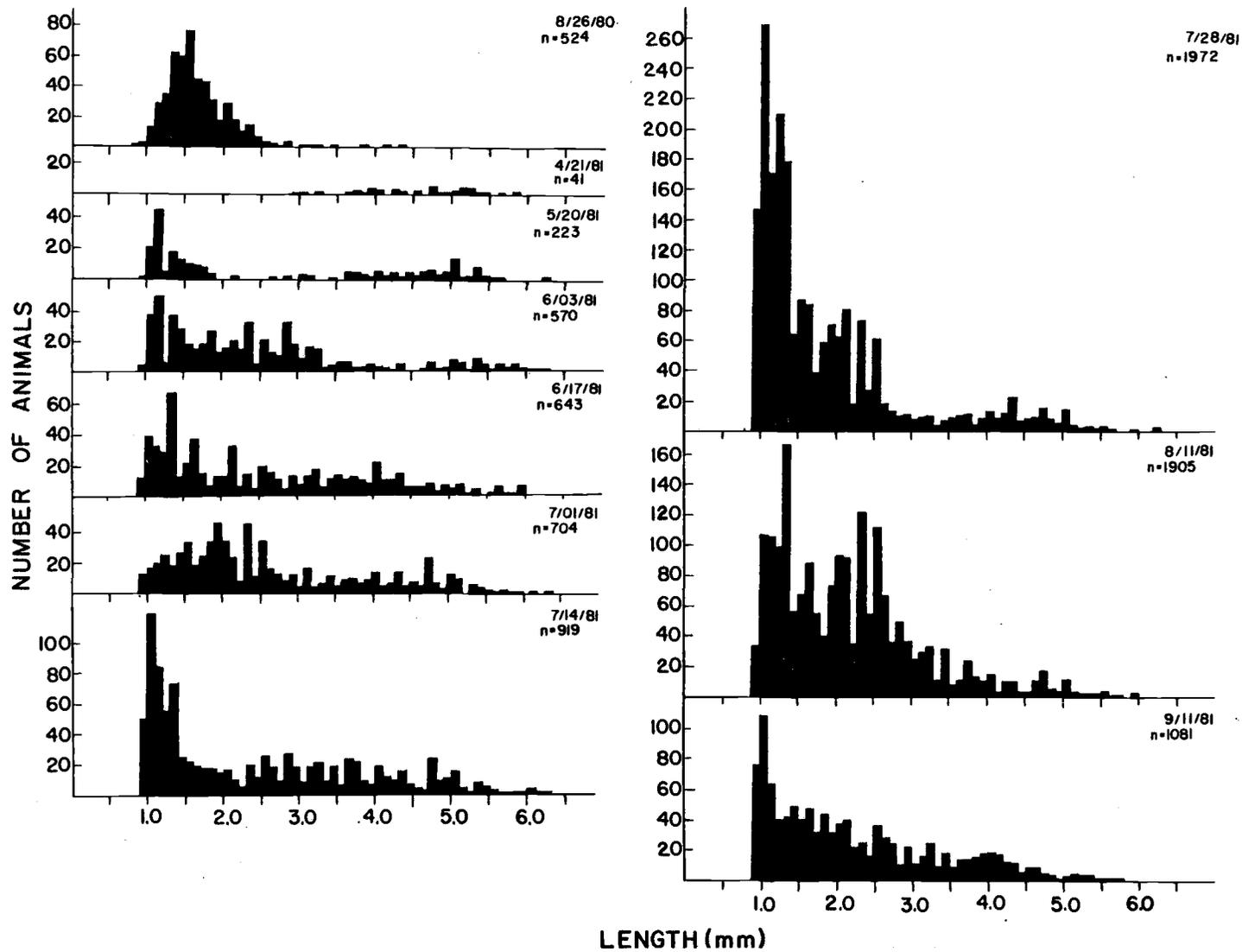


Figure 11. The absolute number size distribution of Corophium salmonis collected from Desdemona Sands.

significant (Table 1), indicating that the mean densities changed significantly over the sampling periods at both sites.

#### Life History Characteristics of *Corophium salmonis*

The sex ratio (M/F) of the Grays Bay population remained around 1.0 throughout the year until early summer (Figure 12). In June and July 1981 the ratio dropped to a low of .587. A Chi Square test (Table 2) showed that only two sample sets, June 17, 1981 and July 14, 1981, had sex ratios significantly different from 1.0. In both cases females outnumbered males. In June there were 115 females and 85 males and in July there were 75 females and 44 males.

For Desdemona Sands, the results of the Chi Square test indicate that the sex ratio was significantly different from 1.0 in August 1980 and the following fall, July 28, August and September 1981 (Table 3). In this case, however, males outnumbered females. There were 176 males and 73 females in August 1980, 421 males and 290 females in July 1981, 648 males and 479 females in August 1981 and 331 males as opposed to 270 females in September 1981.

Mean brood sizes were calculated separately for females with eggs and females with embryos. At Grays Bay 76 females with intact egg broods were collected over the 12 month sampling period. These animals had a mean brood size of 14.17 (Table 4). Only 7 intact embryo brood pouches were found and these contained a mean of 4.00 embryos and a range of 2 to 6 embryos. At Desdemona Sands 85 intact egg broods were examined yielding a mean brood size of 16.10 while 12 intact embryo brood pouches had a mean of 6.83 embryos (Table 4) and a range of 1 to 13 embryos. A Z test was used to test the

TABLE 1. RESULTS OF THE ANOVA ON DENSITY OF COROPHIUM SALMONIS AT GRAYS BAY AND DESDEMONA SANDS.

GRAYS BAY

Source	MS	<u>ANOVA</u> d.f.	F	p
Date	$3.77 \times 10^8$	16	23.89	.005
Error	$1.57 \times 10^7$	68		

C.V. = 26.16%

DESDEMONA SANDS

Source	MS	<u>ANOVA</u> d.f.	F	p
Date	$4.71 \times 10^9$	16	27.17	.005
Error	$1.73 \times 10^8$	68		

C.V. = 18.26%

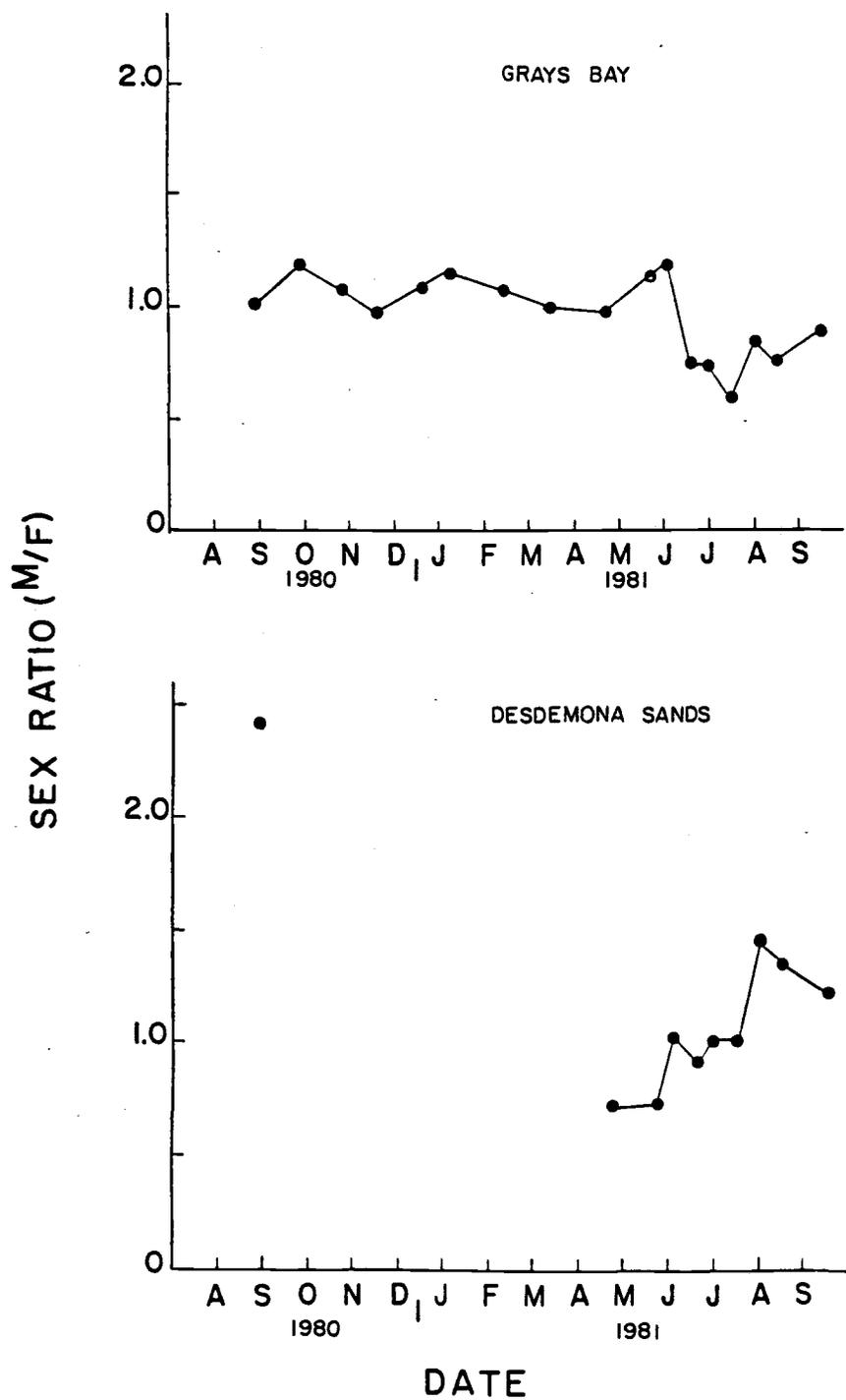


Figure 12. Seasonal sex ratios (M/F) of Corophium salmonis at Desdemona Sands and Grays Bay.

TABLE 2. RESULTS OF THE CHI SQUARE TEST OF SEASONAL SEX RATIOS OF COROPHIUM SALMONIS FOR GRAYS BAY.

Date	Frequency		$\chi^2$	p	M/F
	males	females			
8-28	131	129	.015	NS	1.02
9-25	123	103	1.770	NS	1.19
10-24	72	67	.180	NS	1.07
11-19	121	123	.016	NS	.98
12-18	189	175	.539	NS	1.08
1-15	262	228	2.359	NS	1.15
2-13	310	290	.667	NS	1.07
3-14	289	291	.007	NS	.99
4-21	185	188	.024	NS	.98
5-20	94	83	.684	NS	1.13
6-04	140	118	1.876	NS	1.19
6-17	85	115	4.500	.05	.74
7-01	58	79	3.219	NS	.73
7-14	44	75	8.076	.005	.59
7-28	34	40	.486	NS	.85
8-13	21	28	1.000	NS	.75
9-11	69	77	.438	NS	.90

TABLE 3. RESULTS OF THE CHI SQUARE TEST OF SEASONAL SEX RATIOS OF COROPHIUM SALMONIS FOR DESDEMONA SANDS.

Date	Frequency		$\chi^2$	p	M/F
	males	females			
8-26	176	73	42.606	.005	2.41
4-21	18	25	1.140	NS	.72
5-20	45	61	2.415	NS	.74
6-03	168	163	.076	NS	1.03
6-17	182	198	.674	NS	.92
7-01	254	228	1.403	NS	1.11
7-14	240	231	.172	NS	1.04
7-28	421	290	24.136	.005	1.45
8-11	648	479	25.343	.005	1.35
9-11	331	270	6.191	.025	1.23

TABLE 4. SUMMARY OF STATISTICAL ANALYSIS OF BROOD SIZE OF  
COROPHIUM SALMONIS.

MEAN BROOD SIZE FOR GRAYS BAY.

Type	$\bar{X}$	S	n
egg	14.17	5.449	76
embryo	4.00	1.915	7

MEAN BROOD SIZE FOR DESDEMONA SANDS

Type	$\bar{X}$	S	n
egg	16.10	5.613	85
embryo	6.83	3.589	12

RESULTS OF Z TEST FOR MEAN BROOD SIZE BETWEEN DESDEMONA SANDS  
AND GRAYS BAY (BROODS CONTAINING EGGS).

Z	p
-2.216	>.05

difference between two population means with large sample sizes (McClave and Dietrich, 1979). The Z test indicated that mean egg brood sizes at the two sites differed, with Desdemona Sands having larger broods than Grays Bay (Table 4). A similar test was not done for mean embryo brood size due to the small sample sizes and the difficulty in judging whether or not these broods were intact.

The average length of all mature females, both gravid and non-gravid is presented for each site (Table 5). At Grays Bay a total of 435 mature females were collected. These had a mean length of 5.03 mm. At Desdemona Sands 514 mature females averaged 4.90 mm in length. A Z test found the mean length of the Grays Bay females to be significantly higher than that of the Desdemona Sands females (Table 5) although the difference (0.13 mm) was small.

Mean brood size (Figure 13) and mean length of gravid females were calculated for each site. A one way analysis of variance with date was conducted for both brood size and length of gravid female for each site. Length and brood size both varied significantly over sampling date at Desdemona Sands and Grays Bay (Tables 6 and 7).

To determine if the patterns of change in reproductive state could be related to seasonal effects, the data were subjected to decomposition of the sum of squares which allowed testing of differences within and between the major reproductive seasons (Table 8). For this analysis, the sampling dates were divided into two groups, spring and fall, corresponding to the two reproductive pulses observed. At Grays Bay there was an initial fall appearance of juveniles followed by a spring and a second fall pulse of juveniles. The decomposition of brood size sum of squares according to season

TABLE 5. SUMMARY OF STATISTICAL ANALYSIS OF COROPHIUM SALMONIS  
GRAVID FEMALE LENGTH.

Site	$\bar{X}$	S	n
Grays Bay	5.03	.64	435
Desdemona Sands	4.90	.58	514

RESULTS OF Z TEST FOR MEAN LENGTH BETWEEN DESDEMONA  
SANDS AND GRAYS BAY.

Z	p
3.338	<.05

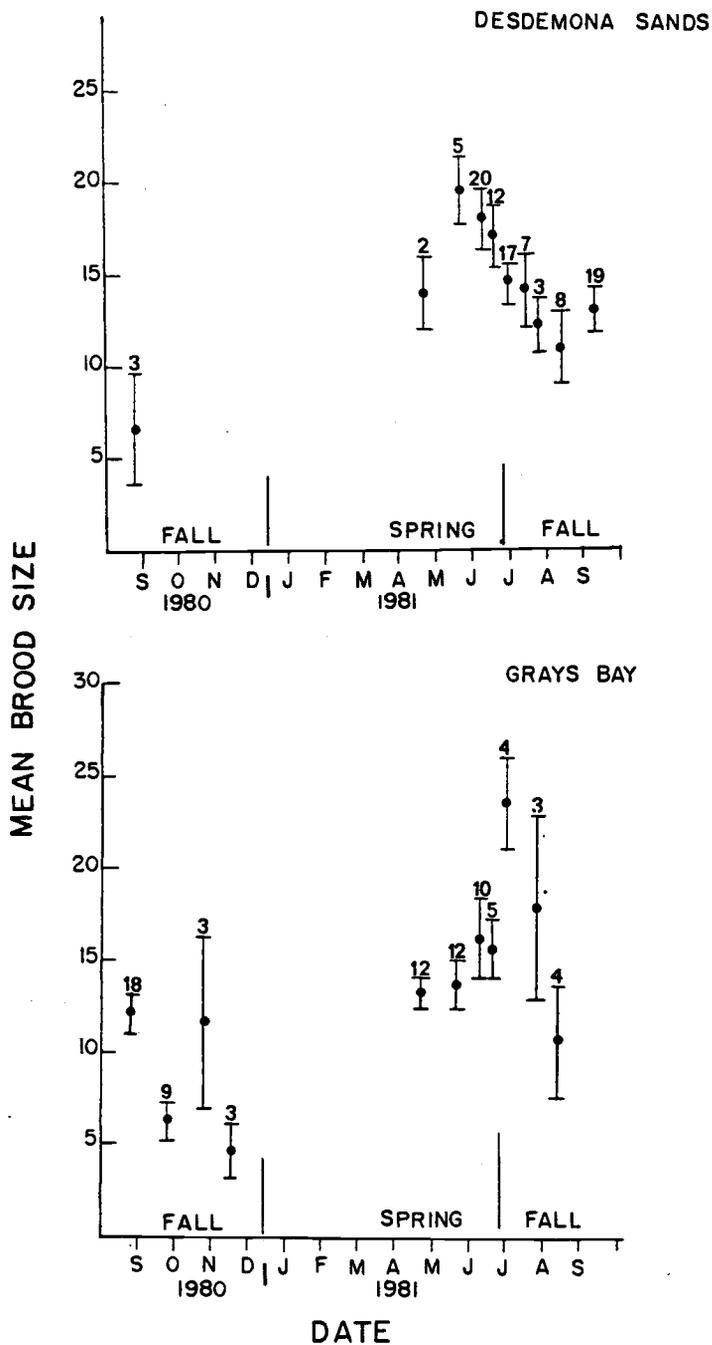


Figure 13. Mean brood size at Desdemona Sands and Grays Bay. Brackets indicate standard error. Numbers associated with each point indicate number of broods examined.

TABLE 6. RESULTS OF ANOVA ON BROOD SIZE AND ON MATURE FEMALE LENGTH OF COROPHIUM SALMONIS COLLECTED FROM GRAYS BAY.

BROOD SIZE

Source	MSE	<u>ANOVA</u> d.f.	F	p
Date	135.24	10	5.77	<.05
Error	23.43	71		

C.V. = 37.09%

MATURE FEMALE LENGTH

Source	MSE	<u>ANOVA</u> d.f.	F	p
Date	1.92	10	10.67	<.05
Error	.18	70		

C.V. = 8.54%

TABLE 7. RESULTS OF ANOVA ON BROOD SIZE AND ON MATURE FEMALE LENGTH OF COROPHIUM SALMONIS COLLECTED FROM DESDEMONA SANDS.

BROOD SIZE

Source	MSE	<u>ANOVA</u> d.f.	F	p
Date	87.61	8	2.45	<.05
Error	35.76	85		

C.V. = 38.97%

MATURE FEMALE LENGTH

Source	MSE	<u>ANOVA</u> d.f.	F	p
Date	2.30	8	9.82	<.05
Error	.23	84		

C.V. = 9.68%

TABLE 8. RESULTS OF THE ANOVA WITH THE DECOMPOSITION OF THE SUM OF SQUARES OF BROOD SIZE OF COROPHIUM SALMONIS COLLECTED FROM GRAYS BAY.

Source	MSE	<u>ANOVA</u> d.f.	F	p
Between spring and fall	296.48	2	12.65	<.05
W/in fall 1	94.14	3	4.02	<.05
W/in spring 1	91.09	4	3.89	<.05
W/in fall 2	112.67	1	4.81	>.05
Error	23.43	71		

at Grays Bay indicated that the brood size within each of the reproductive periods, fall 1980, spring 1981 and fall 1981 did vary significantly by date at the 0.05 level. Additionally, brood size varied significantly at the 0.05 level between the fall 1980, spring 1981 and fall 1981 groups with the spring 1981 broods being generally larger than both the fall 1980 and the fall 1981 groups. A similar pattern was observed for the lengths of mature females at Grays Bay except that the lengths within the fall 1981 grouping were not significantly different at the 0.05 level by date (Table 9). However, the lengths within the fall 1980 and the spring 1981 groups were significantly different at the 0.05 level by date. A significant difference at the 0.05 level also occurred in the values between the spring 1981 grouping and the fall 1980 and fall 1981 groupings. The spring 1981 and fall 1981 females were generally larger than the fall 1980 females. Spring 1981 females were only slightly larger than the fall 1981 females.

Decomposition of brood size and mature female length at Desdemona Sands was confined to the spring 1981 and fall 1981 seasons because the fall 1980 population disappeared in September 1980. At Desdemona Sands decomposition of brood size indicated that the brood sizes did not differ significantly at the 0.05 level within the spring season or within the fall season. However, as at Grays Bay, the spring brood sizes were found to be larger than the fall brood sizes (Table 10). Length of gravid females at Desdemona Sands did not vary significantly at the 0.05 level by date within the fall group, but did vary significantly within the spring group. The values for the length of mature females for the spring were significantly

TABLE 9. RESULTS OF THE ANOVA WITH THE DECOMPOSITION OF THE SUM OF SQUARES OF GRAVID FEMALE LENGTH OF COROPHIUM SALMONIS COLLECTED FROM GRAYS BAY.

Source	MSE	<u>ANOVA</u> d.f.	F	p
Between spring and fall	7.12	2	39.56	<.05
W/in fall 1	.97	3	5.41	<.05
W/in spring 1	.49	4	2.74	>.05
W/in fall 2	.04	1	.19	>.05
Error	.18	70		

TABLE 10. RESULTS OF THE ANOVA WITH THE DECOMPOSITION OF THE SUM OF SQUARES OF BROOD SIZE OF COROPHIUM SALMONIS COLLECTED FROM DESDEMONA SANDS.

Source	MSE	<u>ANOVA</u> d.f.	F	p
Between spring and fall	369.66	1	10.34	<.05
W/in fall	11.88	2	.33	>.05
W/in spring	61.49	5	1.72	>.05
Error	35.76	85		

different at the 0.05 level from the values for the fall mature females (Table 11). The spring females were larger than the fall females.

TABLE 11. RESULTS OF THE ANOVA WITH THE DECOMPOSITION OF THE SUM OF SQUARES OF GRAVID FEMALE LENGTH OF COROPHIUM SALMONIS COLLECTED FROM DESDEMONA SANDS.

Source	MSE	<u>ANOVA</u> d.f.	F	p
Between spring and fall	13.21	1	56.45	<.05
W/in fall	.67	2	2.86	>.05
W/in spring	.75	5	3.21	>.05
Error	.23	84		

## IV. DISCUSSION

Life Cycle of *Corophium salmonis*

The populations of *Corophium salmonis* at both Grays Bay and Desdemona Sands displayed life cycles based on two generations per year. A fall generation of juveniles was produced during late summer and early fall. The reproducing adults then died during the following winter. The juveniles produced in the fall grew and matured throughout the winter and then reproduced the following May and June, and disappeared later in the summer. The spring generation juveniles grew rapidly through the summer and produced the fall generation. Davis (1978) found that *Corophium salmonis* in Youngs Bay, located close to the Desdemona Sands site, also had a two generation per year life cycle. In Youngs Bay overwintering females produced a spring generation by May with the population dominated by juveniles in the summer. This was similar to that found in the present study at Grays Bay and Desdemona Sands. In the Davis study, the proportion of gravid females in the total population increased to 60% in August. These females then produced the fall generation. A study of benthic invertebrates in the Sixes River estuary, Oregon revealed the same reproductive results for *C. salmonis* as the Davis study with a recruitment of juveniles occurring in the spring (Reimers et al., 1979). A study of *C. salmonis* in Grays Harbor, Washington found a population in early spring comprised of overwintering individuals and an increase in reproductive activity in late April and early May (Albright and Armstrong, 1982). Brooding of eggs began in late March 1980 and continued to the end of the

study in September 1980.

Other species of Corophium also have life cycles involving two generations per year. Corophium volutator, a burrowing species like C. salmonis, occurs in intertidal mudflats along the coasts and estuaries of Europe and eastern North America. Watkin (1941) found that in the Dovey Estuary, North Wales, C. volutator produced an overwintering population made up of older mature individuals and juveniles newly hatched in August. The second generation of the year was produced in February, March and April. Fish and Mills (1979) also observed two generations per year for C. volutator in the Dovey estuary, North Wales but spring reproduction commenced in May instead of February. McLusky (1968) found that a C. volutator population in the Ythan estuary, Scotland had one single breeding season per year extending from May to August. Hart (1930) also observed that C. volutator were annual or semiannual reproducers. Differences in the onset of spring reproduction and the number of generations per year are related to differences in the environment. The onset of spring reproduction was found to be correlated with the increase in temperature in the spring. McLusky (1968) reported that 7°C was the minimum temperature needed for C. volutator reproduction. The environment studied by Watkin (1941) may have reached the minimum temperature required by the C. volutator for reproduction earlier in the year.

Juvenile C. salmonis appeared at Grays Bay and Desdemona Sands in May 1981. Temperatures at the two sites in May reached 14°C after winter lows. At Grays Bay the low temperature was 6.5°C in December 1980 after which it began to increase. At Desdemona Sands the low

temperature was 5°C in February 1981. It also increased in the following months. The temperatures at both sites remained in the 17-19°C range throughout the rest of the study. The onset of reproduction at Grays Bay and Desdemona Sands in May 1981 may also be related to the increase in temperatures which occurred that spring and may vary from year to year.

Other Corophium species which have two generations per year include C. arenarium from the Dovey estuary, North Wales and C. insidiosum from the northeast coast of England (Fish and Mills, 1979; Sheader, 1978). C. sextoni from Torbay, England breeds in April and May for a spring generation and in July through September for a summer fall generation (Hughs, 1978). Another species, C. bonelli, although parthenogenic, still exhibits two generations per year (Moore, 1980).

While the populations of Corophium salmonis studied at Grays Bay and Desdemona Sands had sex ratios that were not significantly different from 1.0 through most of the year, during parts of the year the sex ratios did differ significantly from 1.0 at both sites. At Grays Bay the sex ratio dropped in June and July 1981 such that females significantly outnumbered males. This difference may have been due to selective predation on the males. Corophium salmonis provide a major food source for many fish which feed in the Columbia River estuary. Haertel and Osterberg (1967) found that most amphipods consumed by fish in fresh water areas of the estuary were C. salmonis. Coho salmon and chinook salmon captured at Miller Sands had consumed large quantities of C. salmonis especially from March to July (Clairain et al., 1978). Haertel and Osterberg (1967) found

that 50% of the diet of both starry flounder and prickly sculpin in the Columbia River consisted of the amphipod C. salmonis. Prickly sculpin consumption peaked in the spring but starry flounder consumed most during the summer and fall. Starry flounder is the most abundant predator on C. salmonis in Youngs Bay (Higley and Holton, 1975). C. salmonis was heavily preyed upon by both starry flounder and juvenile chinook salmon in the Columbia River estuary during the period of rapid growth from June to September (Higley and Holton, 1975). Some fish guts examined contained only large adult males with well developed second antennae (Higley and Holton, 1975). Male C. spinicorne were often more abundant in stomachs of chinook from the Sixes River estuary. This was also occasionally observed for C. salmonis in chinook stomachs from the Sixes River estuary (Bottom et al., 1982). Since Corophium use the second antennae to forage for food outside the burrow while they remain inside, adult males with larger second antennae may be more prone to predation (Davis, 1978). Males of some species (C. volutator, C. salmonis, and C. spinicorne) are also more active outside the burrow than females which would make them targets for predation (Watkin, 1941; McCarthy, 1973; Bottom et al., 1982; Reimers et al., 1979). During periods of heavy predation such selectivity for males would tend to drop the observed even sex ratio so that females outnumbered males. Albright and Armstrong (1982) reported that C. salmonis greater than 4.00 mm in length generally had a M/F sex ratio less than 1.0 and that it was due to a higher rate of mortality for mature males probably by predation. The higher rate of predation may have been due to the tendency of mature male Corophium to wander over

the tidal flats in search of females, exposing themselves to predation (Albright and Armstrong, 1982). Sheader (1978) and Watkin (1941) both observed that the sex ratios (M/F) of C. volutator declined in June and July and attributed it to die-off of large overwintering males. Die-off again occurred in September and October for males which matured throughout the summer (Watkin, 1941). Either or both factors could have contributed to the change in the sex ratio found at Grays Bay.

The Desdemona Sands population sex ratios, in contrast, were significantly different from 1.0 in late summer and in early fall with males significantly outnumbering females. Males are identifiable at a much smaller size than females, approximately 1.5-2.0 mm, as compared to 2.0-2.5 mm for immature females. This characteristic could lead to males appearing to outnumber females during periods when the population was dominated by juveniles and immatures as was the case for Desdemona Sands in August 1980 and July through September 1981. Davis (1978) found that for Corophium salmonis in Youngs Bay captured in the water column, males generally outnumbered females and for those in the substrate females outnumbered males. However, the sex ratios for the most part did not deviate significantly from 1.0.

Davis (1978) found that female Corophium salmonis in Youngs Bay had a mean brood size of 15.3. Values determined in the present study are very close to this value with a mean brood size of 16.1 found at Desdemona Sands and a brood size of 14.2 found at Grays Bay. Mean brood size for C. salmonis in Grays Harbor, Washington was 11.4 during the spring 1980 but intactness of the broods was not taken into consideration (Albright and Armstrong, 1982). Both Grays Bay and

Desdemona Sands had higher average lengths of mature females than those reported for Youngs Bay. Grays Bay females were 5.03 mm and Desdemona Sands were 4.90 mm, while Davis (1978) reported that most females in breeding condition at Youngs Bay were between 4.00 mm and 4.75 mm. The majority of C. salmonis in Grays Harbor, Washington became sexually mature by 4.5 mm (Albright and Armstrong, 1982). Davis also reported that females were sexable at a length of 1.5 mm while in the present study females were not sexable until 2.0 mm. These differences in length of sexability may be due to different techniques used for measuring individuals. Albright and Armstrong (1982) also found sex of C. salmonis could not be determined for individuals less than 2.0 mm in length.

Davis (1978) found no apparent seasonal trend in mean brood size for the Youngs Bay population over a period of April 1974 through August 1974, January and February 1975 and September, October and December 1975. For both Grays Bay and Desdemona Sands however, mean brood size was observed to differ from spring to fall. At both sites the spring brood size tended to be larger than fall brood size. This difference may be related to the seasonal change in the length of mature females. Spring mature females tended to be larger than those in the fall at both Grays Bay and Desdemona Sands. The spring females derived from the overwintering population had a longer season in which to mature and grow than the females maturing over the summer. Hart (1930) observed that growth of the winter stock of C. volutator was slower than that of the summer stock and the winter stock reached maturity at a larger size. Nair and Anger (1979) also found that the age at which C. insidiosum reached sexual maturity was greatly influenced by temperature. Fish and Mills (1979)

observed that C. volutator and C. arenarium both produced larger broods from the overwintering females than from the summer generation females. They suggest that this was not due solely to the smaller body length of the summer females, but was regulated by the interrelated effects of body length, metabolism, level of food supply and temperature. The larger brood sizes of overwintering females may have reflected different food levels at each season, or it is also possible that high summer temperatures resulted in a reduction of nutrient transfer to the gonads because of increased metabolic utilization. The same factors may be expected to regulate the adult length of spring and fall female Corophium salmonis in the Columbia River estuary. These factors may also explain the differences in mean brood size between Desdemona Sands and Grays Bay where Desdemona Sands had a larger average brood size but smaller average female length than Grays Bay. Temperatures at Grays Bay and Desdemona Sands were much higher in the summer than the winter. Summer temperatures ranged from 16.5°C and 19°C in June 1981 to 17°C in July at Grays Bay. At Desdemona Sands summer temperatures had a range of 15°C in June 1981 to 19°C in August 1981. Winter temperature highs for the sites were 11.5°C in October 1980 at Grays Bay and 11°C in November 1980 at Desdemona Sands. The high summer temperatures found at both sites could have caused reduced nutrient transfer to the gonads as stated by Fish and Mills (1979) and would have resulted in the smaller brood sizes observed in the fall.

Differences observed for broods within the fall and the spring groupings may have been due to inclusion of broods containing embryos. It is difficult to determine whether or not these broods are intact

and as a result inclusion of these broods may have caused low estimates of brood size.

#### Migration of *Corophium salmonis*

The density fluctuations of *Corophium salmonis* observed at Grays Bay and Desdemona Sands can not be explained solely by recruitment of juveniles. Densities at Grays Bay were influenced by adult immigration during the winter and by adult emigration, die-off or predation during the spring. In April 1981 the density at Grays Bay had declined from 29,298/m<sup>2</sup> the previous month to 16,447/m<sup>2</sup>. The decline may have been due to die-off of the large overwintering individuals but the difference in the number of individuals in the larger size ranges was not large enough to explain the total density decline. Predation may have contributed to the decline in the population especially since spring signals the onset of predation by many estuarine fish such as salmon and starry flounder. Also, as stated earlier, adults are more prone to predation than are juveniles and immatures. Whether or not this predation could totally account for the loss of individuals is unknown. Emigration of some of the adults to colonize new habitats may also have occurred. It is unlikely that any single explanation could account for the total decline. It is more likely that a combination of the possibilities would explain the loss.

A different situation occurred at Desdemona Sands, since the entire population disappeared in the fall and adults returned to the site in the spring. Davis (1978) found that *Corophium salmonis* are active vertical migrators. He suggests that these

vertical migrations may be a mechanism to achieve distribution throughout a patchy environment. In this way, the Corophium may leave habitats that have become unsuitable and colonize habitats with newly favorable conditions. This type of migration appears to have occurred at Desdemona Sands. The appearance of Corophium salmonis in April 1981 indicates recolonization of the site when conditions that made the habitat unsuitable in the fall 1980 altered to become favorable again. Fish predation may have contributed to the population decline, however the sand shoals are not common feeding habitats, and fall is not a time of maximum utilization of the estuary by fish. Higley and Holton (1975) found that Corophium salmonis were heavily preyed upon by juvenile chinook salmon and starry flounder from June through September while feeding of salmon occurred on Miller Sands from March to July (Clairain et al., 1978). Although some late summer feeding by fish does occur it is unlikely that predation alone would completely remove the population from the site.

Another possible cause of depopulation at Desdemona Sands is strong currents acting to sweep the animals off the site. However, fall is not the time of heaviest river flow and there was no evidence of scouring at the site as measured by sediment stakes and visual observation. Scouring would be expected in the spring when runoff is highest due to the melt of winter snow pack in the upper basins. Rather than predation or scour, it seems most likely that the animal colonies appear and disappear according to variations in a more subtle environmental parameter.

Among possible factors, water temperature, sediment

characteristics and salinity are three that may determine the suitability of a site as a Corophium habitat. Temperatures measured at the two sites were very similar and did not show any strong difference between Grays Bay and Desdemona Sands. It is therefore unlikely that the dramatic differences in density change at Desdemona Sands were caused by temperature patterns. Hart (1930) observed that the nature of the substratum and the salinity of the water were the main factors leading to the localized distribution of Corophium volutator. Albright and Armstrong (1982) observed however that the C. salmonis distribution and abundance in Grays Harbor, Washington was determined largely by sediment type and beach slope. Salinity did not appear to be as important a factor in controlling C. salmonis distribution and abundance in Grays Harbor as sediment type (Albright and Armstrong, 1982). Sediment characteristics at Desdemona Sands did not change appreciably throughout the study but salinities at the two sites did diverge during the fall (Figures 3 and 4).

The salinity at Desdemona Sands rose in the fall 1980 to greater than 10‰. This rise in salinity was correlated to the disappearance of Corophium salmonis from the site. The subsequent drop in salinity in February 1981 was soon followed by the reappearance of C. salmonis at Desdemona Sands. Therefore, the disappearance and recolonization of Desdemona Sands appear to be in response to yearly salinity fluctuations at the site.

The appearance of adults to the Grays Bay site in the fall occurred simultaneously with the disappearance of the population at Desdemona Sands. Similarly, the decrease in the number of adults in the spring at Grays Bay occurred at the same time as the

reappearance of C. salmonis at Desdemona Sands. Salinity at Grays Bay, where the population was present throughout the year, remained consistently lower, never going above 7‰. This high of 7‰ was also during the fall when fresh water runoff was lowest and salinity intrusion strongest. Populations of Corophium salmonis appeared to be colonizing new habitats in the estuary as salinity conditions became suitable but migrated when salinity increased into areas where the salinities were lower. Studies on Miller Sands (Clairain et al., 1978) where salinities never went above 1.22‰, had density patterns at several stations and tidal levels which were similar to Grays Bay, with peak Corophium salmonis densities occurring during the November to March period. Another study conducted on an intertidal population of Corophium salmonis at the Port of Astoria had a density pattern close to that of the Desdemona Sands population with peak densities occurring in May either due to reproduction or to an influx of individuals into the site (Higley et al., 1982). The site was located along the northeast shoreline of the outer portion of Youngs Bay and would have been subjected to a wide range of salinities during the year.

McLusky (1968) suggested that migrations of Corophium volutator may have occurred in response to salinity. At a site in the Ythan estuary he found that no C. volutator was present when salinities were 0.5 to 1.0‰, but in July as the salinity increased to above 2‰, the Corophium appeared. It appeared that salinity was the critical factor in controlling the distribution and abundance of Corophium volutator (McLusky, 1968). Later, McLusky (1970) found that C. volutator had a stable salinity preferendum of 10 to 30‰

and that the species exhibited a distinct avoidance of low salinities, supporting the migration theory. Mills and Fish (1980) found that the distribution of C. volutator and C. arenarium in the Dovey estuary appeared to reflect their tolerance to low salinities. Because of their distribution, C. arenarium habitats were rarely covered by water of less than 10‰ while C. volutator inhabited areas with salinities as low as 2‰. The authors also found that optimum breeding success and population growth was apparently restricted to an even narrower salinity range than that at which normal embryonic development occurred. Boyden and Little (1973) however, felt that no evidence existed to suggest that salinity preferences were determining the distribution of C. volutator or C. arenarium in the Severn estuary, UK. Siegfried et al. (1980) found that the downstream distribution of Corophium stimpsoni populations within the Sacramento River was regulated by the extent of the salinity intrusion. Hazel and Kelley (1966) observed that both C. stimpsoni and C. spinicorne were limited in their downstream distribution in the San Joaquin Delta by the beginning of the salinity gradient.

Davis (1978) found that Corophium salmonis were active vertical migrators and concluded that dispersal was the most likely reason for the migrations. He stated that long distances could be traversed throughout the brackish water region of the estuary in a few hours with distance and direction variable depending on individual activity related to current direction. Thus it would be possible for widely distributed habitats to be rapidly colonized or abandoned depending on conditions. Davis (1978) observed that his September samples of Corophium salmonis in the surface and midwater strata were older

juveniles between 1.5 mm and 3.0 mm. This was a reflection of the composition of the benthic population at that time in Youngs Bay, and indicated that these older juveniles were the actively moving part of the population in the fall. In the present study the population at Desdemona Sands in August 1980 was also composed almost entirely of older juveniles and it was this population that disappeared in September. The population which recolonized Desdemona Sands in April consisted of older immatures and adults and was a reflection of the population structure at Grays Bay at that time.

Morgan (1965) observed that most C. volutator swam on the ebb tide and that some did swim on the flood tide allowing for both downriver and upriver migration and colonization. Davis (1978) found that C. salmonis had no preference for either ebb or flood tide and would also be capable of both upstream and downstream migrations.

## V. SUMMARY

1. Corophium salmonis collected from Desdemona Sands and Grays Bay in the Columbia River estuary exhibited a two generation per year life cycle. Overwintering individuals produced a spring generation in May 1981. The juveniles then grew throughout the summer and produced a fall generation in July or August.
2. Mean brood size for Desdemona Sands was 16.10 and for Grays Bay, 14.17. Brood sizes and mature female lengths tended to be larger for spring broods than for fall broods.
3. Sex ratios (M/F) at Grays Bay were not significantly different from 1.0 except in June and July 1981 when it dropped below 1.0 and females outnumbered males. At Desdemona Sands the sex ratio was significantly larger than 1.0 in August 1980, July, August and September 1981 when males outnumbered females.
4. The population of Corophium salmonis disappeared from Desdemona Sands in September 1980 and reappeared in April 1981. Observed salinity fluctuations at Desdemona Sands suggest salinity controlled migrations into and out of the site.

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