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Title: <u>DIEL ACTIVITY OF BENTHIC CRUSTACEANS IN THE</u>

<u>COLUMBIA RIVER ESTUARY</u>

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Swimming activity of six benthic peracarid and decapod crustaceans was studied in Youngs Bay, Oregon, an embayment of the Columbia River estuary. Densities of species in the water were determined through horizontal plankton net tows and epibenthic sled tows. Several benthic grab samples were taken to characterize the structure of the infaunal populations. Sampling was conducted in a subtidal region of the bay day and night over several diel and tidal cycles from September 26 to 30, 1975. Animals captured in the water column and in the substrate were characterized according to length, sex, maturity, and body color.

The life-history pattern of the tube-dwelling, infaunal amphipod <u>Corophium</u> <u>salmonis</u> in Youngs Bay was also studied using grab samples collected from April 1974 to September 1975. Animals were characterized according to length, sex, and maturity. This species is the most abundant and extensively distributed macrofaunal resident of the bay, and was the most abundant benthic species captured in the

water column. Swimming activity is discussed in reference to the seasonal pattern of reproductive activity.

Nocturnal activity was the dominant pattern expressed by the resident benthic crustaceans in the subtidal region. Participants included the infaunal amphipods *Corophium salmonis* and *Eohaustorius estuarius*, the epifaunal amphipod *Corophium spinicorne*, and three epibenthic species; the amphipod *Anisogammarus confervicolus*, the mysid *Neomysis mercedis*, and the sand shrimp *Crangon franciscorum*. All of these species were present in the water at relatively high densities during the night and nearly absent there during the day. Densities rapidly increased just after sunset and decreased by sunrise. Although not all tide-light phase relationships were sampled, tidal periodicity in the activity appeared absent.

Mostly juvenile *C. salmonis*, *E. estuarius*, and *N. mercedis* were present in the upper water column, while adults and juveniles both were present in the epibenthic and benthic (for the infaunal amphipods) regions. Among several alternatives considered (molting, reproductive activities, feeding), dispersal from crowded or deteriorating habitats seems the most likely explanation for the appearance of these benthic juveniles in surface waters.

Swimming *C. salmonis* differed from non-swimming ones in sex ratios and coloration. About 60% of the animals taken in the water column were males, while only about 40% of those in the substrate

were males. Among several comparisons made, most deviations from a 1:1 sex ratio were statistically significant. The color of C. salmonis was darker in non-swimmers and lighter in swimmers, according to pigment distribution in integumental melanophores. Several behavioral and physiological responses in crustaceans, including chromatophores and activity, are under neurohormonal control. A model, based on prevailing knowledge of neurohormonal systems in crustaceans, is developed depicting the possible interactions of factors involved in the integration and control of these responses.

Diel Activity of Benthic Crustaceans
in the Columbia River Estuary

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INTRODUCTION

Marine organisms are subject to pervasive periodic fluctua-

tion in their environment driven by various geophysical cycles.

Most notable are those associated with the solar day and year cycles,

and the major periodicities of tidal oscillations. Consequently,

many physiological and behavioral responses of marine plants and

animals are also rhythmic in expression.

One of the more overt classes of rhythmic behavior in aquatic

organisms is the various forms of swimming activity exhibited by

benthic crustaceans inhabiting shallow coastal waters. Many of

these species periodically swim into the overlying water column.

Timing of activity is typically synchronized to particular phases of

the diel light and/or tidal cycles. The primary participants are

peracarids, especially gammaridean amphipods, isopods, cumaceans,

and mysids; and decapods, particularly natantia.

This study was conducted to observe rhythmic swimming by

macrofaunal benthic crustaceans in Youngs Bay, a shallow embay-

ment of the Columbia River estuary near Astoria, Oregon. Previous

work reported by Higley and Holton (1975) and Higley et al. (1976)

had shown several species of peracarids and a decapod to reside in

the bay. These include two infaunal amphipods. Corophium salmonis
and Eohaustorius estuarius, an epifaunal amphipod, Corophium
spinicorne, and four epibenthic species; the amphipod Anisogam-
marus confervicolus, the isopod Gnorimosphaeroma oregonensis,
the mysid Neomysis mercedis, and the decapod Crangon francis-
corum.

The primary objectives of this study were to determine which
species swim into the overlying water column, and to determine as
far as possible the probable functions of the activities. To these
ends, animals were collected by net and grab samplers day and
night over a five day period during the fall of 1975. This sampling
regime was designed to specifically identify:

1) the height above the substrate species swim to,

2) the timing of occurrence of individuals in the water
    column,

3) the proportions of the infaunal populations below the study
    site that were active and non-active, and

4) the types of individuals from the populations which were
    active.

The second objective of this study was an assessment of the
consequence of swimming activity in this dynamic tidally-dominated
hydrographic system upon the structure and dynamics of a resident
infaunal population. Corophium salmonis was studied because of its

wide abundance in the bay. This study was designed to identify:

1)   the life-history pattern of $\underline{C}$. <u>salmonis</u> in the bay,

2)   the possible magnitude of transport into or out of the

        bay resulting from swimming in the water,

3)   and any relationship between seasonal reproductive activity

        and swimming activity.

BACKGROUND

Biological Rhythms

The expression of most overt biological rhythms will cease when the organism is isolated from stimuli associated with the environmental fluctuation in which the rhythm is synchronized. These rhythms are exogenous and result from direct responses to perceived environmental changes. However, some rhythms will persist in isolation from external stimuli, suggesting an internal timing mechanism. Many different internally-mediated, or endogenous, rhythms have been observed in plants and animals, and all such overt responses have come to be known as "biological clocks." An overt rhythmic response, however, may result from the interaction of one or more endogenous and/or exogenous rhythms having the same or different frequencies. For an extensive description of endogenous rhythms, refer to the Cold Spring Harbor Symposium of Quantitative Biology on "Biological Clocks" (1960), Aschoff (1965), Menaker (1971), Palmer (1975), and DeCoursey (1976). The following is a brief description of the more important properties of endogenous rhythms relevant to this study.

Aschoff (1960) states that the only unambiguous evidence for a true endogenous rhythm is a periodic behavior which progressively deviates from the environmental rhythm, from which the organism

has been isolated. If the frequency remains synchronized, he argues that an unknown or overlooked environmental stimulus may still be mediating the rhythm. An endogenous rhythm which is completely isolated from relevant stimuli becomes "free-running" and only approximates the natural period. The expressed rhythm is said to "decouple" from the natural fluctuation. Because the internal oscillator only approximates the natural fluctuations in frequency when isolated, endogenous rhythms have acquired the names of "circadian" and "circatidal" for rhythms with free running periods of approximately 24 h and 12.4 h, respectively (see Palmer, 1975).

Under natural conditions, however, circadian and circatidal rhythms are continually adjusted so that the expressed period matches the natural period. All periodic factors in the environment which are effective in adjusting, or entraining, the phase and period of an internal oscillator to synchony with the natural cycle are called Zeitgebers, or "time givers." One to several factors may entrain a biological rhythm. However, when several factors can operate, one is typically more effective than the others. The more effective factors are usually the more reliable indicators of the critical environmental cycle.

The primary mechanism of synchronization by the Zeitgeber is the adjustment of the phase relationship between the expressed and natural cycles (Aschoff, 1960; Bruce, 1960). Some event of the Zeitgeber, for example dawn in the diel light cycle or maximum

hydrostatic pressure for the tidal cycle, indicates its phase. The internal oscillator varies in its sensitivity and response to the relative phase the Zeitgeber. Thus, if the biological rhythm is lagging behind the phase of the Zeitgeber, the internal oscillator is advanced some degree. If on the next cycle the biological rhythm is still lagging the Zeitgeber, the internal oscillator is advanced some more. If the rhythm precedes the Zeitgeber in phase, then it will be delayed some degree. Thus, during each cycle, the phase relationship can be slightly adjusted as needed.

Typically, the internal oscillator will only adjust slowly, in small changes, to a large change in the Zeitgeber phase. Enright (1970, 1976) points out the ecological usefulness of this "inertia" resisting phase-shifting. The pervasive environmental cycles may have an occasional irregular component generating a single mis-timed, and confusing, stimulus. For example, a storm may greatly perturb factors associated with a tidal excursion. The inertia of the internal oscillator causes entrainment to the average of the previous few environmental fluctuations experienced. The effect of single, mistimed stimuli is thus greatly reduced.

Swimming Activity Rhythms of Benthic Crustaceans

Reported swimming activities by benthic crustaceans may be classified as tidal or diel, based on the dominant period of overt

rhythmicity. The swimming activity of intertidal species has, by

necessity, a tidal periodicity regulated by the time of immersion at

high water. In the first section following, several studies performed

at intertidal beaches are discussed to illustrate the variety of tidal

activity rhythms, including the possible interaction with diel and

semi-lunar month periodicities, that can be expressed. Nocturnal

swimming activity by subtidal species has long been recognized as

a common and complex behavior. Watkins (1941) and Williams and

Bynum (1972) give good, brief discussions of many older observations

of nighttime activity. In the second section, a selection of studies are

discussed to illustrate the variety of nocturnal rhythms that can be

expressed. Finally, in the third section, the several activities

thought to be performed by benthic crustaceans swimming in the

water column are discussed.

Tidal Periodicities

Several species of the haustoriid amphipod genus Bathyporeia

and the oedicerotid amphipod genus Pontocrates occupy distinct

horizontal zones situated from the high intertidal region down to

the subtidal region of sandy beaches in the British Isles (Watkin,

1939, 1941a; Coleman and Seagrove, 1955a, 1955b; Fincham, 1970a).

Intertidal species swam at night during high tide, but were captured

only over their respective habitats. A mixture of sexes and

developmental stages, ranging from juveniles to gravid females, were active. Very few individuals were present in the water during daytime high tides. Subtidal species of these amphipod genera were abundant in nighttime samples taken over the subtidal sands (Bossanyi, 1957), but were rare in intertidal samples. Other intertidal peracarid species active at night over their habitats included the isopod Eurydice pulchra and the cumacean Cumopsis goodsiri.

The overt activity rhythm of the intertidal species is composed primarily of an endogenous tidal rhythm which is enhanced by darkness. Bathyporeia pelagica (Fincham, 1970b), B. pilosa (Preece, 1971), and Eurydice pulchra (Jones and Naylor, 1970; Fish and Fish, 1972) exhibited an endogenous tidal rhythm with swimming beginning at or just after expected high tide and persisting for a few hours. Individuals do not swim continually during the period of activity, but rather swim in bouts of several seconds duration (Watkin, 1939, 1941a; Coleman and Seagrove, 1955b). Endogenous tidal activity was suppressed by light. Animals observed under natural day-night illumination only swam after expected high tides when they occurred during darkness. When B. pelagica and B. pilosa were observed under constant dim light or darkness, all tidal peaks of activity were equal in magnitude. Thus, the expressed rhythms had an endogenous tidal and an exogenous diel component of periodicity.

There is apparently an additional exogenous component in the

activity rhythm of E. pulchra (Watkin, 1941a; Jones and Naylor, 1970; Fish and Fish, 1972). The isopod was observed swimming at the water's edge as it progressed up the beach on rising flood tides. Thus, activity began during flood tide, presumably stimulated by exogenous factors, but continued during ebb tide by endogenous control.

Other sand-burrowing intertidal peracarid crustaceans exhibiting tidal rhythmicity have been studied on open beaches in Southern California. Here they are exposed to mixed semi-diurnal tides often having markedly different tidal amplitudes and periods between extreme water levels each lunar day. Enright (1963) observed that the oedicerotid amphipod Synchelidium n. sp. migrates across the beach in the uprush zone. Individuals emerge from the sand when immersed, swim briefly, then reburrow as the wave wash recedes. Enright (1963) and Klapow (1972a) observed that another intertidal resident, the isopod Excirolana chiltoni, remains localized in the high intertidal and emerges at high water when washed over by waves. As a wave crashes and sand containing the isopods is suspended, they burrow down. As the water begins to recede, they emerge and swim into the flow, thus working to maintain their position on the beach.

The rhythmicity of these species is endogenous with the periodicity and magnitude of activity closely correlated with the periodicity and tidal amplitude of the previous few tidal excursions experienced

before collection (Enright, 1963; Klapow, 1972a). Peak activity corresponds to expected ebb tide, and, unlike the British Isle intertidal peracarids, magnitude of activity is unaffected by the diel light cycle. Klapow (1976), in addition, noted that newborn E. chiltoni, hatched from a gravid female one day after her capture and isolation in the laboratory, immediately expressed the same fully-developed tidal activity as other adults collected at the same time. This very early expression of endogenous rhythmicity emphasized to Klapow the apparent ecological importance of the timing of the activity.

Synchelidium n. sp., like Eurydice pulchra, is active near the water's edge during flooding tides (Enright, 1963). Because this activity is not expressed under constant conditions in the laboratory, the amphipods are presumably active in response to exogenous stimuli. Enright (1961) observed that this species responds to changes in hydrostatic pressure by scrambling and darting about the aquarium. He suggested, therefore, that the amphipods are stimulated to swim by the crashing of waves, which sweeps them up the beach on a flooding tide. However, they remain active by endogenous cue during ebb tide.

This same pattern of tidal rhythmicity was observed for the tube-dwelling Corophium volutator inhabiting estuarine mudflats (Vader, 1964; Morgan, 1965). Animals emerge in flooding water,

follow the water line up the beach, and return on the ebb. Morgan

(1965) showed that animals collected from intertidal sites exhibited

an endogenous tidal rhythm beginning at high slack tide and continuing

for a few hours of the ebb tide. Animals collected from semi-isolated,

tideless brackish water pools exhibited continuous, low-level activity

with no evidence of rhythmicity. Unfortunately, no observations

were made of laboratory or field activity under day-night illumination

for the intertidal and tideless animals, thus the possible existence

of an exogenous nocturnal rhythm is not known.

A final pattern of tidal activity rhythmicity is expressed by

subtidal peracarid crustaceans which migrate into the intertidal

region at night with flooding tides. The amphipods Nototropis

(=Atylis) swammerdami and Gammarus locusta (Watkin, 1941a;

Coleman and Seagrove, 1955b; and Fincham, 1970a) and the mysid

Schistomysis spiritus (Watkin, 1941a; and Coleman and Seagrove,

1955a) occurred in high densities over intertidal sands at nighttime

high tides. These species migrated throughout the year, while

Fincham (1970a) noted greater densities of N. swammerdami and

G. locusta during spring and summer. Essentially only juveniles

partook of the activity. Coleman and Seagrove (1955a) noted that the

mysid tended to swarm at the water's edge and would follow it through

the tidal excursion, while N. swammerdami would remain in the lower

intertidal region. Although many species in subtidal waters were

active at night (Bossanyi, 1957), only a few species migrated into the intertidal at night.

The tidal activities of Bathyporeia pilosa (Preece, 1971), Eurydice pulchra (Fish and Fish, 1972), and Excirolana chiltoni (Klapow, 1972b; and Enright, 1972) are superimposed on a semi-lunar month cycle. B. pilosa and E. pulchra are more active around night-time high tides during spring and falling spring tides and show little or no activity during neap and rising spring tides. E. chiltoni, at least, migrates higher in the intertidal zone with spring tides and lower with neap tides (Klapow, 1972a). These rhythms are endogenous in both species.

Endogenous tidal rhythms can only be entrained by conditions associated with the tidal cycle as experienced by the organism in its habitat. Intermittent swirling of water or sand and water simulating the tidal cycle change in wave-generated turbulence entrained a circatidal rhythm in the following intertidal sand-burrowing peracarids inhabiting exposed beaches: Eurydice pulchra (Jones and Naylor, 1970), Excirolana chiltoni (Enright, 1965; Klapow, 1972a), and Synchelidium n. sp. (Enright, 1963). In addition, Enright (1972) suggested that the fluctuation in wave turbulence arising from greater wave-crash energy higher on beaches during spring tides may be sufficient to entrain the observed semi-lunar month rhythm in E. chiltoni. Attempts to entrain tidal rhythmicity in these intertidal species with

fluctuations in hydrostatic pressure were successful only for

E. pulchra (Jones and Naylor, 1970). They found, however, that

wave-generated turbulence was much more effective in entrainment

than cyclic hydrostatic pressure. However, in intertidal regions not

subjected to large waves, hydrostatic pressure may be more impor-

tant. Fish and Fish (1972), working with E. pulchra from a protected

estuarine beach, suggested that hydrostatic pressure is the primary,

and perhaps the sole, entraining stimulus for these isopods. Morgan

(1965), working with Corophium volutator from an intertidal mudflat,

found hydrostatic pressure to be the only entraining stimulus.

Enright (1963, 1970, and 1976) speculated on the ecological

usefulness of the expressed endogenous tidal rhythms for Excirolana

chiltoni and Synchelidium n. sp. Animals stranded by a receding

tide after having moved up the beach with a rising tide are likely to

die from dessication. Therefore, they must remain active in wave

back-wash as the tide first ebbs. However, irregularity in the

progression of the water-line across the beach arises from such

factors as surf beat and storms. Enright suggested that an endoge-

nous tidal rhythm, entrained as an average of the last few tidal excur-

sions experienced, is a more reliable cue to when ebb tide begins than

any direct stimulus from a receding tide.

Diel Periodicities

Many species of peracarid and decapod crustaceans found in or close to substrate in coastal waters have been observed to swim into the water column at night (Fish, 1925; Russell, 1925, 1927, 1931; Bossanyi, 1957; Herman, 1963; Thomas and Jelley, 1972; Williams and Bynum, 1972; and Hobson and Chess, 1976). Typically, a few species tend to be much more abundant than others in the water. The density of most species generally decreases towards the surface (Russell, 1925; Bossanyi, 1957), however, some species swarm in the surface waters. Russell (1931) noted that while the mysid Leptomysis gracilis congregated near mid-water in a 51 m water column, the mysid Anchialina agilis swam to the surface. This division was also noted in two species of cumaceans: Diastylis rostrata stayed at mid-depth while Bodotria scorpioides went to the surface.

Very few of the nocturnally-active animals were captured in daylight samples. Russell (1927) failed to catch any of the benthic species he reported to be nocturnally-active, and concluded that they either re-entered the sediment or, for the mysids, stayed on or very close to the bottom. Bossanyi (1957), using an epibenthic sled, captured occasional swarms of some non-burrowing amphipods and mysids. Hobson and Chess (1976) observed, while diving, infaunal

species reburrowing in the sand bottom and epibenthic species returning to the shelter of kelp fronds just before sunrise.

Seasonal differences in the density and types of individuals which swim at night have been observed by Fish (1925), Tattersall (1938), Bossanyi (1957), Herman (1963), and Williams and Bynum (1972). Many of the differences have been attributed to seasonal reproductive behavior (Fish, 1925; Herman, 1963; Williams and Bynum, 1972). Bossanyi (1957) obtained evidence to suggest that some intertidal and shallow subtidal sand-burrowers may move offshore during winter and return by summer. During summer, Tattersall (1938) often captured mysids at various stages of development, including breeding adults, while during winter captured predominantly juveniles. He suggested that the relatively low catch of juveniles during summer, the period of their maximum production, resulted because they were higher in the water column and thus avoided capture by the epibenthic sled used. Fish (1925) observed large numbers of amphipods and cumaceans in surface waters at night during their respective breeding seasons. Usually, a mixture of developmental stages, including gravid females, was captured.

A variety of endogenous and exogenous nocturnal rhythms have been observed. Enright and Hamner (1967) studied an assemblage of coastal crustaceans first under simulated day-night illumination and then under constant dim light. Three types of nocturnal biological

rhythms were exhibited by benthic species. First, the amphipod Nototropis (= Atylis) sp. and the isopod Exosphaeroma sp. exhibited an endogenous rhythm which persisted for several days under constant illumination. Secondly, the amphipod Tiron sp. exhibited an endogenous rhythm that was expressed for only one cycle, suggesting a timing mechanism analogous to an hour-glass. Animals which swam up at the beginning of darkness returned, under constant illumination, at the time of expected sunrise. They did not swim up at the next time of expected sunset. The time of sunrise was apparently anticipated by an endogenous cue and the return migration began without sensing a change in light intensity. Presumably, the experimental animals would not swim to the surface again until another period of daylight then sunset was experienced.

The final type of rhythm exhibited was exogenous. The mysid Metamysidopsis elongata swam to the surface at darkness and swam down when illuminated. Exogenous nocturnal rhythmicity has also been observed in the isopods Idothea chelipis and I. baltica, and in the amphipod Gammarus oceanicus by Jansson and Kalländer (1968), and in the amphipod Tritaeta gibbosa by Jones et al. (1973).

Functions of Swimming Activities

Swimming activity by infaunal and epibenthic crustaceans is a complex behavior. Activity occurs in different habitats, is

expressed by different developmental stages, and is regulated by various environmental cycles. Compounding the complexity, however, is the probability that swimming activity serves several different functions for these benthic species. These functions can be divided into three categories: 1) various processes related to reproduction and molting, 2) feeding, and 3) juvenile dispersal.

Many peracarids and decapods molt while present in the water at night. Lloyd and Yonge (1947) report that the decapod <u>Crangon</u> <u>vulgaris</u> left the substrate at night to molt, while Corey (1970) captured a high proportion of newly molted <u>Iphinöe</u> <u>trispinosa</u>, a cumacean. Mysids usually molt at night between 2000 h and 2400 h, after which very few remain in the upper water column (Tattersall and Tattersall, 1951; Clutter, 1969). Anger and Valentin (1976) and Valentin and Anger (1977) observed while diving that the cumacean <u>Diastylis</u> <u>rathkei</u> also emerged at sunset, molted, and returned to the sand by midnight. This cumacean was primarily active over a period of about one week during the several months of observations. The researchers estimated that during peak activity, about 15% of the infaunal population swam during a night, and that about 65% of the entire population molted in a few days.

This last observation implies synchronization of molting, and is supported by Klapow's (1972b) study of semi-lunar month rhythmicity in the isopod <u>Excirolana</u> <u>chiltoni</u>. Many individuals, all of various

developmental stages, molted during their "active" phase at spring tide. In addition, this semi-lunar month rhythm of molting was endogenously expressed in the laboratory. The remarkable synchrony of molting by various developmental stages suggests that, in some way, the intermolt periods are adjusted to multiples of the nearly 15 day period between spring tides.

In mature peracarids, several reproductive processes are carried out in conjunction with molting. Female peracarids generally release ripe eggs through genital pores into the ventral brood pouch immediately after molting, while the new exoskeleton is still soft (Barnes, 1974). Klapow (1972b) speculated that copulation in _E. chiltoni_ occurs after molting during the semi-lunar month activity during spring tides. Similarly, the presence of many ovigerous female _Bathyporeia pilosa_ active during falling spring tides and the observation by Watkin (1939) of a 15 day development time between egg fertilization and hatching, led Preece (1971) to suggest that _B. pilosa_ may swim to release offspring into the water, lay new eggs, and copulate.

Nocturnal reproductive activity is particularly well-coordinated in mysids. Gravid female mysids will swim up in the water at night, release the offspring from the brood pouch, molt, lay ripe eggs into the new brood pouch, and copulate, all in rapid succession (Tattersall and Tattersall, 1951; Clutter, 1969). Clutter (1969) noted that mature

female _Metamysidopsis_ _elongata_ repeated this cycle every ten days.

Male peracarids can find newly molted and receptive females by detecting a released pheromone. Clutter (1969) observed that male _M._ _elongata_ within 5 cm of a molting or newly molted adult female immediately swam faster and in a convoluted pattern, apparently in search of the female. The success rate of eventually finding the female, after first detected, was 50%. Males will not attempt to copulate with females not having ripe eggs, and will attempt to copulate with other males which have just mated with a female. Females of the amphipod _Tritaeta_ _gibbosa_ are sessile on sponges and ascidians, and only males are active at night (Jones et al., 1973). Fincham (1974) suggested that these males may locate receptive females by detecting pheromones, citing Dahl et al. (1970), who demonstrated that male _Gammarus_ _duebeni_ responded to a female pheromone.

Some predaceous peracarid and decapod crustaceans swim at night to feed. Watkins (1941a) noted that the isopod _Eurydice_ _pulchra_ preyed on swimming animals in the lab, and in the field observed them to emerge at night to feed with the incoming tide and to sink to the sand with the retreating tide. He also suspected that feeding activity occurred during daylight. Jones and Naylor (1970) observed a behavioral difference between starved and satiated _E._ _pulchra_. Starved isopods were photopositive, while satiated ones were

photonegative. This suggested to the researchers that in daylight,
when the isopods are washed out of the sand by a crashing wave,
starved animals begin to swim, presumably to feed, while satiated
ones reburrow. In darkness, however, there is no apparent photo-
taxic response and more isopods probably remain active. Species
of the decapod genus Crangon, though omniverous, are generally
predaceous (Plagmann, 1939, cited in Muus, 1967; Lloyd and Yonge,
1947; Muus, 1967). Generally, they remain buried in substrate during
daylight and are active at night, in part, to feed (Havinga, 1929,
cited in Lloyd and Yonge, 1947; Herman, 1963; Green, 1968).

Hughes' (1968) laboratory study of the nocturnal swimming
activity of the predaceous pink shrimp Penaeus duorarum is an ex-
ample of how the timing of prey availability and the diel light cycle
both act to entrain the activity rhythm. During daylight, these shrimp
remain buried in sand and emerge at night to swim and feed. This
rhythm will persist for several cycles under constant conditions
and in the absence of feeding. Animals maintained under a day-night
illumination regime, and thus endogenously entrained to that rhythm,
showed evidence of an exogenous response when the lights were
turned off during the expected daylight period. They slowly emerged
over the first 90 minutes of darkness; most, however, soon re-
burrowed. The activity was probably not fully expressed because it
was contradictory to the animal's physiological state. Six days were

required for complete entrainment to a 120° phase shift in an imposed light-dark cycle. If a shrimp was hungry, it would emerge, even in light, when food was placed in the aquarium. The shrimp would emerge 24 hours after feeding, cued endogenously, without the stimulus of more food. If shrimp were given food upon emergence in darkness, they became completely entrained to a 120° phase shift in an imposed light-dark cycle in only three days, as opposed to the six days required without feeding. The time of feeding, presumably at night when prey are available, and the diel light cycle are both components of the shrimp's Zeitgeber.

In many species only juveniles are active at night (e.g., Foxon, 1936; Tattersall, 1938; Watkin, 1941a; and Corey, 1970); or, as noted for Gammarus locusta by Blegvad (1922), juveniles may be active in a different region of their habitat from the adults. Foxon (1936) noted that only older juvenile cumaceans swam while younger ones remained in the sand, and suggested that nocturnal activity may be delayed until sexual maturity is approached. Perhaps implicit in his suggestion is that activity is delayed until the molt from the last juvenile to first mature instar with immediate copulation and egg fertilization. However, active juveniles of many species are not near maturity, leading many researchers to suggest activity may facilitate dispersal (e.g., Watkin, 1941a; and Corey, 1970). Advantage to dispersing individuals may be conferred under situations of

crowding, competition, or a deteriorating habitat (Emlen, 1973).

Wilson (1975) pointed out that the best colonizing females are those

with the highest reproductive value; these are typically the older

immatures.

The Columbia River Estuary

Sedimentation and Geomorphology

The lower Columbia River is a coastal plain estuary composed

of two distinct geomorphic regions (Hubbell and Glenn, 1973). In

one region, above Columbia River Mile 30 (CRM 30), the river runs

in a main channel 1 to 2 km wide during low discharge at mean lower

low water, and is contained between steep valley walls 3 to 5 km

apart. There are several large permanent islands bounded by small

channels and sloughs. Most of the river bottom in this region is

covered by sand deposits formed into sand waves (Whetten et al.,

1969).

The river broadens below CRM 30 into the second geomorphic

region, containing the estuary (Figure 1). Water flow becomes less

channelized and spreads over the entire width of the estuary at high

tide. Consequently, sand has been deposited as vast shallow flats

and shoals throughout much of the central region. Many flat, bare

sand islands are exposed at low tide, especially off Youngs Bay and
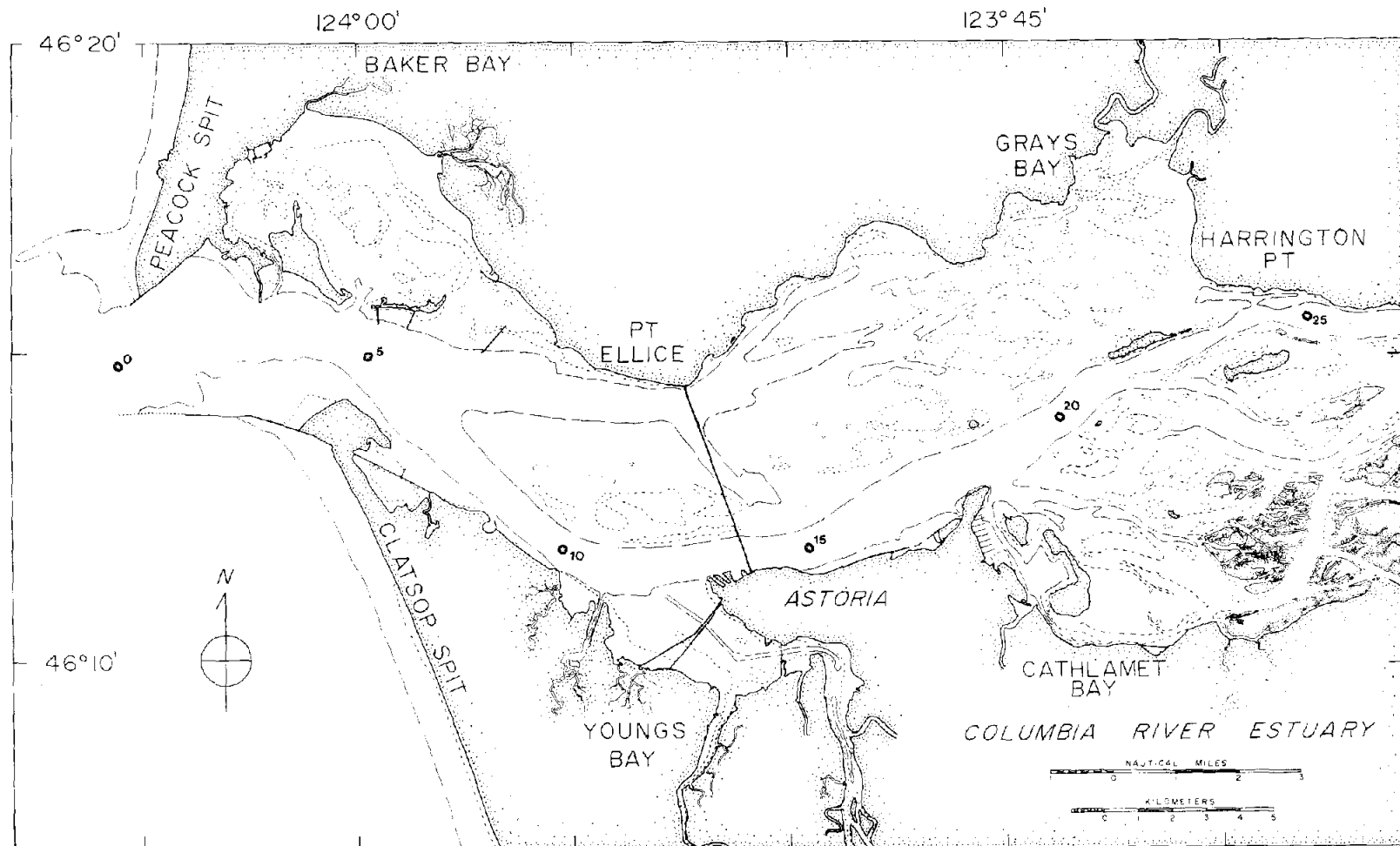
Figure 1. The Columbia River estuary. Areas exposed at mean lower low water are enclosed by —··—··—·· , and the 18 foot (5.5 m) contour is indicated by — — — . River mile distance is shown at five mile increments. Adapted from NOAA C & GS charts 6151 (1974) and 6152 (1972).

upstream to Harrington Point (Figure 1). Several semi-permanent,

vegetated islands, surrounded by channels and sloughs, occupy much

of the upper end of the estuary. These islands are occasionally

inundated at high tide. Four large, shallow embayments (Baker

Bay, Youngs Bay, Grays Bay and Cathlamet Bay) drain adjacent

highlands through small rivers. Extensive deposits of mud have

formed in these bays, along shorelines, and in the lee of some of the

sand islands.

Hydrography

The Columbia River discharges about twice as much fresh

water into the North Pacific Ocean as all of the other rivers in

Washington, Oregon and California combined. The mean annual

discharge at the mouth is 7,300 m^3/s, while monthly mean values

range from 3,000 to 20,000 m^3/s (Neal, 1972). However, estimated

instantaneous discharges off Astoria, Oregon often exceed 60,000

m^3/s during ebb flows at high discharge (Lutz et al., 1975). Highest

discharges occur in the spring and early summer due to the melt of

winter snow pack in the upper basins. Lowest flows occur during

late summer and early fall. Large discharges of short duration,

occasionally equaling spring runoff in rate, can occur in winter from

local heavy rainfall.

The tides at the Columbia River are the mixed, semi-diurnal

type typical of the eastern North Pacific coast, with two high waters and two low waters each lunar day, all of different heights. At the mouth, mean and diurnal tide ranges are 1.7 m and 2.3 m, respectively. The extreme tidal range, however, may exceed 4 m. Tidal waves are amplified upriver, reaching maximum amplitude at Youngs Bay (near CRM 12) where mean and diurnal ranges are 2.0 and 2.6 m, respectively (Neal, 1972).

The unusual combination of large river discharge and strong tidal currents results in a very dynamic hydrologic regime. Flow reversals occur with moderate frequency at Prescott, Oregon (CRM 73), and even occasionally occur at discharges exceeding 8,500 m^3/s (Snyder and McConnell, 1973). Neal (1972) estimated flushing times in the estuary of 1/2 to 5 days, depending on discharge and method of calculation. Lutz et al. (1975), working near Astoria, Oregon, observed near-surface velocities up to 2.4 m/s during ebb flow and up to 1.8 m/s upstream during flood flow.

During most of the year, the estuary is partially mixed. During low discharge, the salinity intrusion may extend to Harrington Point (CRM 23) at higher high waters and to CRM 17 at lower low waters (Neal, 1972). During high discharges, the intrusion is usually confined to the lower several miles of the estuary.

The north channel conveys, on the average, 73% of the total water flow in the estuary, and the circulation pattern is complicated

by lateral exchange between the north and south channels (Lutz et al., 1975). During all discharges except those between 4,000 m^3/s and 5,400 m^3/s, more water is conveyed up the north channel during floods than returns during the next ebb. Presumably, entering water encounters an easier and more direct route up the north channel, and the south channel, although longer and more circuitous, conveys downstream flow more effectively because of its continuous deep path through the estuary. The excess water flows laterally through the small channels across the central shoal region of the south channel. Thus, there is usually clockwise circulation in the estuary. Only when discharges fall between 4,000 m^3/s and 5,400 m^3/s does circulation flow in the opposite direction.

The direction of net water transport off Astoria, Oregon (CRM 13 to CRM 17) is complicated by a complex bottom topography and the occasional intrusion of the salt wedge through the area. Lutz et al. (1975) reported flow predominance values in the region at various river discharges. These values represent the percentage of total flow averaged over a tidal cycle directed downstream. At low discharge (2,270 m^3/s), net flow is directed upstream near the bottom in the north channel, in a middle channel across the central shoal region, and in the south channel (Figure 2). Net upstream flow, in addition, persists in the middle channel even during high discharge when net flow is downstream throughout the water column in the north and
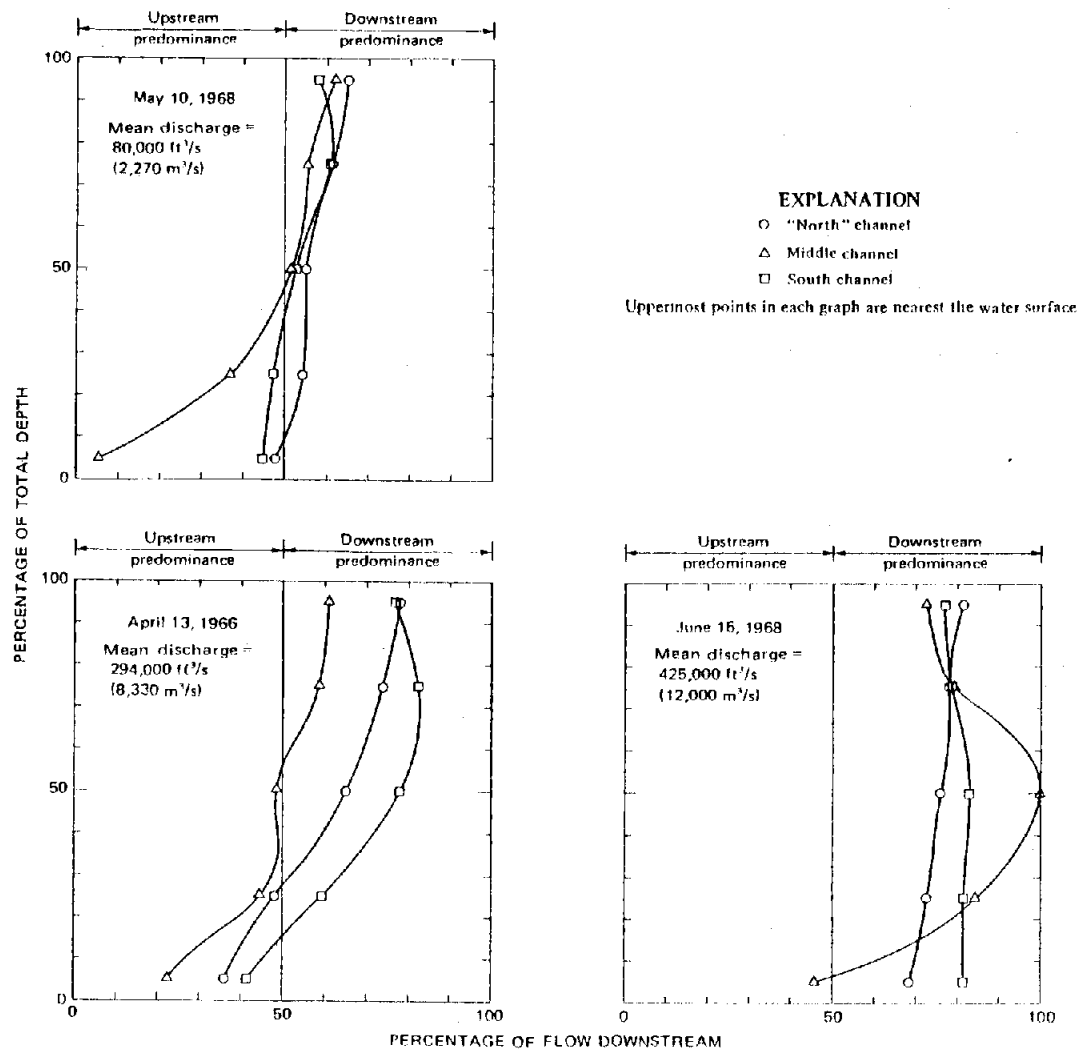
Figure 2. Flow predominance of the Columbia River off Astoria, Oregon under different discharge rates. Taken from Lutz et al. (1973).

south channels.

Youngs Bay

Youngs Bay is a broad, shallow embayment opening onto the
south channel of the lower Columbia River estuary between CRM 10.7
and 12.4 (Figure 1). A navigational channel extends up the center of
the bay 2 miles where it splits; one channel leads south into the
Lewis and Clark River, and another leads east into the Youngs River.
Channel depth varies from 3 m to over 30 m (at MLLW) within the
bay. Nearly one-third of the area at high water, especially along
the south-west shoreline, is exposed as mud flats at low water.

Measurable salinity occurred in the bay during all seasons
except the spring freshet in 1974 (Higley and Holton, 1975; OSU,
Ocean Engineering Program, 1975). High tide salinity near the
bottom at the causeway (U.S. Highway 101) ranged near 0‰ during the
freshet to over 15‰ during the fall. Surface salinity ranged near 0‰
to over 5‰ in the fall, and measurable salinity was found upriver
to mile 12.

The water circulation pattern in Youngs Bay is influenced by
two major features (Figure 3). First, most of the water flowing
into and out of the bay is conveyed along the main navigational chan-
nel. Near-surface current velocities through here may reach 1.0
m/s. The second feature, an obstruction to some flow, is the
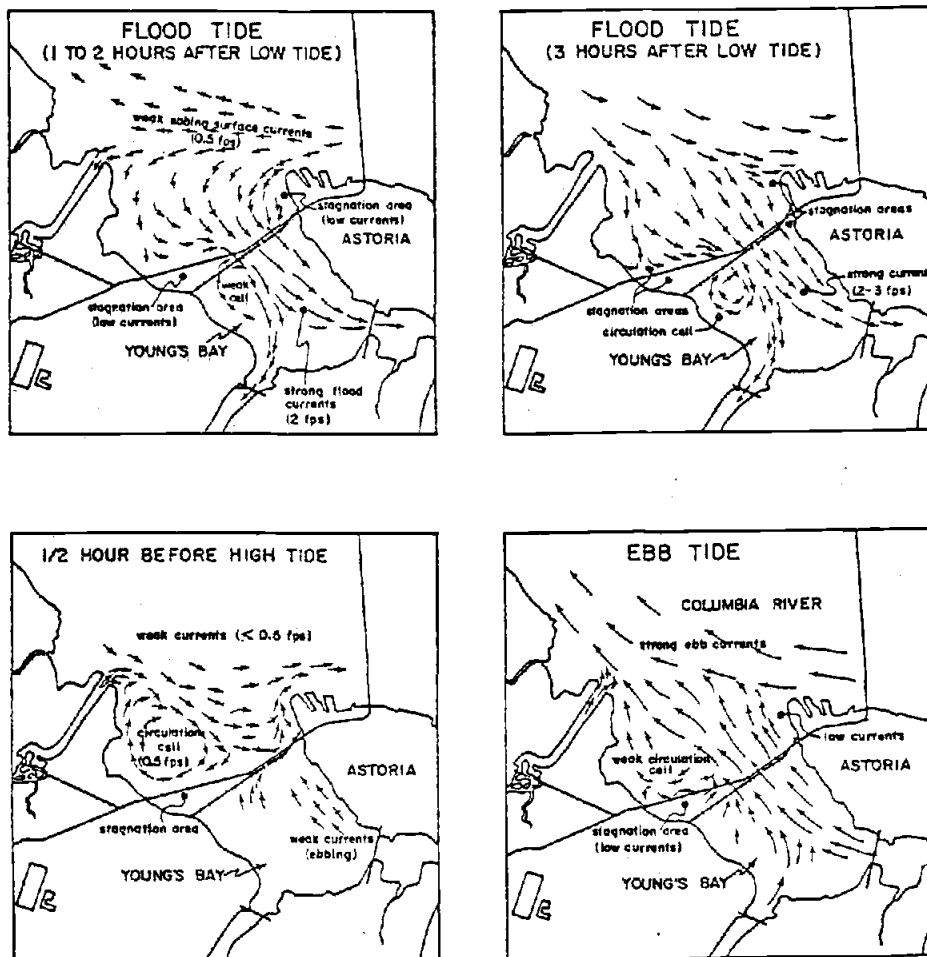
Figure 3. Water circulation patterns in Youngs Bay, Oregon at different tide stages. Taken from OSU, Ocean Engineering Program (1975).

causeway spanning the mouth of the bay. Nearly one-half of the road, beginning at the south shoreline, is supported by a filled base which acts as a barrier to water flow. Consequently, at various tide stages, weak circulation gyres may form on either side of the fill.

Sediment texture distribution and deposition rates reflect this water circulation pattern (OSU, Ocean Engineering Program, 1975; Johnson and Cutshall, 1975). Youngs River and Lewis and Clark River fine sediments settle out along the south shoreline between the causeway fill and the river mouths. These deposits are composed mostly of silt- and clay-sized particles. The region between the fill and the mouth of the Skipanon waterway also contains a large proportion of silt and clay. Columbia River fine sand dominates deposits beneath the high velocity water zones of the deeper channels in the bay and most of the mouth region downbay of the causeway.

The area of shallow tidal flats along the south shoreline has greatly increased since the beginning of the century (OSU, Ocean Engineering Program, 1975). Construction of the entrance jetties to the Skipanon waterway and the causeway have undoubtedly led to increased deposition of fine sediment. The causeway was constructed in 1964, and Johnson and Cutshall (1975) estimated that the deposition rate immediately upbay of the fill has been 4 cm/year since. Clear-cut logging on the local drainage basins and dredge spoil disposal may also have accelerated sediment deposition within the bay.

Benthic Fauna

Columbia River Estuary Benthic Crustacean Fauna

The Columbia River estuary, although a very dynamic system,

supports a rather diverse benthic crustacean fauna relative to other

estuaries (Haertel and Osterberg, 1967). The Pacific Northwest

shore fauna is characteristically rich in the number of euryhaline

species within represented genera and families relative to the North

Atlantic Coast (Bousfield, 1958). Many of these species inhabit the

Columbia River estuary where, because of the large tidal ranges and

great variations in river discharge, they are subjected to wide fluctu-

ations in salinity. There are two distinct faunal assemblages within

the estuary primarily distinguished by their different salinity toler-

ances. Within tolerable salinity regions, however, the distribution

and abundance of species is strongly related to sediment character.

One assemblage, best characterized as marine-brackish, is

composed primarily of marine species which invade brackish bays,

river mouths, lower estuaries, and regions of freshwater seepage

on coastal beaches. The sand burrowing amphipods Eohaustorius

washingtonianus, E. sawyeri, and Paraphoxus milleri were found

in sand deposits ranging from outside the mouth of the river up to

the central estuary off Youngs Bay (Higley and Holton, in prep.).

Densities were near or less than 100 per m^2. The distribution of

another amphipod, Corophium brevis, sporadically captured in the lower estuary, is unclear. This is a tube-building marine species, sometimes found extensively in sediment or on pilings in high salinity bays such as Netarts Bay (Stout, 1976), which probably inhabits only the first few miles of the estuary. However, it does occasionally occur in Youngs Bay, but probably is accidentally transported this far upstream with the salinity intrusion.

Several additional marine-brackish species belong to the decapod genus Crangon and the mysid genera Archeomysis and Neomysis. Higley and Holton (in prep.) report C. stylirostrus only near the mouth of the river, and Haertel and Osterberg (1967) report C. nigricauda in 30‰ + salinity water in the river. Higley and Holton (in prep.) found A. grebnitzkii extending upriver only as far as about CRM 8. Haertel and Osterberg (1967) report two species of Neomysis in the higher salinity regions of estuary. N. rayii was reported to occur in water only down to 18‰ salinity, and N. kadiakensis was found in water down to 5‰ salinity.

The second assemblage can be characterized as freshwater-brackish. The amphipod Corophium salmonis is the most conspicuous member of this assemblage, and is extensively found in fine sand and muddy deposits in sheltered areas from the central estuary near Youngs Bay up to at least the mouth of the Willamette River at Portland, Oregon (Higley et al., 1976; Higley and Holton, in prep.;

Sandborn, 1973). Densities of this species are often quite high, usually exceeding 10, 000 per m^2. A species of Neomysis was also found this far upriver by Sandborn (1973). He identified it as N. awatchensis; however, in the extensive work reported in Higley and Holton (in prep.), only the morphologically very similar N. mercedis was found in the upper brackish and lower freshwater reaches of the river.

Additional species belonging to the freshwater-brackish assemblage include two amphipods and a decapod. The amphipod Eohaustorius estuarius is moderately abundant in fine and medium sand in the central and upper estuary, especially in the region off Astoria, Oregon and in the mouth region of Youngs Bay. It is occasionally taken downstream as far as Baker Bay (Higley and Holton, in prep.). The amphipod Anisogammarus confervicolus was consistently captured off the mouth of Baker Bay by Misitano (1974) and was encountered throughout the entire estuary and into the freshwater reach by Higley and Holton (in prep.). Haertel and Osterberg (1967) report the salinity distribution of the sand shrimp Crangon franciscorum in the estuary as 0‰ to 30‰.

The distributions of two additional species in the estuary, Corophium spinicorne and the isopod Gnorimosphaeroma oregonensis, are not well enough known to assign them to either assemblage. Both species are common in Youngs Bay (Higley and Holton, 1975).

C. spinicorne was sporadically captured in the lower estuary and outside the mouth of the river (Higley and Holton, in prep.). Observations of this species in the Sacramento-San Joaquin Delta suggest it is broadly euryhaline, occurring in water of full salinity to fresh, but is restricted from high salinity regions in the estuary by two other marine species of this genus (Filice, 1958; Aldrich, 1961; Hazel and Kelley, 1966). In the Columbia River, C. spinicorne should probably be considered a brackish water species. Haertel and Osterberg (1967) describe its salinity distribution in the estuary as 5‰ to 30‰.

The isopod G. oregonensis is reported to be notoriously euryhaline, occurring in water of full salinity to fresh (Menzies, 1954). There is a morphological difference between individuals found in high and low salinity and each has been described by Menzies (1954) as a subspecies. Whether they are genetic subspecies or the morphological difference is just related to salinity is not known. In the Columbia River, this species has been found throughout the estuary, from Clatsop Spit to Grays Bay (Higley and Holton, in prep.). More work is needed to determine "subspecies" distributions before assignments to assemblages can be made.

Youngs Bay Benthic Fauna

The amphipod Corophium salmonis and oligochaete worms

dominate macroinfaunal densities in Youngs Bay (Higley and Holton, 1975; Higley et al., 1976). For these studies, macroinfauna was defined as animals living in sediment which are retained on a 0.425 mm screen. $\underline{C}$. $\underline{salmonis}$, found intertidally and subtidally in mucous and mud tubes in soft sediment, commonly occur at densities exceeding 10,000 per m^2 and occasionally exceed 40,000 per m^2. Highest densities are found in sheltered regions of the bay where sandy mud deposits accumulate. Oligochaetes are captured at comparable densities in muddy areas, and are more abundant in deposits composed mostly of silt and clay. Densities for these worms may be underestimates of real values because some were probably lost through the 0.425 mm screen upon sieving. Regardless, on a weight basis, the larger $\underline{C}$. $\underline{salmonis}$ comprises most of the bay's infaunal biomass standing stock.

Several other infaunal taxa, though less abundant, are common in intertidal and subtidal deposits. The burrowing amphipod $\underline{Eohaustorius}$ $\underline{estuarius}$ is found in the mouth region of the bay but restricted to sandy deposits ranging from clean medium-fine sand to muddy fine sand. Densities of this species are commonly less than 1000 per m^2. The nereid polychaete worm $\underline{Neanthes}$ $\underline{limnicola}$ and the bivalve mollusc $\underline{Macoma}$ $\underline{baltica}$ are distributed throughout the bay in sandy to muddy deposits, and are usually present in densities less than 1000 per m^2. Nemertean worms apparently occur

sparsely in fine sediment.

Meiofauna were abundant in a few 3.5 cm cores taken in Youngs Bay sediment, with harpacticoid copepods, nematode worms, and ostracods commonly found (Higley and Holton, 1975). In a deposit of primarily silt and clay, harpacticoid copepod densities (predominantly Canuella canadensis with some Ectinosoma sp.) exceeded 200, 000 per m^2 in the upper 1 cm layer of sediment, while in a sandy mud deposit, densities were near 50, 000 per m^2 in the surface layer. Densities decreased markedly with depth. Nematodes and ostracods were less abundant, occurring in densities near 30, 000 per m^2 in the upper 1 cm layer in the fine mud deposit and near 10, 000 per m^2 in the surface of the sandy mud deposit. In sand, all meioinfaunal densities were typically less than 10, 000 per m^2 in the various 1 cm layers of sediment.

Some epibenthic crustaceans commonly occur in the bay, although their distributions and abundances are not well known. The amphipod Anisogammarus confervicolus, the mysid Neomysis mercedis, and the sand shrimp Crangon franciscorum were occasionally taken by grab sampler (Higley and Holton, 1975), although this gear is not effective in capturing these species. Otter trawl samples taken during this project suggest that C. franciscorum and N. mercedis can be quite abundant during the summer and fall.

The shoreline surrounding Youngs Bay harbors a faunal

assemblage different from that in the intertidal and subtidal mud deposits. Corophium spinicorne builds mucous and detritus tubes on firm surfaces such as vegetation, pilings, and rocks along the shoreline. The isopod Gnorimosphaeroma oregonensis and the ampharetid polychaete Amphicteis floridus are abundant in and around the vegetated areas. A. confervicolus is often found among vegetation at high water and around plant rhizomes or beneath rocks along the shoreline when exposed at low water.

MATERIALS AND METHODS

Swimming Activity Rhythms

Sampling

The mouth region of Youngs Bay, that area downstream of the causeway and inside of the entrance to the bay, was selected as the study site for several reasons. First, the water circulation pattern in the region is simple and well-known. The magnitude of water transport into and out of the bay by tidal action can be estimated. Secondly, several grab samples taken throughout 1974 and in part of 1975 were available for study of the seasonal changes in population structure of infauna. Finally, the sampling gear and methods used by Higley and Holton (1975) had proven effective for work in that area, and were available for use.

A tow line was established that extended from the Milcap buoy near the mouth of the Skipanon Waterway half-way across the bay, a distance of about 1 km (Figure 4). The line was nearly perpendicular to the dominant direction of water circulation into and out of the bay (Figure 3). It was situated between a persistent circulation gyre along the southwest shoreline and the dredged ship channel near the opposite shore. Water depth gradually increased away from the Milcap buoy along the tow line from about 4 m to 6 m (MLLW). Two months prior to sampling, a section of chain spread between otter trawl doors was
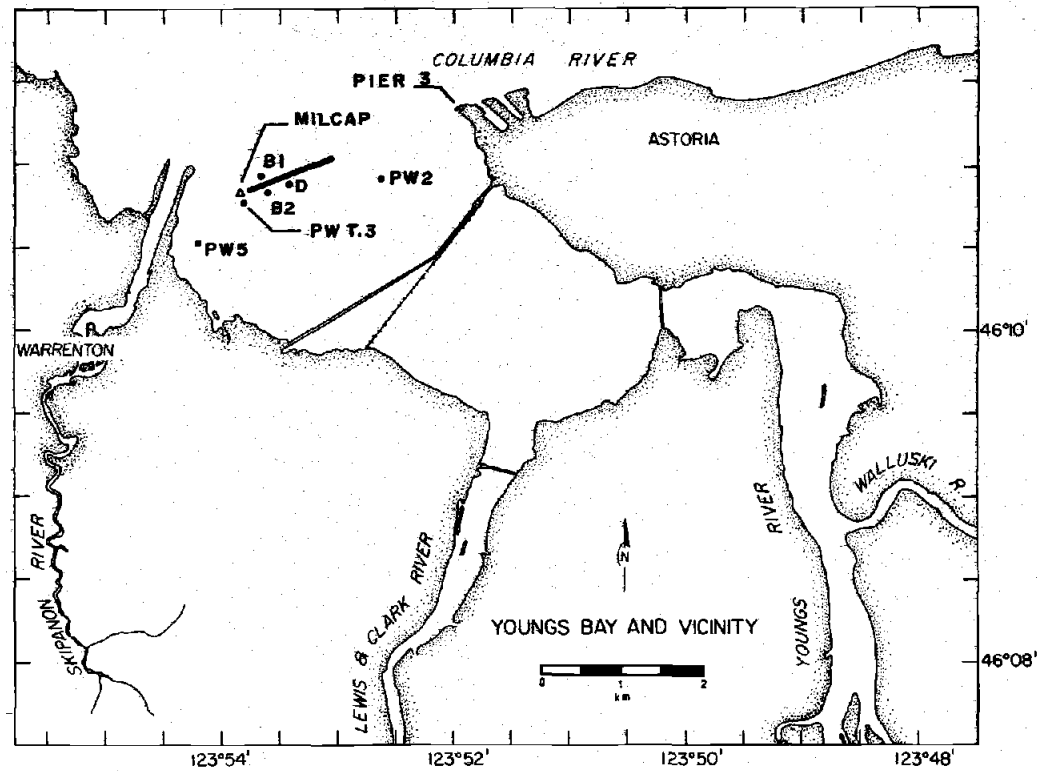
Figure 4. Location of sampling stations in Youngs Bay, Oregon. Heavy line shows 1975 tow zone, and dots indicate 1974 and 1975 grab sample stations.

dragged over the substrate to determine if the tow line was free of obstructions (e. g., sunken logs) to sampling gear. It is believed that there was sufficient time for benthic populations to recover from this disturbance prior to sampling.

Collections of swimming animals were made with a plankton net towed horizontally in three sampling strata: 1/2 m below the surface (surface), 2 m above the substrate (midwater), and 1/3 m above the substrate (epibenthic). The substrate was also sampled using a grab sampler so that the structure of the infaunal populations could be characterized.

The same 1/2 m plankton net (150 cm long; 0.425 mm mesh) was used to collect all water column samples. For surface and midwater sampling, the net was fixed to a 1/2 m ring, while for epibenthic sampling, it was fixed to the variable-height epibenthic sled described by Higley et al. (1977). The sled has a closing device which allows it to collect uncontaminated epibenthic samples. A flow meter (General Oceanics model 2030/31) suspended in the mouth of the net measured the volume of water filtered during each sample collection. Lighted buoys were anchored at each end of the tow line for nighttime sampling. All samples were immediately preserved in 5% formaldehyde solution neutralized with sodium borate.

Surface and midwater tows were usually 7 to 10 minutes in duration and filtered about 100 cubic meters of water. Epibenthic

tows were usually 5 minutes in duration and filtered about 40 cubic meters of water. Tow speeds were about 2 knots. For surface tows, the top of the net fished 1/2 m below the water surface. For mid-water tows, the net was quickly lowered until a lead weight fixed at the end of the tow line and hanging 3 m below the net was felt dragging along the bottom. Wire angle was kept at 45°, so the center of the net opening rode about 2 m above the substrate. For epibenthic samples, the bottom of the rectangular mouth frame opening (53 cm wide by 26 cm high) was set to ride 1/3 m above the substrate.

Benthic samples were collected from an anchored boat using a Smith-McIntyre grab sampler (Smith and McIntyre, 1954; actual mouth area of sampler was 0.107 m^2). After each set of replicate grabs, the anchor line was let out a few meters so that the next set was collected from an adjacent area. No sample appeared to have been taken from an area previously sampled. The depth of sample in the grab was measured at its deepest point as an indication of the grab's effectiveness in penetrating and removing substrate. A 3.5 cm plastic tube was used to remove a 8 cm deep subsample of substrate from the sample for sediment particle size analysis. The sample was washed on a screen trough (0.408 mm by 0.457 mm mesh) and the residue retained preserved.

Re-rigging between samples took about 1/2 hour, which did not allow more than two strata to be sampled with sufficient frequency to

accurately define the timing of the rhythms. Consequently, sampling

was performed in four sequential series:

1) a series of 17 epibenthic samples from late morning
through the evening of September 26,

2) a series of 33 alternating surface and midwater samples
from the afternoon of September 27 to the afternoon of
September 28,

3) a series of 10 replicate sets of grab samples from the
afternoon of September 28 to the morning of September 29,

4) and another series of 13 epibenthic samples around the
sunset of September 29 and the sunrise of September 30.

Figure 5 presents a summary of the times all samples were taken in

relation to the periods of darkness and the extreme water levels.

Benthos samples were taken from three stations. Five replicate

grab samples were collected at 1540 h on September 28 at Station D

located 30 m upbay of the midpoint of the tow line (Fig. 4). Very

few Corophium were observed so the benthic sampling station was

relocated. Three replicate grab samples were collected at 1745 h

on the same day from Station B1 half-way between Station D and the

Milcap buoy. A sufficient number of Corophium was collected at this

site to indicate the population structure. Subsequently, four more

sets of replicate samples were collected at Station B1, and four sets of

replicate grab samples were collected from Station B2, located across
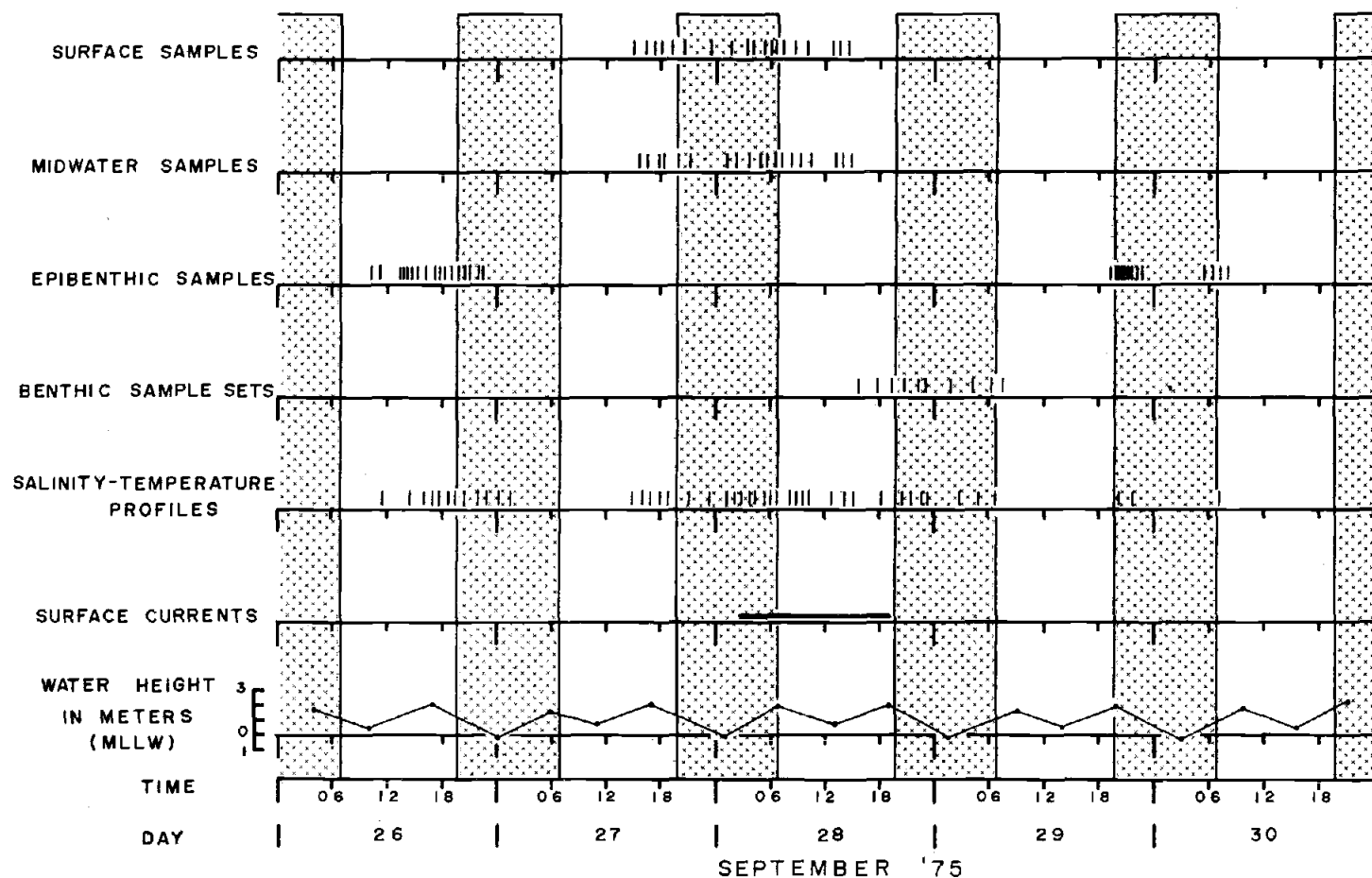
Figure 5. Sampling schedule followed for the swimming activity rhythms study. Each net sample, set of benthic samples, and salinity-temperature cast is represented by a short vertical line (ꟾ). Periods of darkness are shaded. Extreme water heights are based on records taken at the Tongue Point gauge corrected to the Astoria Port Docks. A heavy line indicates when surface current velocity was measured.

the tow line from Station B1.

Environmental conditions were measured concurrently with animal collection, and the times of measurement are presented in Figure 5. Before each sample, ambient skylight intensity was visually classified into one of four classes: (1) daylight, (2) darkness, (3) dusk, beginning when the late afternoon sky first began to darken and ending when the sky was at the ambient nighttime darkness, and (4) dawn, beginning when the night sky first began to lighten and ending when the sky was at the full morning ambient light intensity. Dusk and dawn each lasted almost an hour.

A Savonius rotor type current meter (Hydroponics Model No. 460) was used to measure water speed and direction at Station D. The meter was suspended 1-1/3 m below the water surface and recorded from 0300 h to 1830 h, September 27.

A portable, in situ inductive salinometer (Industrial Instruments Co. Model RS5-3) was used to measure salinity and temperature at one-meter intervals through the water column. Over a period of 44 hours from September 26 to 28, 30 profiles were obtained at Station D. Eight profiles were taken at the benthic stations, B1 and B2, during grab sampling. Eight additional profiles were taken at Station D.

Sample Analysis

All net and grab samples were rinsed in water and transferred

to 40% isopropanol within one week of collection. Some of the net

samples and all of the benthic samples were quantitatively split to

a manageable size using a Folsom plankton sample splitter (McEwen

et al., 1954). Rose Bengal stain was added to benthic subsamples 24

hours or more before sorting to selectively stain animals red, making

them easier to see among the wood and plant debris in the sample.

Each sample or subsample was sorted in a white enamel pan, and

the various benthic crustacean taxa were counted and placed in sepa-

rate vials. In addition, most pelagic and infaunal groups were also

enumerated, but not removed.

After all of the samples were completely sorted, taxa were

identified as far as time and experience allowed. All benthic crusta-

ceans were identified to species. Other benthic infaunal groups and

the several pelagic groups were identified to higher taxonomic

categories (usually order or class).

Members of the genus Corophium were sorted under a stereo-

microscope according to the presence or absence of densely setose

second antennae, which allows rapid and accurate differentiation of

C. spinicorne and C. brevis (densely setose) from the predominant

C. salmonis (sparsely setose) (Shoemaker, 1949). All densely setose

Corophium were identified to species. Approximately 50% of the

Corophium with sparse setation were identified to species, and all

were C. salmonis. Other species than these may have been captured

and not noticed; however, their frequency of occurrence would have been very low. A single specimen of C. insidiosum was found, which is the first report of this species in the Columbia River estuary.

Other common benthic crustaceans were identified as follows. Each Eohaustorius captured in net samples and most of those captured in grab samples were identified to species; all were E. estuarius. Many adult Anisogammarus and Neomysis were identified to species, and all were A. confervicolus and N. mercedis. All Crangon captured were identified as C. franciscorum, and all Gnorimosphaeroma as G. oregonensis. In all subsequent discussion, these species names will be used even though every individual was not identified and a few rare additional species may have been unnoticed.

Benthic crustaceans taken in net and grab samples were characterized according to size, sex, body color (for Corophium), and maturity. Corophium salmonis, being the most abundant macro-infaunal crustacean in the sediment and in the water column, was most intensely studied. C. spinicorne was also sufficiently abundant in the samples to warrant study, and provides an interesting comparison with C. salmonis. Water column and benthic samples from which individuals were removed for examination are listed in Appendix A.

Body length was measured as the distance from the tip of the rostrum to the tip of the telson while the specimen was held flat on its dorsal surface (Blegvad, 1922; Watkin, 1941b). The measurement was made using a calibrated ocular micrometer mounted in a

stereomicroscope. Animals were placed in 0.25 mm size classes with an estimated accuracy of measurement of about ± 0.05 mm.

The sex of _Corophium salmonis_ was determined based on the dimorphic characters of the second antennae (Shoemaker, 1949). Sex was easily determined on animals longer than 1.50 mm. Smaller individuals showed an unusually high proportion of the female-type second antennae. Subsequent examination of many newly hatched _C. salmonis_ still retained in the brood pouch showed that at birth (length from 0.75 mm to 1.00 mm), all individuals have the female-type antennae. Characteristically, they bear two distal spines on the third segment, and one central and one distal spine on the fourth segment (Figure 6). By 1.50 mm, males lose these four spines and acquire the characteristic distal hook on the fourth segment. This transition presumably occurs in stages over several molts because intermediate forms showing both characters are seen. Bradley (1906) misinterpreted these morphological changes with development, and Shoemaker (1949) incorrectly revised Bradley's work. Since other sexual characters, such as genital papillae in males and oostigites in females, are not evident in individuals smaller than 1.50 mm, they were classified as unsexable juveniles.

No reliable dimorphism exists between male and female _C. spinicorne_ of any size, other than the presence of genital papillae and oostigites. These characteristics were present in all individuals
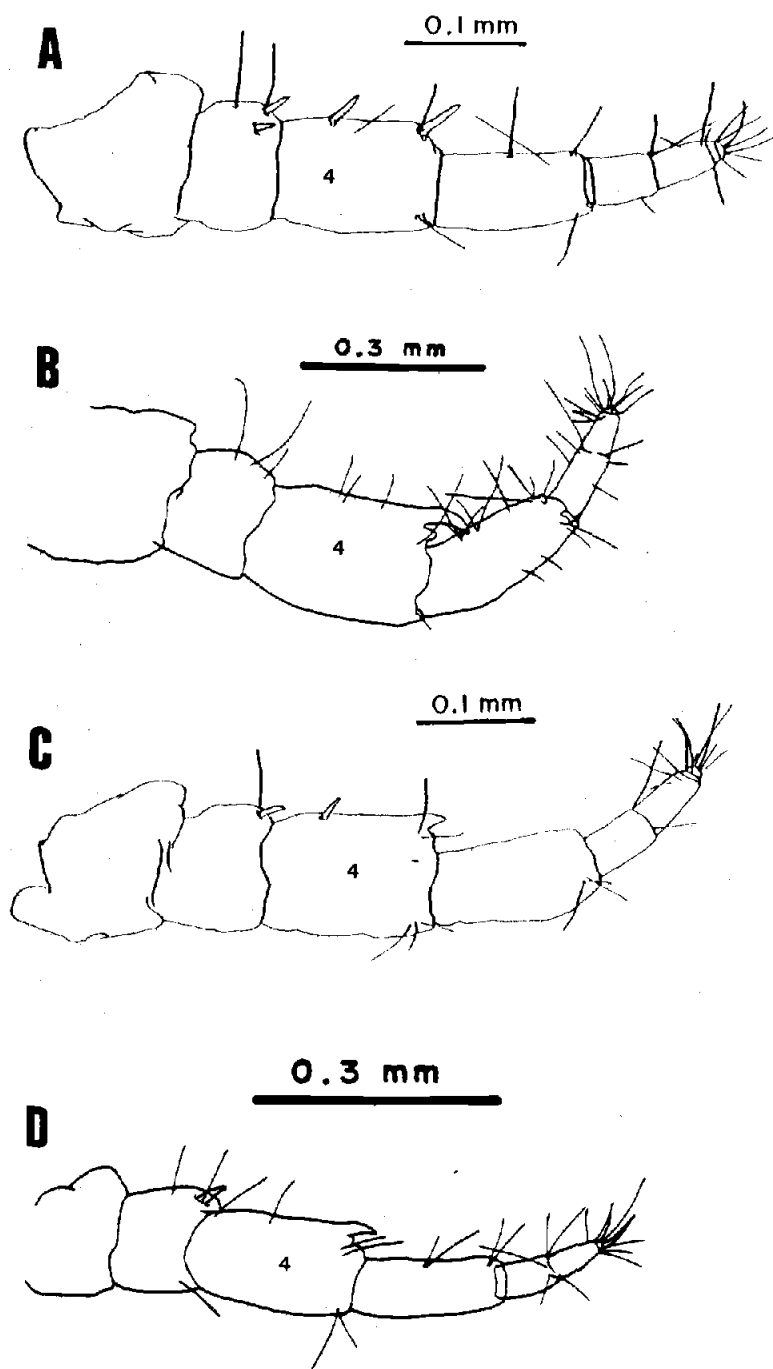
Figure 6. Morphology of the second antennae of <u>Corophium</u> <u>salmonis</u>. The fourth segment of each antenna is labelled. A. Characteristic morphology of females longer than 1.50 mm. B. Characteristic morphology of males longer than 1.50 mm. C, D. Intermediate morphology of juvenile males, based on two individuals 1.4 mm long. See text for a discussion of the developmental changes in morphology.

longer than 2.00 mm, and in some between 1.50 mm and 2.00 mm.
Those without either characteristic were classified as unsexable juveniles.

Females were divided into four discrete maturity categories
based on oostigite morphology: (1) females without enlarging oosti-
gites, signifying older juveniles which have not yet begun to sexually
mature; (2) females with intermediate-sized oostigites, indicating the
beginning of maturation; (3) females with full-sized oostigites, indi-
cating that maturity has been reached; and (4) females with oostigites
bearing marginal setae. Classification in category 4 indicates that
the female is in breeding condition. She may be carrying eggs or
offspring. If she is not, then either she just released all offspring
or is about to lay eggs into the brood pouch.

Classification by this scheme is a useful representation of
the continuous maturation of gammaridean amphipods. However,
some biases may have developed in data collection. First, the
judgment of whether oostigites had begun to develop or had reached
full size was difficult to make in a few cases. The tendency was to
classify females with very small oostigites in category 1 and females
with large oostigites in category 3. This probably resulted in a
slight underestimation of category 2. Secondly, marginal setae are
acquired when a female molts and releases eggs into the brood pouch.
These setae may be lost at the next molt if new eggs have not ripened.
Therefore, some older females who have ceased reproduction or who

have entered a reproductive resting phase may have been placed in category 3 when they belonged in category 4.

The ovigerous condition of each female Corophium was noted. Females were classified as gravid or non-gravid by the presence or absence of one or more eggs or juveniles within the marsupium, a ventral brood chamber formed by the ventral body surface and the oostigites bearing marginal setae. The clutch size of each gravid female was counted, and the firmness with which the clutch was held by the enfolding oostigites was noted. Eggs are firmly held in the marsupium during early development. Later, as the eggs near hatching, the oostigites begin to unfold and eggs and juveniles may sometimes be easily removed. Some of these females may have lost all or some of their offspring during sample sieving and handling. As will be indicated, some of the clutch size data discussed later are based solely on counts of clutches considered to be whole and intact.

Early in the study, varying degrees of diffusion and concentration of a dark pigment within the melanophores in the integument of Corophium salmonis were noticed. Because there seemed to be some correlation between melanophore state and locality of capture, all Corophium were classified according to the following scheme. The standard categories of chromatophore expansion stages were developed by Hogben and Slome (1931). These stages are diagrammed in Figure 7. When all or nearly all of the melanophores were punctate (classes
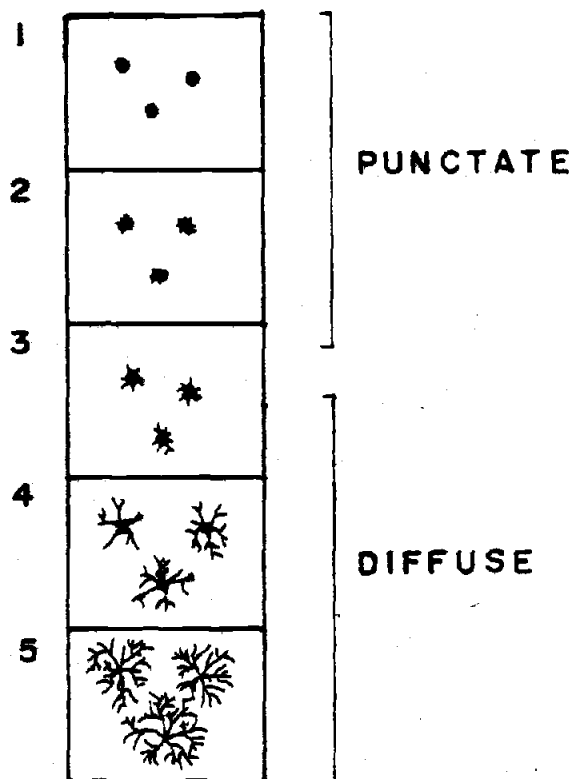
Figure 7. Arbitrary classification used in characterizing the stage of pigment diffusion in chromatophores. The classification is adapted from Hogben and Slome (1931).

1 and 2), the Corophium was called "punctate." If several melano-phores were distinctly stellate or more diffused (classes 3, 4, and 5), the specimen was called "diffuse." Whole-body drawings of some typical specimens falling into these two categories are shown in Figure 8.

Samples from which the amphipods Eohaustorius estuarius and Anisogammarus confervicolus, and the mysid Neomysis mercedis, were removed for examination are listed in Appendix A. Of the 211 E. estuarius captured in net samples, all were taken during or near darkness. All water column specimens were examined, and 173 were in satisfactory condition for measurements. Animals from some representative benthic samples were also measured. In preserved Eohaustorius, the urosome bearing the telson is tucked beneath the body ventral to the pleopods. Therefore, body length was taken from the tip of the rostrum to the posterior edge of the body segment bearing the last pair of pleopods. Sex was determined by noting the presence of genital papillae in males and oostigites in females. These characters were evident on individuals larger than 1.25 mm; smaller animals were classified as unsexable juveniles.

N. mercedis and A. confervicolus were abundant in the water column only at night. Approximately 100 specimens of each species were selected from nighttime samples at each stratum for measurement. Body length was taken from the tip of the rostrum to the base
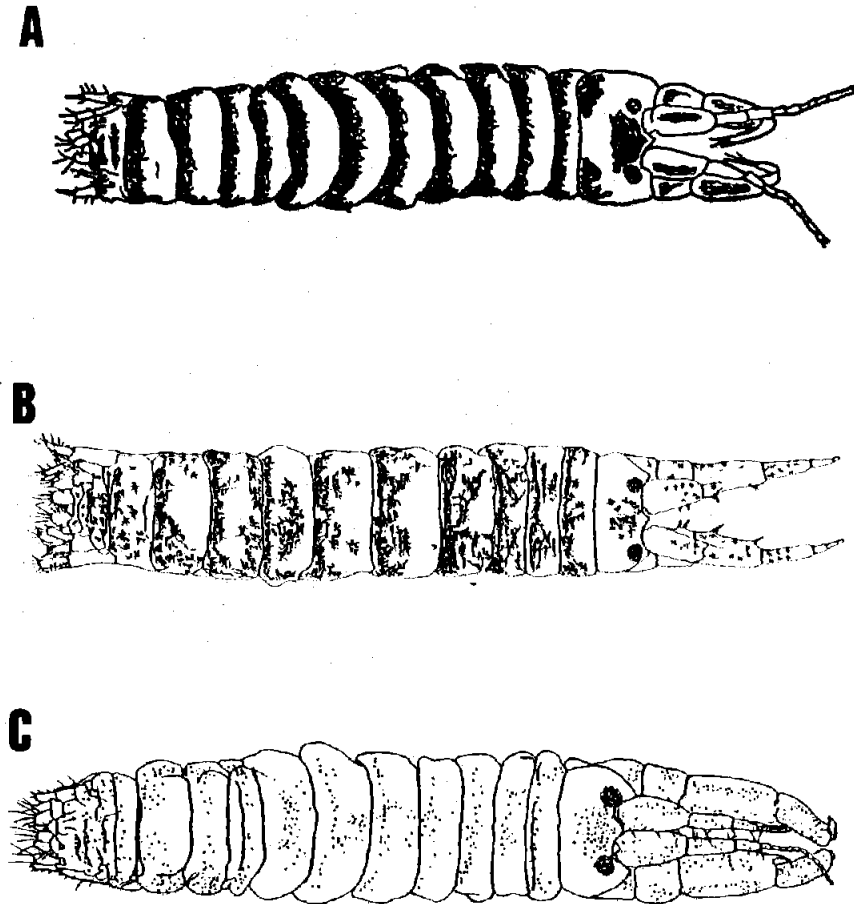
Figure 8.   Whole-body drawings of <u>Corophium</u> <u>salmonis</u> having
melanophores in different stages of diffusion.   A. Diffuse.
B. Diffuse.   C. Punctate.

of the telson in <u>N</u>. <u>mercedis</u> and to the tip of the telson in <u>A</u>. <u>confer-</u>
<u>vicolus</u>. No attempt was made to determine the sex of these species.

<div align="center">Life-History of <u>Corophium salmonis</u></div>

Life history data were collected on <u>Corophium salmonis</u> from
grab samples taken in the mouth region of Youngs Bay over a 17
month period in 1974 and 1975. A random subsample (Folsom splitter)
of animals from each grab was studied to determine the relative size
structure of the population; the relative abundance of immature,
mature, and gravid females; and the average production of offspring.

Twelve unreplicated grab samples were selected for examina-
tion. Eleven of these were collected as part of a previous study
reported by Higley and Holton (1975), and one was collected during
the swimming activity study. Samples used were the following:

(1)   9 at Station PW 5: April 17, May 7, May 30, June 18,

      October 12, and December 3, 1974; and January 2,

      January 29, and February 24, 1975.

(2)   1 at Station PW 2: July 9, 1974.

(3)   2 at Station PW T3: August 6, 1974 and September 2, 1975.

See Figure 4 for location of these stations.

These grab samples were collected and processed in the manner
described for the swimming activity study. However, only a single
sample was taken on each date. Each sample was split with a Folsom

plankton sample splitter until a subsample with about 500 C. salmonis

was obtained. The subsamples were stained with Rose Bengal stain

for 24 hours or more, placed in a white enamel pan and all C.

salmonis removed. These animals were then split until a fraction

containing 100 to 200 was obtained. Each of these individuals was

characterized in the manner described in the swimming activity

rhythms section.

RESULTS

Swimming Activity Rhythms

Environmental Conditions

Precipitation levels and river discharge during sampling were typical of late summer conditions at Youngs Bay. Columbia River discharge over the 1975 water year (October, 1974, through September, 1975) was 7703 m^3/s, close to the 1958 to 1972 15-year average of 7726 m^3/s. In 1975, precipitation was slightly higher than average during February and lower than average during September. The monthly mean Columbia discharge at the mouth for September was 3322 m^3/s, 96% of the 1958 to 1972 15 yr average. High pressure established over the Pacific Northwest on September 18, 1975, and a series of weak low pressure systems moved through at the end of the month.

Salinity-temperature profiles taken on September 28 and 29 (Figure 9) show the intrusion of cooler marine water at high tide establishing a temporary two-layer flow system. At Youngs Bay, such systems are common only during low river discharge in the late summer and fall. Maximum salinity at the bottom reached 23.2‰, while at the surface reached only 7‰ (Appendix B). Salinity was highest about 2 hours after maximum water height.

Figure 9.   Water depth, near-surface water velocity, and selected
salinity-temperature profiles for the period 1800 h on
September 28 to 1800 h on September 29, 1975, at Station
D. Complete salinity-temperature records are in Appen-
dix B. Water depth was measured by shipboard fathometer
prior to collection of each salinity-temperature profile.
Extreme water height relative to MLLW, based on records
taken at the Tongue Point gauge corrected to the Astoria
Port Docks, is shown. The speed and direction of water
flow extracted from the continuous record at 30 minute
intervals are shown. The direction of water flow as shown
in Figure 10 has been simplified to either upstream or
downstream.
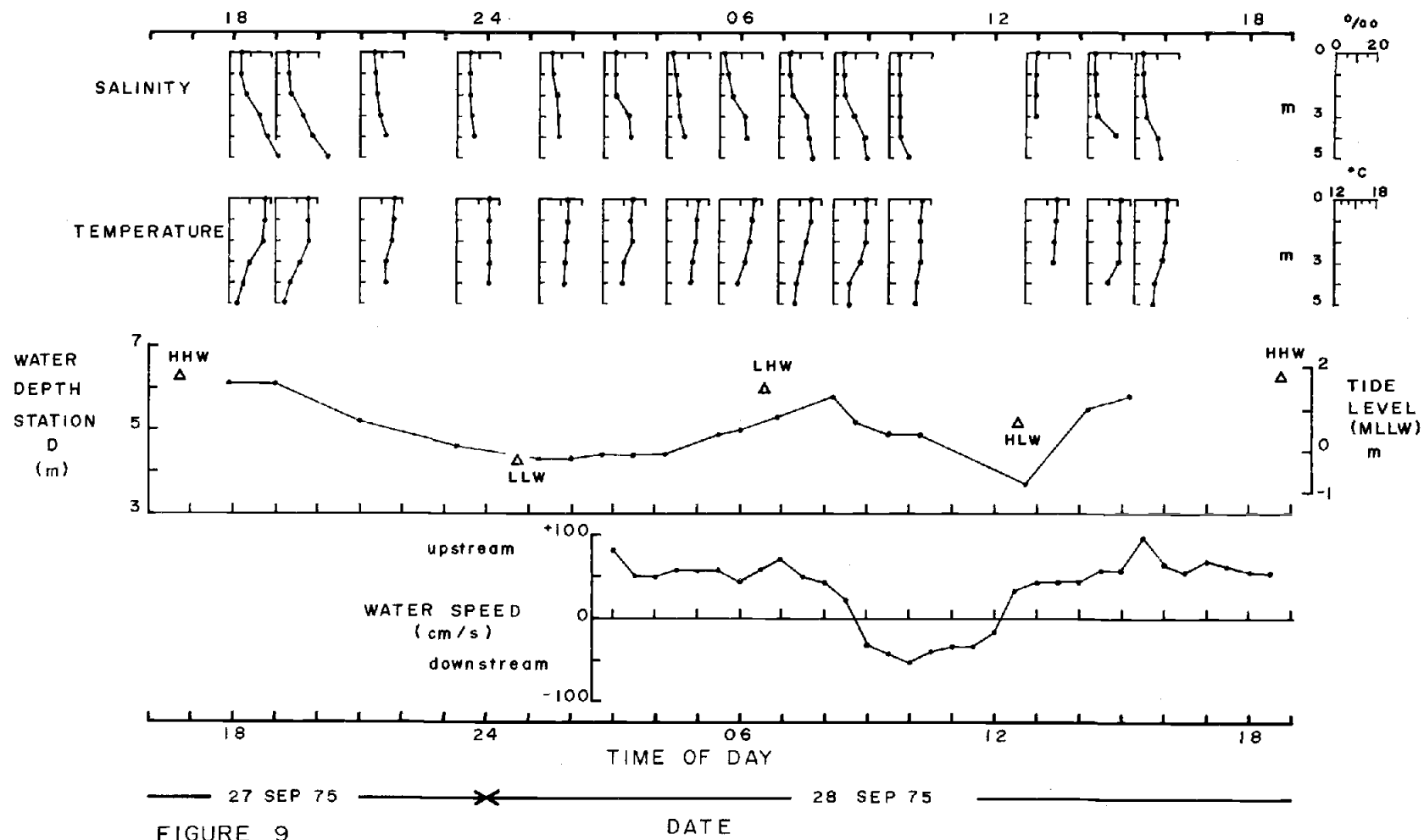
FIGURE 9

The direction of water flow through the tow zone (Figure 10) corresponded closely to the pattern of water circulation described by OSU, Ocean Engineering Program (1975). The dominant direction of flow is parallel to the dredged ship channel. There is little rotation in direction as flow reverses from flood to ebb and back to flood. Water speed stayed near 50 cm/s, and occasionally approached 100 cm/s during the floods (Figure 9). Speed appeared highest about 3 hours after maximum water height, while OSU, Ocean Engineering Program (1975) reported a 3 1/2 to 4 hour lag.

Fauna

Animals caught in the upper water column (the surface and midwater strata combined) were members of three faunal assemblages: estuarine endemic zooplankton, coastal zooplankton, and estuarine benthic crustaceans (Table 1). Copepods (calanoids and cyclopoids) and cladocerans comprised the estuarine endemic zooplankton catch. Oftentimes they were quite abundant. Coastal zooplankton immigrants into Youngs Bay were infrequently captured. Included in this group were several scyphomedusae, pagurid (hermit crab) zoea, and Leptocottus armatus (staghorn sculpin) larvae. In addition, three cirriped (barnacle) nauplii, and a single Engraulis mordax (northern anchovy) larva were captured. Several estuarine benthic crustaceans were quite abundant at times in the upper water column, as will be
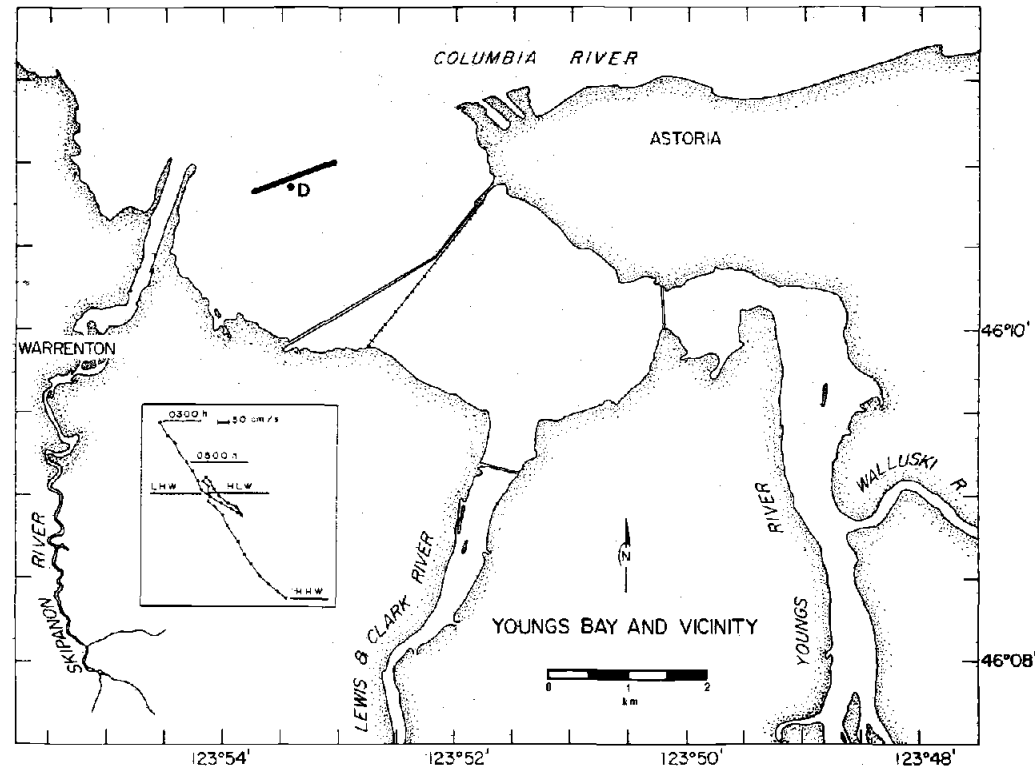
Figure 10. Progressive vector plot of near-surface current velocities measured at Station D. The plot is shown in the insert, and is oriented in the same direction as the map. Speed and direction of flow were extracted from the continuous record at 30 minute intervals from 0300 h to 1830 h, September 28, 1975. These values are represented as vectors placed head to tail. Vectors taken at 0300 h and 0500 h are illustrated for reference. The times of lower high water (LHW), higher low water (HLW), and higher high water (HHW) are shown. A scale of vector length to water speed is given.

Table 1. Relative abundance of taxa captured in the swimming activity rhythms study. xx indicates high abundance, x indicates moderate to low abundance, and - indicates rare.

Taxon	Surface	Midwater	Epibenthic	Benthic
Coelenterata				
Scyphozoa		-	-	
Nemertinea			x	x
Nematoda				xx
Annelida				
Polychaeta			x	xx
Oligochaeta			x	xx
Mollusca				
Bivalvia			x	x
Arthropoda				
Crustacea				
Cladocera	xx	xx	xx	
Copepoda	xx	xx	xx	xx
Cirripedia nauplii			-	
Mysidacea				
Neomysis mercedis	xx	xx	xx	
Isopoda				
Gnorimosphaeroma oregonensis	x	x	x	
Amphipoda				
Corophium salmonis	xx	xx	xx	xx
Corophium spinicorne	x	x	x	
Corophium brevis		-	x	
Corophium insidiosum			-	
Anisogammarus confervicolus	xx	xx	xx	-
Eohaustorius estuarius	x	x	x	x
Paraphoxus milleri		-		
Decapoda				
Crangon franciscorum	x	x	x	
Paguridae zoea		x	x	
Insecta				
Chironomidae larvae				x
Chordata				
Teleostei				
Leptocottus armutus	x	x	x	
Eugraulis mordax		-		

discussed later.

The epibenthic stratum (also called the lower water column) contained most of the animals present in the upper water column and some from the substrate below. The oligochaetes and nemerteans were similar in size to those in the sediment. The polychaetes and bivalves, however, were all quite small (less than 3.00 mm in length), while the sediment contained a moderate proportion of large adults. These benthic forms were probably swept up into the epibenthic region by water currents. The small size of the polychaetes and bivalves suggests also that they may have been in the process of settling to the bottom or been distributed closer to the surface than the larger ones and more susceptible to resuspension by water currents.

The infaunal benthic assemblage in the tow zone was like that observed in Youngs Bay previosuly by Higley and Holton (1975). Several worm phyla were present, all moderately abundant except for the more scarce nemerteans. Oligochaetes and nematodes, though individually small, were numerically abundant. Polychaetes, on the other hand, were less abundant, but a moderate portion were large in size. The polychaetes appeared to be the nereid <u>Neanthes</u> <u>limnicola</u> and the bivalves appeared to be <u>Macoma</u> <u>baltica</u>, based on work reported by Higley et al. (1976).

Only two species of macroinfaunal crustaceans, the amphipods

Corophium salmonis and Eohaustorius estuarius, were common in grab samples. The epibenthic crustaceans Anisogammarus confervicolus, Neomysis mercedis, and Crangon franciscorum may have been present during sampling, but the grab sampler is ineffective in capturing them. Four species of Corophium were captured in the water column, as opposed to one species in grab samples. This strongly suggests that crustacea entered the study site from other substrate or salinity regions within or from outside the estuary.

<center>Swimming Activities of Benthic Crustaceans</center>

Ten species of benthic crustaceans were captured in the water column (Table 1). Densities of the eight most abundant species in each sample in each stratum are presented in Appendix C. Two species, Corophium salmonis and Eohaustorius estuarius, were commonly captured in grab samples, and their densities are also presented in Appendix C along with densities of the other infauna. An occasional Anisogammarus confervicolus was captured in grab samples; however, these values are not representative of their abundance.

It was originally hoped that changes in density and structure of infaunal populations resulting from migration into the water column by some members of these populations could be observed. This was not possible for the following reasons. Only a small fraction of each

infaunal population was present in the water column at any one time
(see Appendix C). The decrease in the density of C. salmonis, for
example, resulting from the migration was much less than the varia-
tion in density between replicate grab samples (coefficient of variation
for replicates was about 20%: 17% for 2A, 2B and 2C; and 24% for 6A,
6B, and 6C; Appendix C). In addition, the variation in mean density
among sampling periods 1, 2, and 6 was even greater. Thus, high
variation among grab samples prevented detection of population
changes resulting from swimming activity. For this reason, only
a selection of the grab samples was analyzed to characterize the
infaunal population structures.

Densities of the six most abundant species in the water column
are plotted in Figures 11-16. Because the dominant period of activity
was diel, surface, midwater, and epibenthic data are all aligned
over a common axis, although collected on different days. This al-
lows comparison of data for all strata taken at the same time of day
and in the same ambient light condition, although it assumes no
important changes in patterns of density occurred during the sampling
week. This approach should be valid for detecting large patterns
of density change.

Corophium salmonis, Anisogammarus confervicolus, and Neomysis mercedis

The amphipods Corophium salmonis and Anisogammarus

<u>confervicolus,</u> and the mysid <u>Neomysis</u> <u>mercedis</u> were the most abundant benthic crustaceans in the watercolumn.

<u>C</u>. <u>salmonis</u> was distinctly more abundant in the water column at night than during the day (Figure 11). Of the 35 daylight samples, 15 contained no <u>C</u>. <u>salmonis</u> while only 3 contained more than 25/100 m^3. In contrast, nighttime densities of 500/100 m^3 were common and several approached 1000/100 m^3.

<u>C</u>. <u>salmonis</u> appeared to emerge into the epibenthic stratum immediately prior to dusk (Figure 11). During the first series of samples around sunset on September 26, densities increased gradually from the last daylight sample into the nighttime samples. This pattern of gradual increase through dusk was also seen during the second series on September 29; however, only one daylight sample was taken so events prior to this time are not known.

<u>C</u>. <u>salmonis</u> appeared in the upper water column sometime during the first 1 1/2 hours of darkness. Few were captured in the last samples just before or at night fall, but many were present when the next samples were taken about 1 1/2 hours later. When precisely they arrived in the upper water column is not known. However, Morgan (1965) observed that <u>C</u>. <u>volutator</u> can swim up at speeds near 2 to 3 1/2 cm/s. Thus, <u>C</u>. <u>salmonis</u> in the 4 m to 8 m water column may have arrived at the surface well before the first samples 1 1/2 hours into night.

Figure 11. Density of <u>Corophium salmonis</u> in three water column
strata over a diel cycle in Youngs Bay, Oregon. Dark-
ness (shaded area) is bounded by dusk and dawn (unshaded
enclosures). H indicates high tide and L low tide.
The + sign indicates densities less than $25/100 \text{ m}^3$,
while the O indicates zero densities. Data are tabu-
lated in Appendix C.
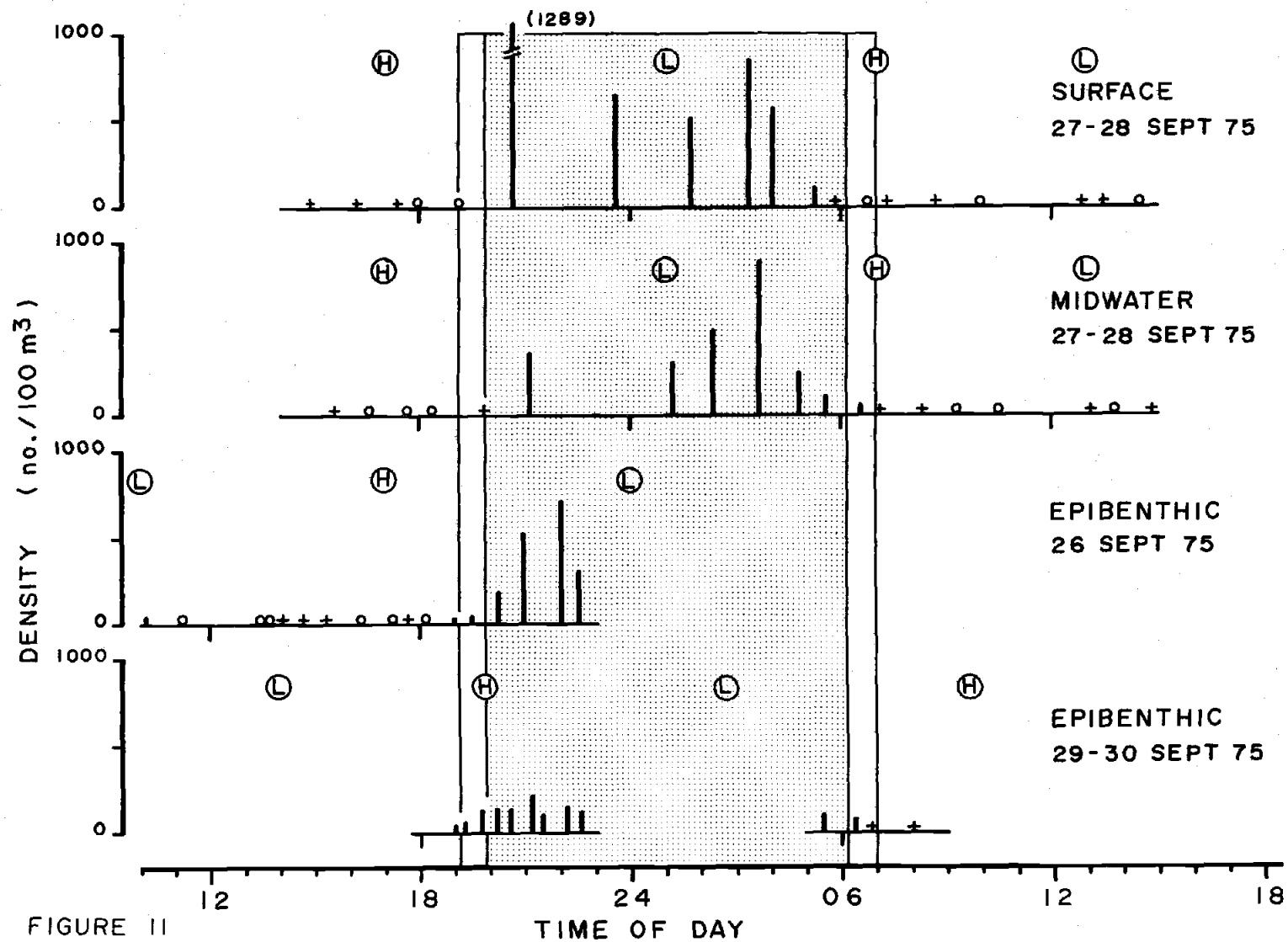
FIGURE II

C. salmonis began to disappear from the upper water column about 2 hours prior to sunrise (Figure 11). After surface and mid-water samples #9, densities decreased gradually towards dawn. In the third epibenthic series on September 30, a decrease in density at sunrise was evident; however, events in the 2 hour period prior to sunrise are not known.

A. confervicolus, much like C. salmonis, was abundant in the water column only at night (Figure 12). Most daylight samples contained no individuals. Nighttime densities in the upper water column were commonly 100 to 200/100 m^3, while densities reached 500 to 1000/100 m^3 during the first epibenthic series.

A. confervicolus density increased during the first epibenthic series beginning with the dusk sample (14E), and was distinctly higher in the upper water column by the time the first darkness samples were taken. This pattern is similar to that exhibited by C. salmonis, but is not as marked because A. confervicolus was less dense in the upper water column than C. salmonis. Because of this, a pattern of decreasing density prior to sunrise is not as evident.

N. mercedis, like the amphipods C. salmonis and A. confervicolus, was nocturnally active in the water column (Figure 13). Nighttime densities reached 100 to 200/100 m^3. However, the nighttime densities prior to midnight were distinctly lower than those after. Densities increased immediately at dark during the first

Figure 12. Density of <u>Anisogammarus confervicolus</u> in three water
column strata over a diel cycle in Youngs Bay, Oregon.
Darkness (shaded area) is bounded by dusk and dawn
(unshaded enclosures). H indicates high tide and L
low tide. The + sign indicates densities less than
$25/100 \text{ m}^3$, while the O indicates zero densities. Data
are tabulated in Appendix C.

FIGURE 12

DENSITY (no./100 m³)

SURFACE
27-28 SEPT 75

MIDWATER
27-28 SEPT 75

EPIBENTHIC
26 SEPT 75

EPIBENTHIC
29-30 SEPT 75

(1134)

TIME OF DAY

71
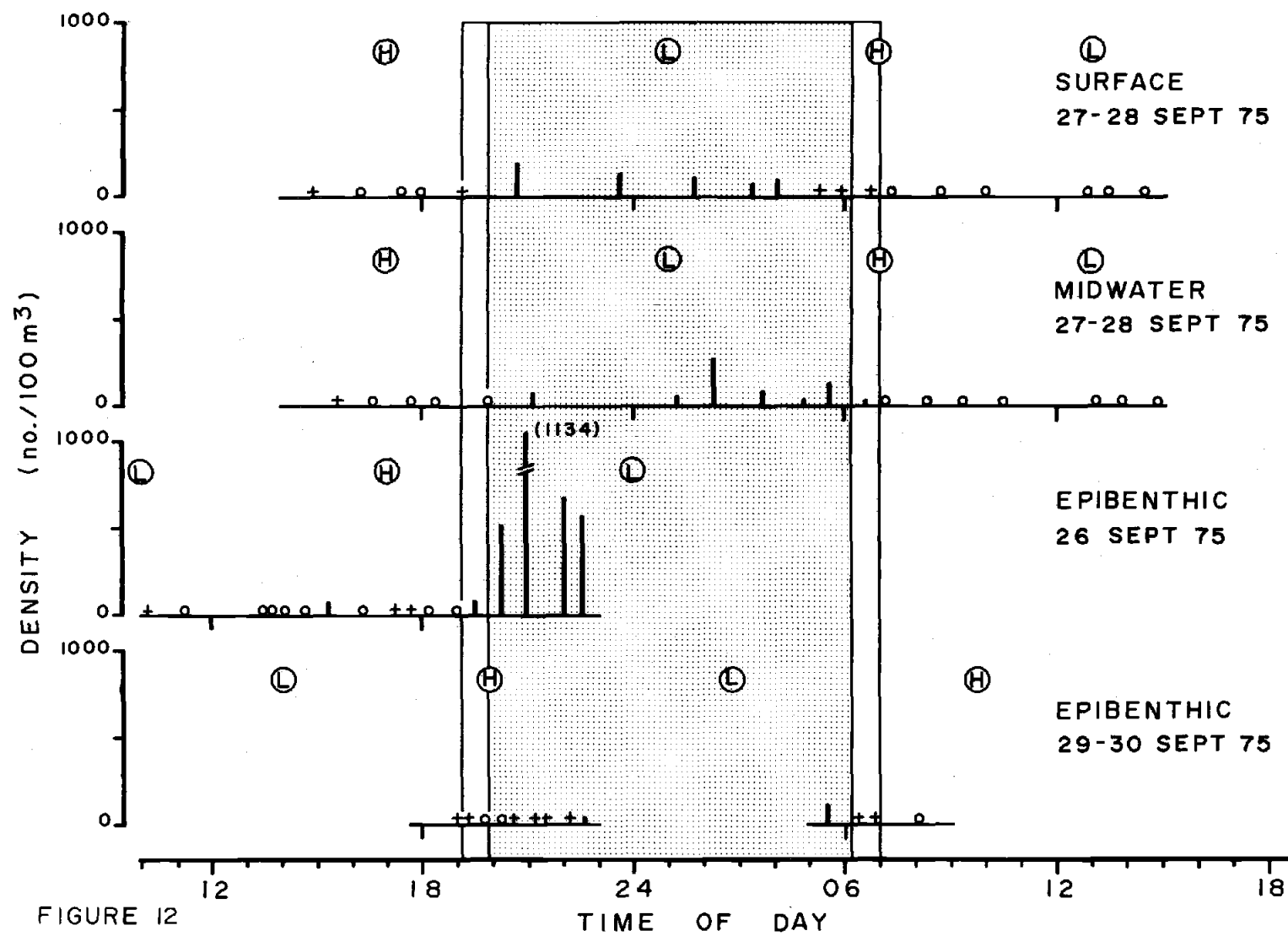
Figure 13. Density of <u>Neomysis mercedis</u> in three water column
strata over a diel cycle in Youngs Bay, Oregon. Dark-
ness (shaded area) is bounded by dusk and dawn (unshaded
enclosures). H indicates high tide and L low tide.
The + sign indicates densities less than $25/100 \text{ m}^3$,
while the O indicates zero densities. Data are tabu-
lated in Appendix C.
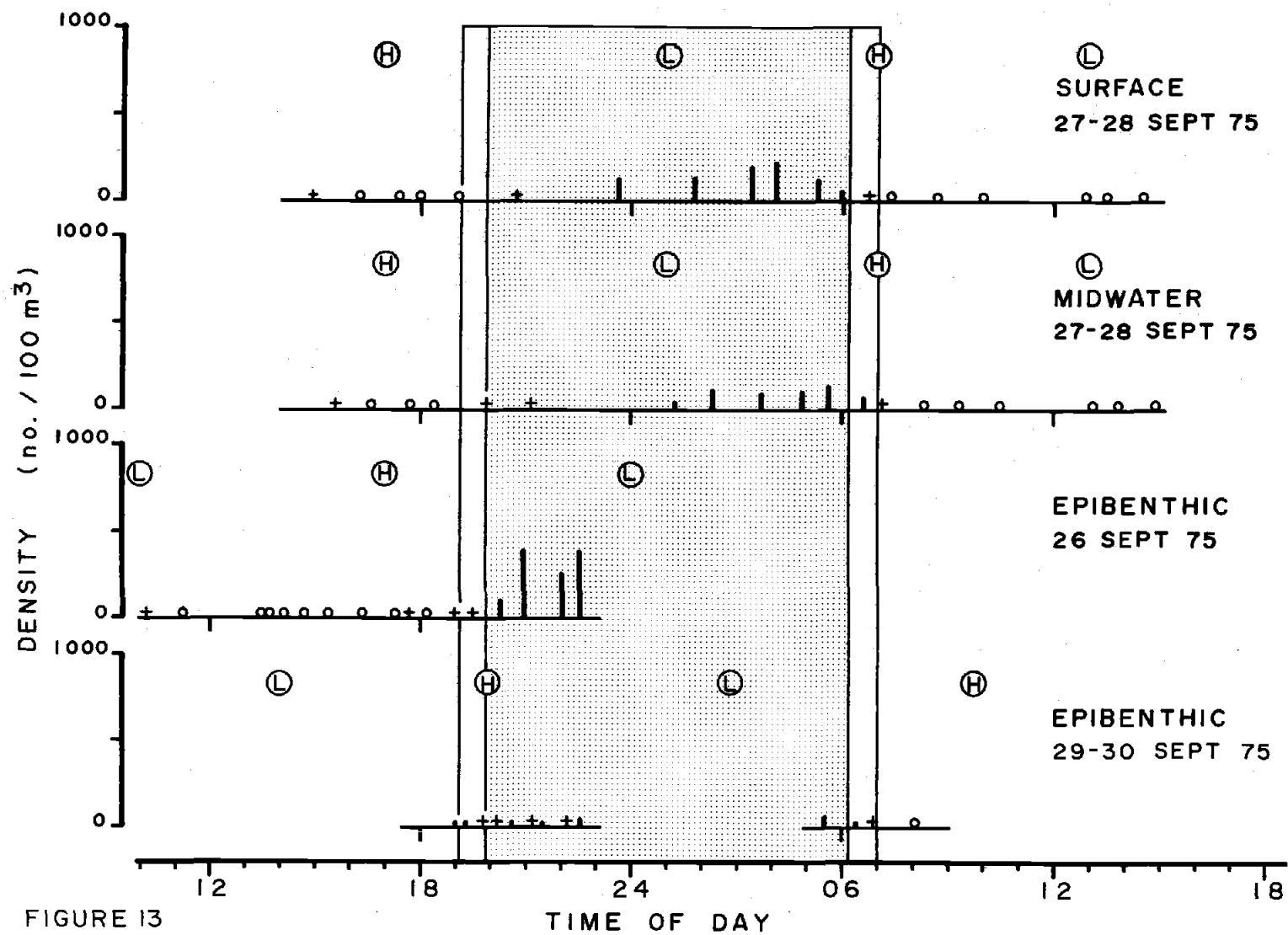
FIGURE 13

epibenthic series. $\underline{N}$. $\underline{mercedis}$ may take more time to reach the upper water column, or some other environmental factor may affect the timing of their movements. They disappeared from the upper water column by sunrise.

Lacking replicate samples, sample variability associated with estimates of animal density in the water is unknown, confounding comparison among strata and among species. The changes in density indicated by sequential tows may reflect time changes in the magnitude of swimming activity so variability among tows is not an estimate of sample variability. The densities of $\underline{C}$. $\underline{salmonis}$ at night, before the cessation of activity near sunset, fluctuated near 700/100 m^3 in the surface stratum (range 527 to 1289/100 m^3, 5 samples), and near 400/100 m^3 in the midwater stratum (range 306 to 891/100 m^3, 4 samples). Lacking estimates of sample variability alone, a test for significant difference can not be made, and all that can safely be said is that densities of $\underline{C}$. $\underline{salmonis}$ appeared slightly higher in the surface stratum than in the other water column strata.

Comparisons of the upper water column data with the epibenthic data are confounded not only by sample variability but also by possible differences in environmental conditions not associated with the diel light cycle thought to regulate the activities. The second series of epibenthic samples was collected two diel cycles after the upper water column samples, and the light-tide phase relationship had

shifted about 90°, so that sunset during the second epibenthic series occurred at high slack water instead of ebb tide. The first series of epibenthic samples was collected one diel cycle before the upper water column samples, and the light-tide phase relationship was very similar for these two series.

In comparing upper water column data with data from the first epibenthic series, C. salmonis was more evenly distributed throughout the water column at night (Figure 11), while A. confervicolus and N. mercedis were distinctly more dense in the epibenthic stratum (Figures 12 and 13). Since environmental conditions were quite similar, the data suggest that the infaunal species, C. salmonis, swims higher into the water column than do the two epibenthic species.

Densities of these three species were distinctly lower during the second epibenthic series than during the first (Figures 11, 12, and 13). This difference is especially apparent for A. confervicolus, which was present during the first series at densities near 600/100 m^3 and only near 10/100 m^3 during the second. It is unfortunate that neither epibenthic series was continued through the night to give a more complete look at activity during different tide stages. However, the data obtained strongly suggest that nighttime densities of these species in the epibenthic stratum were greater at night during ebb flow than during high slack.

Eohaustorius estuarius, Corophium spinicorne, and Crangon franciscorum

Eohaustorius estuarius, a sand-burrowing amphipod, is the only other common macroinfaunal crustacean species in Youngs Bay (Higley and Holton, 1975). It was absent from daylight net samples but was present in most nighttime samples (Figure 14). Similar to A. confervicolus and N. mercedis, E. estuarius was more abundant in the epibenthic region during the first series than in the upper water column. This is in contrast to the other infaunal species, C. salmonis, which was more evenly distributed throughout the water column at night. The pattern of nocturnal activity appears similar to those observed for the three species discussed in the previous section.

Another species of the genus Corophium, C. spinicorne, was also frequently captured in the water column (Figure 15). Individuals were common in nighttime tows taken in the midwater and epibenthic strata, while usually absent from tows taken there during daylight. However, C. spinicorne was present in the surface stratum, day and night. Densities throughout the water column were distinctly higher at night, but no other benthic crustacean was captured as consistently throughout the day.

The decapod Crangon franciscorum, much larger in size than the peracarid species captured, was taken only in nighttime samples

Figure 14. Density of <u>Eohaustorius estuarius</u> in three water column strata over a diel cycle in Youngs Bay, Oregon. Darkness (shaded area) is bounded by dusk and dawn (unshaded enclosures). H indicates high tide and L low tide. The + sign indicates densities less than $3/100 \text{ m}^3$, while the O indicates zero densities. Data are tabulated in Appendix C.
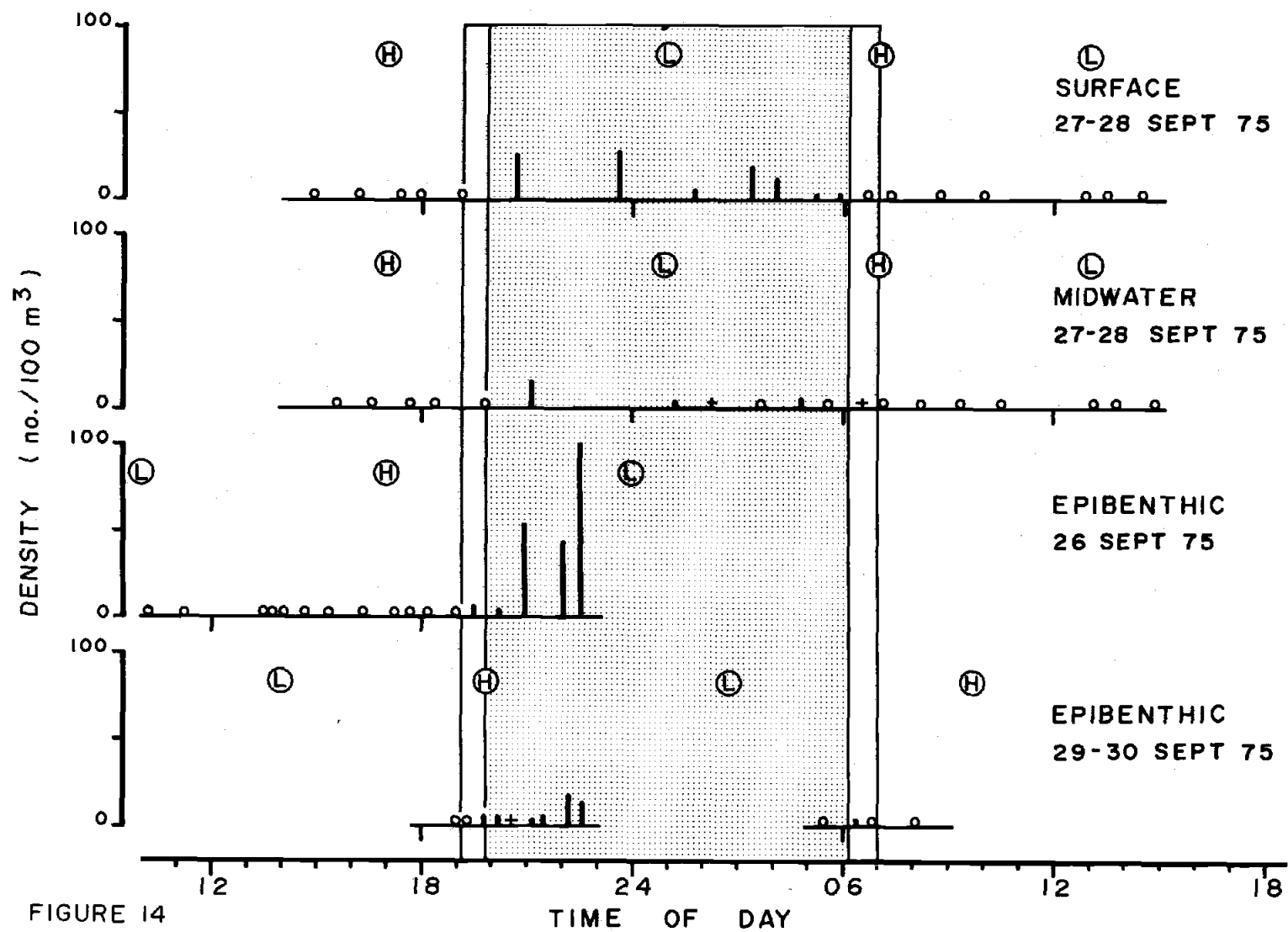
FIGURE 14

Figure 15. Density of <u>Corophium spinicorne</u> in three water column strata over a diel cycle in Youngs Bay, Oregon. Darkness (shaded area) is bounded by dusk and dawn (unshaded enclosures). H indicates high tide and L low tide. The + sign indicates densities less than $3/100 \text{ m}^3$, while the O indicates zero densities. Data are tabulated in Appendix C.

FIGURE 15

SURFACE
27-28 SEPT 75

MIDWATER
27-28 SEPT 75

EPIBENTHIC
26 SEPT 75

EPIBENTHIC
29-30 SEPT 75

DENSITY (no./100 m³)

TIME OF DAY
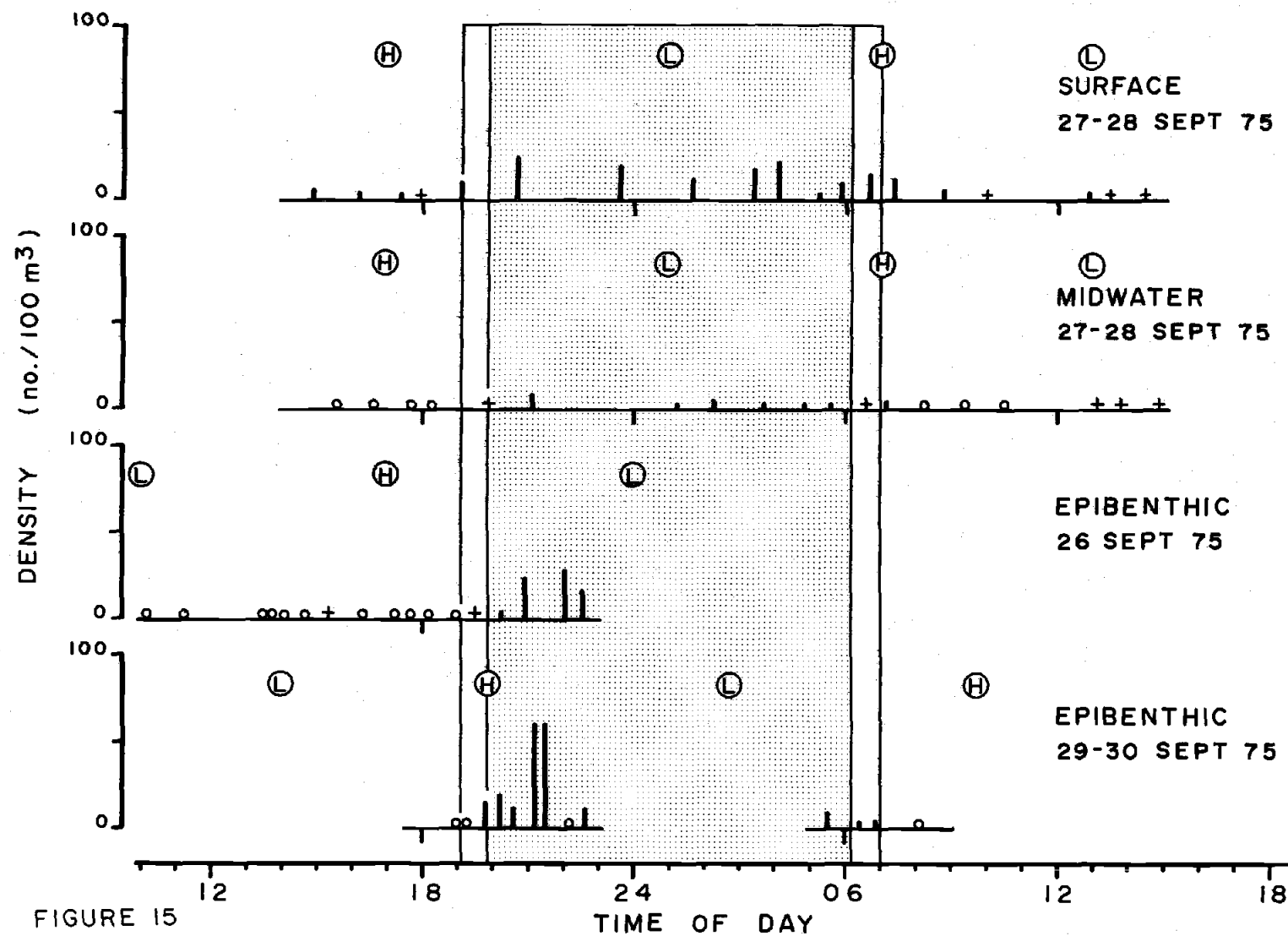
(Figure 16). Most were captured in the epibenthic stratum. Densities in the first epibenthic series were near 25/100 m^3. The activity rhythm of C. franciscorum involving density increases at sunset was similar to those seen for C. salmonis, A. confervicolus, N. mercedis and E. estuaris.

Gnorimosphaeroma oregonensis and Corophium brevis

The isopod Gnorimosphaeroma oregonensis was captured in seven nighttime, one dusk, and one daylight sample (Appendix C). However, densities were very low (about 1/100 m^3). Menzies (1954) cited additional observations of nocturnal activity, and because in Youngs Bay these isopods are primarily distributed along the shore-line, swimming activity at night may have been mostly localized there.

One additional species of the genus Corophium, C. brevis, was captured consistently aroung nighttime high tides in both the first and second epibenthic series (Appendix C). Densities were near 10/100 m^3. This species is primarily distributed in more saline water downstream of Youngs Bay (Higley and Holton, in prep.), and was probably swept into the tow zone with the salinity intrusion.

81

Figure 16. Density of Crangon franciscorum in three water column
strata over a diel cycle in Youngs Bay, Oregon. Dark-
ness (shaded area) is bounded by dusk and dawn (unshaded
enclosure). H indicates high tide and L low tide. The
symbol O indicates zero densities. Data are tabulated
in Appendix C.
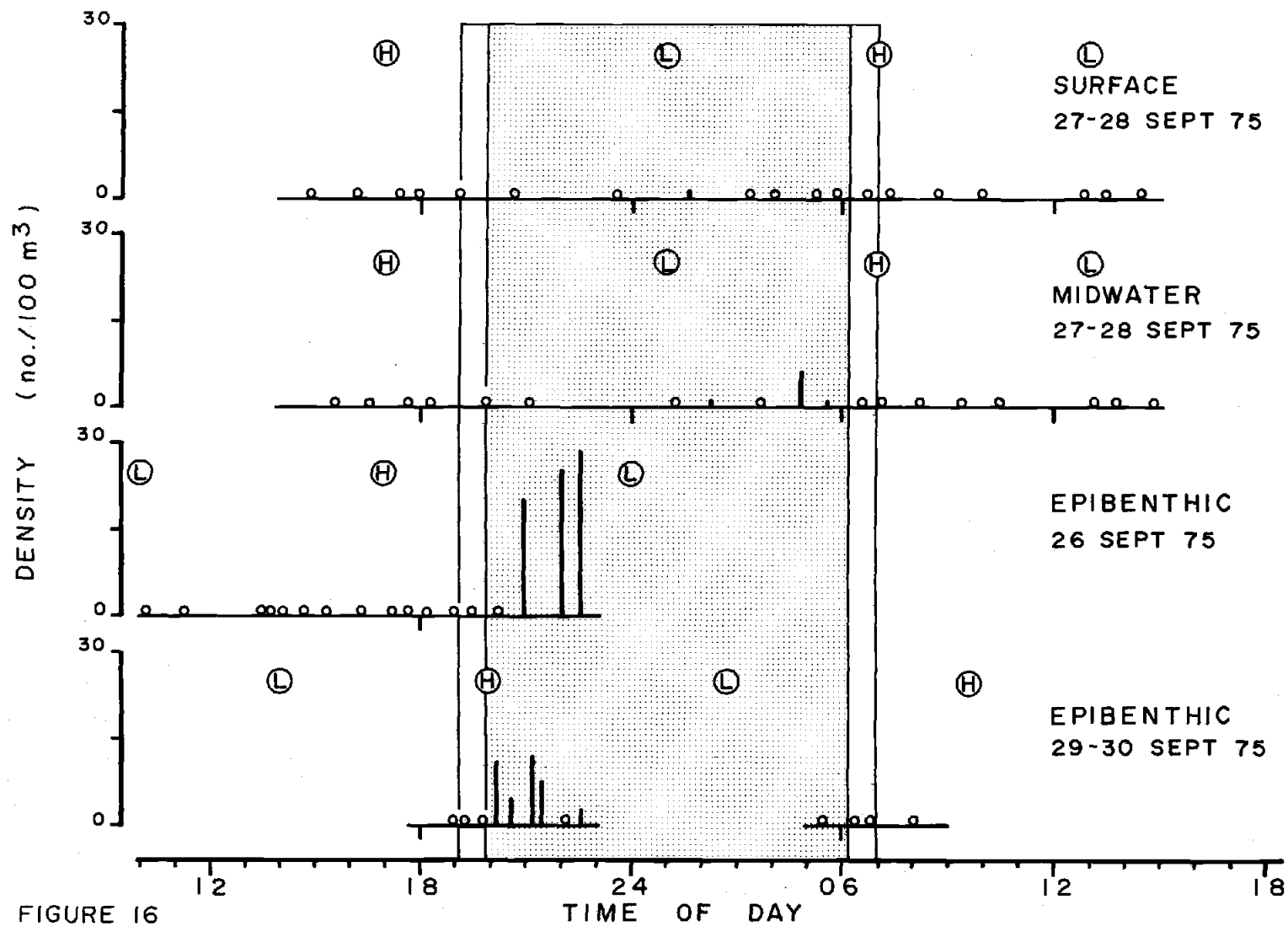
FIGURE 16

Characteristics of Swimming Animals

Length, Sex, Maturity, and Body Coloration
of Corophium salmonis and C. spinicorne

Body length, sex, maturity, and body coloration were deter-
mined for 1578 Corophium salmonis and 159 C. spinicorne. Animals
captured at each of the three water column strata during the three
light conditions of daylight, transition light (dusk and dawn), and
darkness were examined. In addition, C. salmonis from selected
benthic samples taken during daylight and darkness were examined;
no light condition is designated, and this data is taken to reflect the
benthic population structure.

Corophium salmonis

For C. salmonis captured in the water column, males generally
outnumbered females, while for those remaining in the sediment,
females outnumbered males (Table 2). Looking at the water column
data combined, about 60% of the animals, at each light condition,
were male, while in the substrate, only about 40% were male.

Tests for a significant departure from a hypothetical 1:1 sex
ratio were performed on data for each stratum-light condition category,
and the results are shown in Table 2. For sample sizes less than or
equal to 25, the exact probability of obtaining the observed values

Table 2. Sex ratios and melanophore states of Corophium salmonis and C. spinicorne. Water column data have been combined into three light categories: (1) daylight, (2) transition (dusk and dawn), and (3) darkness. Benthic data are from daylight and darkness samples. Data from water column samples have also been combined as a separate category (water column). Results are given for the tests for significant departure from a 1:1 sex ratio next to the fraction male values.

		Surface			Midwater			Epibenthic			Water Column			Benthic
Corophium salmonis		Day	Trans	Dark	Day	Trans	Dark	Day	Trans	Dark	Day	Trans	Dark	
Sex:	Melanophores:													
Male	Punctate	4		170	1	33	105	12	35	142	17	68	417	2
	Diffuse	7		3	2	0	1	20	21	66	29	21	70	195
Female	Punctate	0		110	3	18	97	8	27	81	11	45	288	0
	Diffuse	1		3	2	0	4	9	15	49	12	15	56	286
TOTAL		12		286	8	51	207	49	98	338	69	149	831	483
Fraction	Punctate	.33		.98	.50	1.00	.99	.41	.63	.66	.41	.76	.85	< .01
Fraction	Male	.92**		.60**	.38	.65	.51	.65	.57	.62**	.67**	.60*	.59**	.41**
Corophium spinicorne														
Sex:	Melanophores:													
Male	Punctate	0	1	0	1	1	0	0	0	1	1	2	1	
	Diffuse	24	10	8	3	0	3	1	1	7	28	11	18	
Female	Punctate	0	1	1	0	0	1	0	0	0	0	1	2	
	Diffuse	18	15	11	3	1	1	0	1	8	21	17	20	
TOTAL		42	27	20	7	2	5	1	2	16	50	31	41	
Fraction	Punctate	0	.07	.05	.14	.50	.20	0	0	.06	.02	.10	.07	
Fraction	Male	.57	.41	.40	.57	.50	.60	1.00	.50	.50	.58	.42	.46	

*0. 05 > P > 0. 01.

**P < 0.01.

and all greater deviations from a 1:1 ratio were calculated assuming

a binomial population with $p = q = 0.5$ (Sokal and Rohlf, 1969). For

sample sizes greater than 25, the X^2_{adj} test statistic, which approxi-

mates the χ^2 - distribution was calculated (Sokal and Rohlf, 1969).

The Yates correction for continuity was used in all of these latter

calculations. The null hypothesis was that the animals were selected

from a population with a 1:1 sex ratio. Failure to reject the null

hypothesis, of course, does not confirm the 1:1 ratio, but just indi-

cates that there was insufficient evidence to conclude that it was

false.

Although the sex ratios differed from 1:1 by an apparently

small amount, these differences were statistically significant when

adequate sample sizes were obtained (Table 2). At night, when

many animals were captured in the water column, sex ratios signifi-

cantly favored males in the surface and epibenthic strata. The sex

ratio of C. salmonis in the substrate significantly favored females.

The sex ratio of nocturnally active C. salmonis, therefore, did

not reflect the sex ratio of non-active ones. This suggests that the

active animals were not just a random selection of those in the sub-

strate. A further anlaysis will be presented later addressing the

possible interaction between animal size and sex ratios.

With small exception, C. salmonis captured in the upper water

column at night had punctate melanophores, while those in the

substrate had expanded melanophores (Table 2). In the epibenthic stratum at night, however, there was a mixture of animals having either punctate or expanded melanophores. Very few had melanophores in an intermediate stage of expansion. The proportion of C. salmonis with punctate melanophores was lower in the water column during daylight than during either transition light or darkness. Thus, the condition of punctate melanophores was strongly associated with nocturnal activity in the upper water column.

Multiway tests of independence were performed on the data in Table 2 to determine the degree of association among melanophore state, sex, light condition, and stratum for Corophium salmonis in the water column. The log likelihood ratio test (Sokal and Rohlf, 1969) was used in a three-way contingency table format. In the terminology of these types of tests, each parameter compared is a factor while each of the different possible states of a parameter is a level. For example, melanophore state is a factor with two levels, punctate and diffuse; while light condition has three levels, daylight, transition light, and darkness.

The first set of tests determined the relationship between melanophore state, sex, and light condition at each of the three water column strata. The results are presented in Table 3. An overall test of independence among the three factors was performed with the null hypothesis being independence. Acceptance of the null hypothesis

Table 3. Results of three-way contingency table tests made on the data in Table 2. Factors are abbreviated as follows: LT = light, SX = sex, ML = melanophore state, ST = strata, SF = surface stratum, MW = midwater stratum, and EB = epibenthic stratum.

	Surface		Midwater		Epibenthic	
Hypothesis tested	d. f.	G	d. f.	G	d. f.	G
LT x SX independence	2	5.834	2	3.886	2	1.032
LT x ML independence	2	39.496**	2	20.444**	2	11.182**
SX x ML independence	1	.666	1	1.578	1	.302
LT x SX x ML interaction	2	.468	2	1.146	2	1.410
LT x SX x ML independence	7	46.464**	7	26.994**	7	13.926

	Darkness	
Hypothesis tested	d. f.	G
ST x SX independence	2	6.234*
ST x ML independence	2	168.406**
SF vs MW	1	.054
SF + MW vs EB	1	168.352**
SX x ML independence	1	.566
ST x SX x ML interaction	2	3.092
ST x SX x ML independence	7	178.300**

*0.01 > P > 0.05.

**P < 0.01.

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indicates that the product of the probabilities of each of the particular

levels of the factors allows prediction of the probability of a single

observation, which is the occurrence of an individual of a particular

melanophore state and sex during a particular light condition. The

probability for each factor level is obtained in these three-way tables

from the marginal totals, which are sums over the other two factors.

The overall independence G value and its degrees of freedom

may be partitioned into components to examine the independence of

the factors in more detail. Tests of independence of each pair of

factors were performed, with the null hypothesis being independence.

The two-factor tests are interpreted in an analogous fashion to the

three-factor test. A test of overall interaction of the three factors

was also tested, with the null hypothesis being interaction. Accep-

tance of the null hypothesis indicates that the degree of association be-

tween some pair of factors, measured by the two-way G value, differ

at different levels of the third factor. If there is interaction among

the three factors, then they can not be independent. However, the

hypothesis of overall independence may be rejected with or without

interaction existing among the three factors. In other words, the

three factors, though not independent, may or may not relate in

the specific manner implied by overall interaction.

At each stratum, the dependence of melanophore state and light

condition was highly significant (Table 3). This result is particularly

evident in surface and midwater data but to a lesser degree in the epibenthic data. This is expected because of the moderate proportion of diffuse animals in the epibenthic-darkness category and their absence from the upper water column-darkness category (Table 2). As a result, only in the epibenthic region was there insufficient evidence to reject the overall independence of the three factors.

There was evidence for overall interaction among the three factors as evidenced by the failure to reject the null hypothesis at each stratum. To determine where the interaction existed, two-way G values for each pair of factors at each level of the third were calculated. The association between melanophore state and light condition was stronger for males than for females. Sex, per se, however, was independent of either melanophore state or light condition. Thus, even though both males and females were predominantly punctate at night, the association between these two levels was greater in males than in females.

The second set of tests determined the degree of association between melanophore state, sex, and water column stratum during the same light condition. Darkness data were selected for analysis because sample sizes are large (greater than 200 for each stratum). A three-way test was performed on these data in the same manner as in the first tests, and the results are presented in Table 3. The rejection of the null hypothesis of overall independence of the three

factors was significant, and the G value and its degrees of freedom were further partitioned. Of the three tests of independence between the pairs of factors, only stratum and melanophore state were dependent. This G value and its two degrees of freedom were partitioned into two additional tests to determine the nature of the dependence. The first tested whether the melanophore states were independent between the two upper water column strata, surface and midwater. This test showed no evidence for rejecting the null hypothesis. The second tested whether the melanophore states were independent between the upper water column and the lower water column (epibenthic stratum). This test showed that essentially all of the dependence of melanophore state with stratum arose from the difference in melanophore state between the upper and lower water column.

Essentially all of the C. salmonis captured in the surface and midwater strata at night were older juveniles between 1.50 and 3.00 mm in length (Figure 17). Of those in the substrate, however, there was a small but distinct proportion of young juveniles less than 1.50 mm in length and a moderate proportion of adults longer than 3.50 mm. Still, most of the benthic population was between 1.50 mm and 3.00 mm in length. The length distribution of epibenthic animals was more similar to that of the benthic population than to that of the upper water column population in showing a small proportion of individuals less than 1.50 mm and greater than 3.50 mm in length.

Figure 17. Length-frequency distributions of <u>Corophium</u> <u>salmonis</u> from water column and benthic samples. Water column data have been combined into three light categories: (1) daylight, (2) transition (dusk and dawn), and (3) darkness. Benthic data are from daylight and darkness samples. Sample size is shown at the upper right of each histogram. Median length class is indicated by .

DAYLIGHT   TRANSITION   DARKNESS

FIGURE 17

LENGTH CLASS (mm)

FRACTION
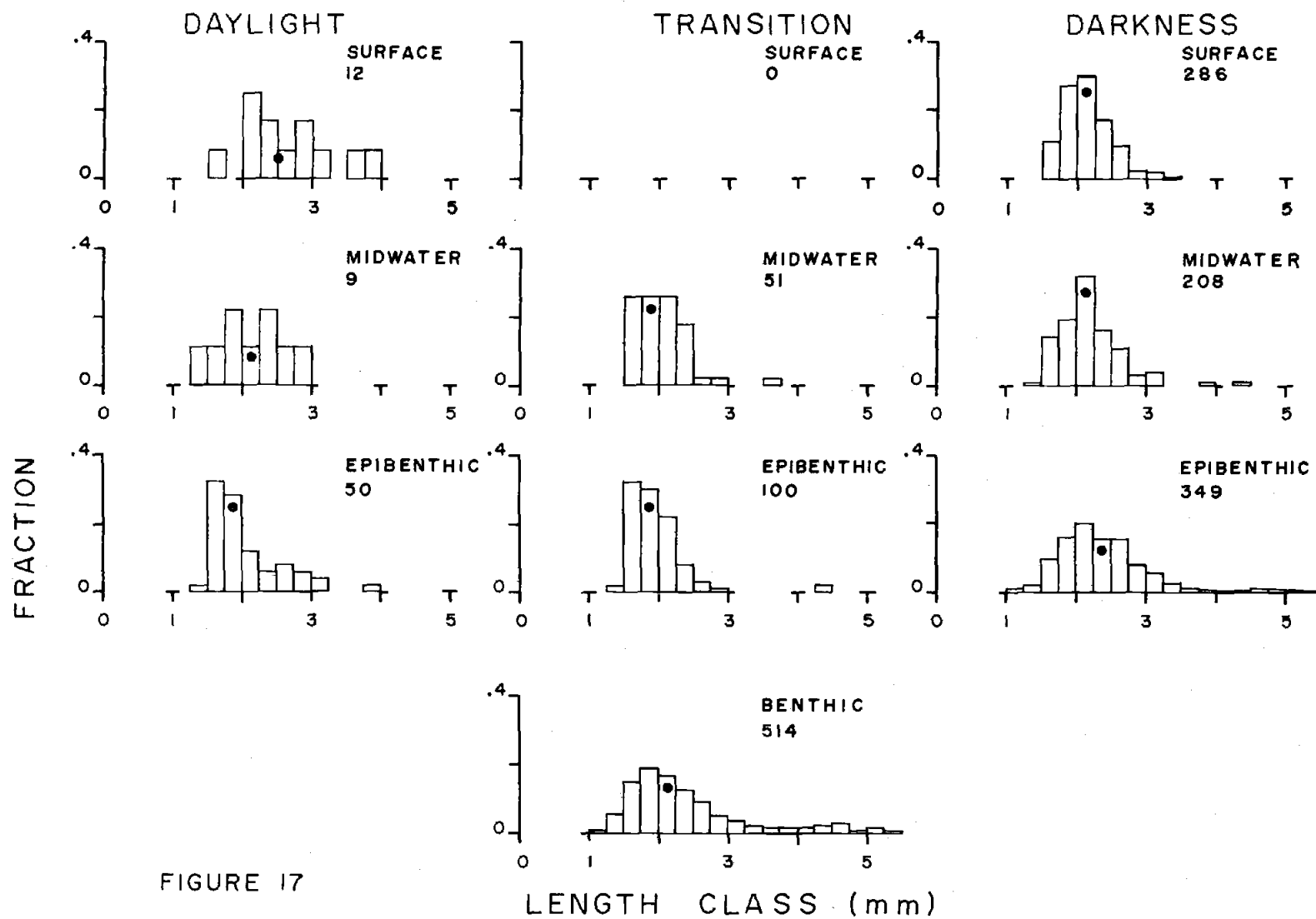
Comparisons of length distributions of individuals captured in the water column during daylight and transition light were hampered by small sample sizes. Most individuals, however, like those captured in the upper water column at night, were between 1.50 mm and 3.00 mm in length. The midwater-transition, epibenthic-daylight, ana epibenthic-transition distributions (sample sizes greater than 50 for each) appeared similar and had the same median class. Both of these epibenthic distributions, however, had a much lower proportion of longer individuals than the epibenthic-darkness distribution.

Based on nighttime water column data and benthic data, the length distributions of males and females were very similar at each stratum (Figure 18). The moderate proportions of individuals longer than 3.50 mm in the epibenthic and benthic regions, however, was composed of more females than males.

As stated, males were more abundant in the water column at night than females, while females were more abundant in the substrate than males (Table 2). However, only a restricted size range of the individuals present in the substrate, that is, those between 1.50 mm and 3.00 mm, swam to the upper water column (Figure 17). It is reasonable to assume that individuals found in the water column represent a portion of the benthic population. The higher proportion of males in the water column may thus be explained two ways. First, it is possible that sex does not influence the response of an individual
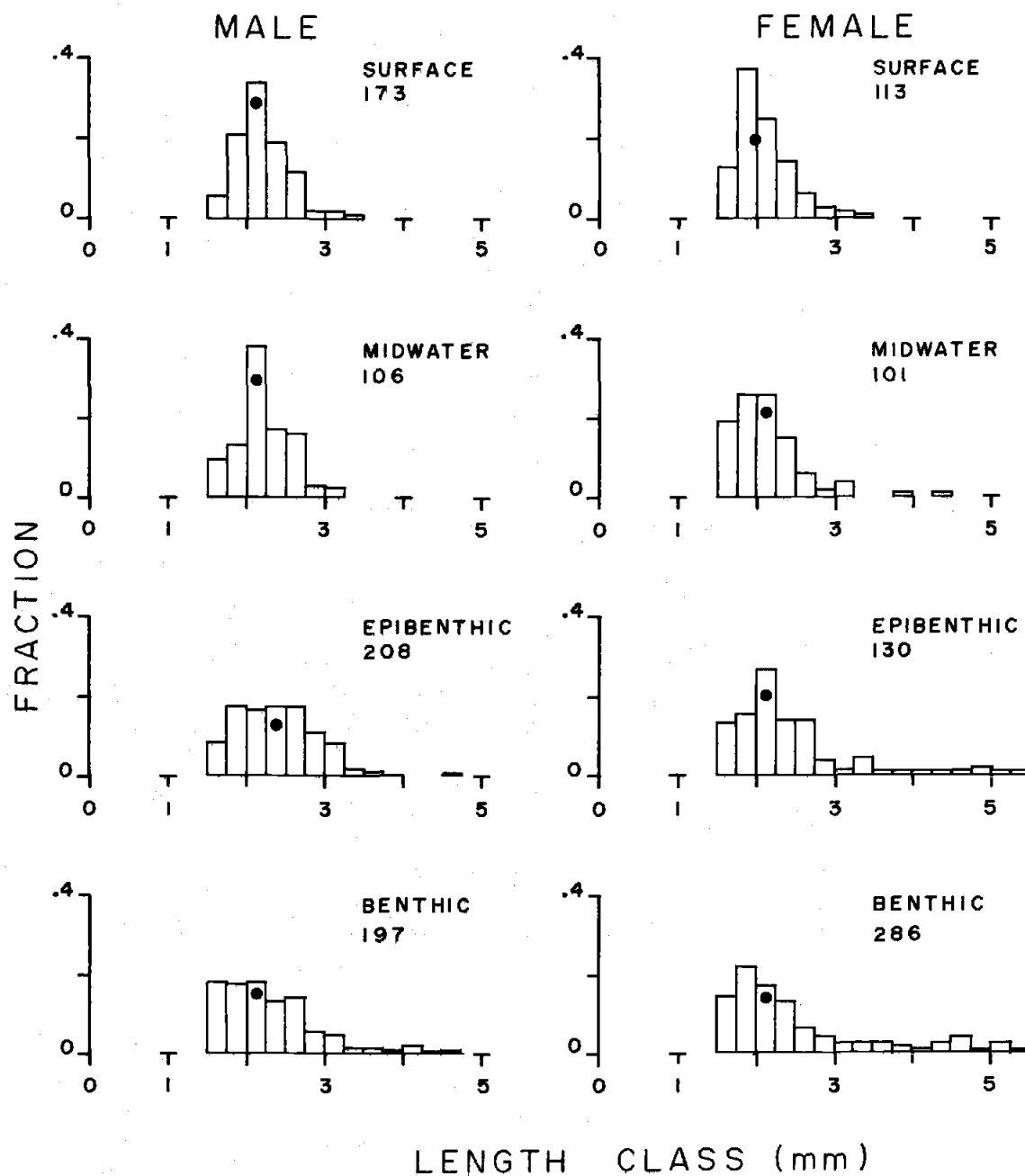
Figure 18. Length-frequency distributions of Corophium salmonis
according to sex. Water column data are from darkness
samples, and benthic data from daylight and darkness
samples. Sample size is shown at the upper right of
each histogram. Median length class is indicated by ⊕ .

to leave the substrate, in which case the benthic sex ratio for the
1.50 mm to 3.00 mm size group only should be skewed towards
males, like the sex ratio of animals in the water column. Or, it is
possible that the sex ratio of 1.50 mm to 3.00 mm individuals in
the substrate, like that for all individuals in the substrate combined,
is skewed towards females, and a higher proportion of males than
females leaves the substrate.

To examine these alternative hypotheses, sex ratios were
calculated for individuals between 1.50 mm and 3.00 mm in length
and for those greater than or equal to 3.00 mm using benthic data and
nighttime data from each water column stratum. The results are
presented in Table 4. The null hypothesis that the samples were
drawn from a population having a 1:1 sex ratio was tested by calculat-
ing either the exact binomial probability or the X^2_{adj} test statistic in
the manner explained for the data of Table 2.

The sex ratios of both length groups of individuals in the sub-
strate were skewed towards females. The deviation from a 1:1 ratio
was statistically significant in the group ≥ 3.00 mm, and very nearly
significant at the 0.05 level in the group between 1.50 mm and 3.00
mm. Only the epibenthic data were of sufficient sample size of indi-
viduals ≥ 3.00 mm to allow statistical comparison. Although not
statistically significant, 60% of these large individuals were males,
a value very similar to the percentage of males between 1.50 mm and

Table 4. Results of tests for significant departure from 1:1 sex ratios for two size groups of <u>Corophium salmonis</u> (1.50 mm to 3.00 mm, and ≥ 3.00 mm). Data are from darkness water column samples, and from daylight and darkness benthic samples.

	Surface		Midwater		Epibenthic		Benthic	
	1.50-3.00 mm	>3.00 mm	1.50-3.00 mm	>3.00 mm	1.50-3.00 mm	>3.00 mm	1.50-3.00 mm	>3.00 mm
No. males	169	4	103	3	183	25	172	25
No. females	110	3	95	6	113	17	223	63
TOTAL	279	7	198	9	296	42	395	88
Fraction male	.61*	.57	.52	.33	.62**	.60	.44	.40*

*.01 < P < .05.

**P < .01.

3.00 mm present in the surface and epibenthic strata at night. These results therefore support the second hypothesis, that is that a slightly higher proportion of males than females left the substrate and swam in the water column.

For the most part, the length distributions of punctate and diffuse individuals were similar in each stratum for water column-darkness and benthic data (Figure 19). In the epibenthic stratum, where there was a mixture of both types of individuals, the central portions of the distribution between 1.50 mm and 3.00 mm were very similar. The moderate proportion of individuals larger than 3.00 mm, which is a characteristic of the lower water column and not the upper water column, was composed of slightly more diffuse than punctate individuals. Very few diffuse individuals in the upper water column at night and very few punctate individuals in the benthos were captured.

Up to this point, the comparisons of length distributions between males and females (Figure 18) and between punctate and diffuse individuals (Figure 19) were made with water column-darkness data because sample sizes were large. In an attempt to make reliable comparisons with the less extensive daylight and transition light data, the surface and midwater data were combined into upper water column to increase sample sizes and compared to the lower water column (epibenthic) data (Figure 20).
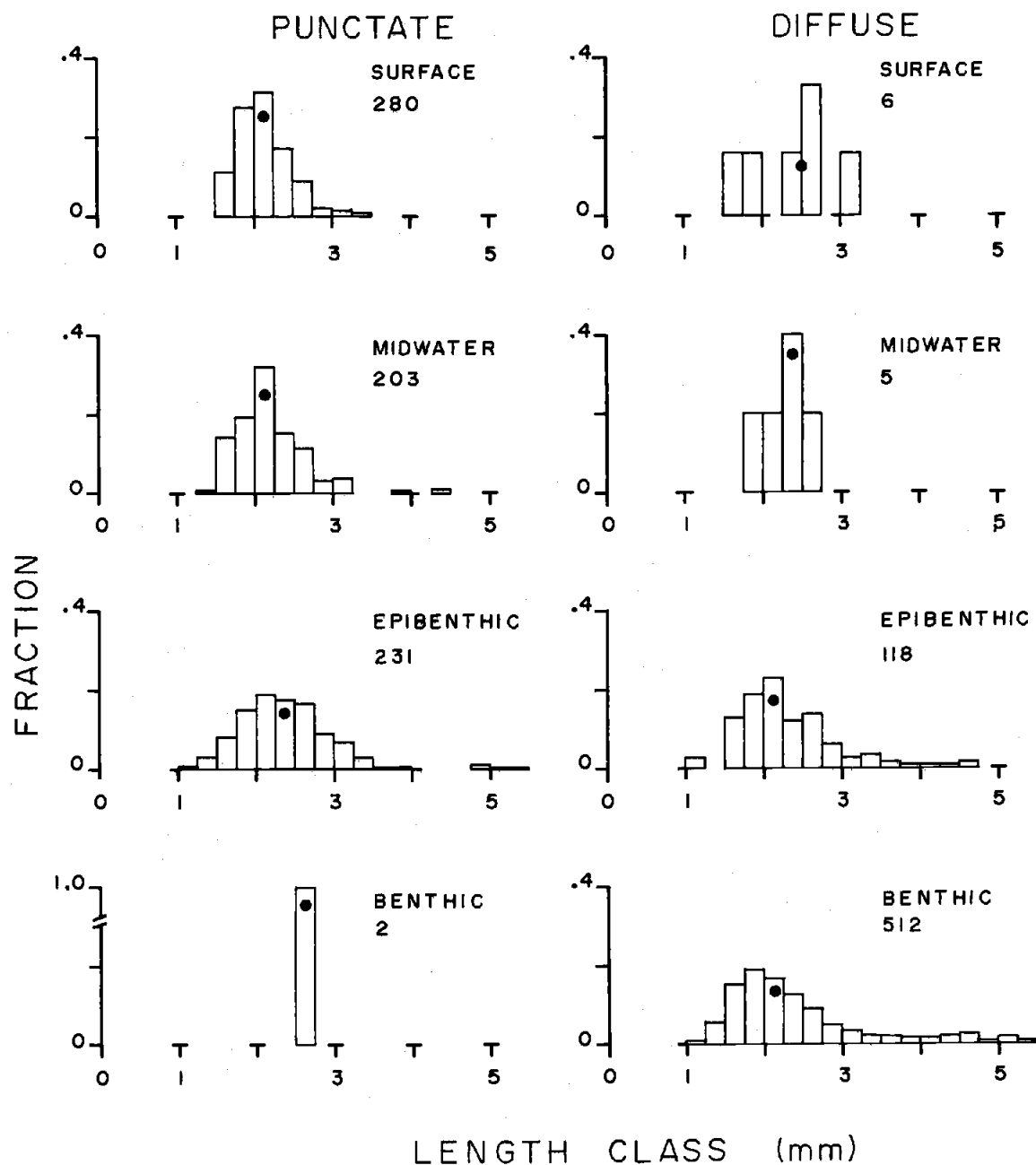
Figure 19. Length-frequency distributions of <u>Corophium</u> <u>salmonis</u> according to melanophore state. Water column data are from darkness samples, and benthic data from daylight and darkness samples. Sample size is shown at the upper right of each histogram. Median length class is indicated by ● .
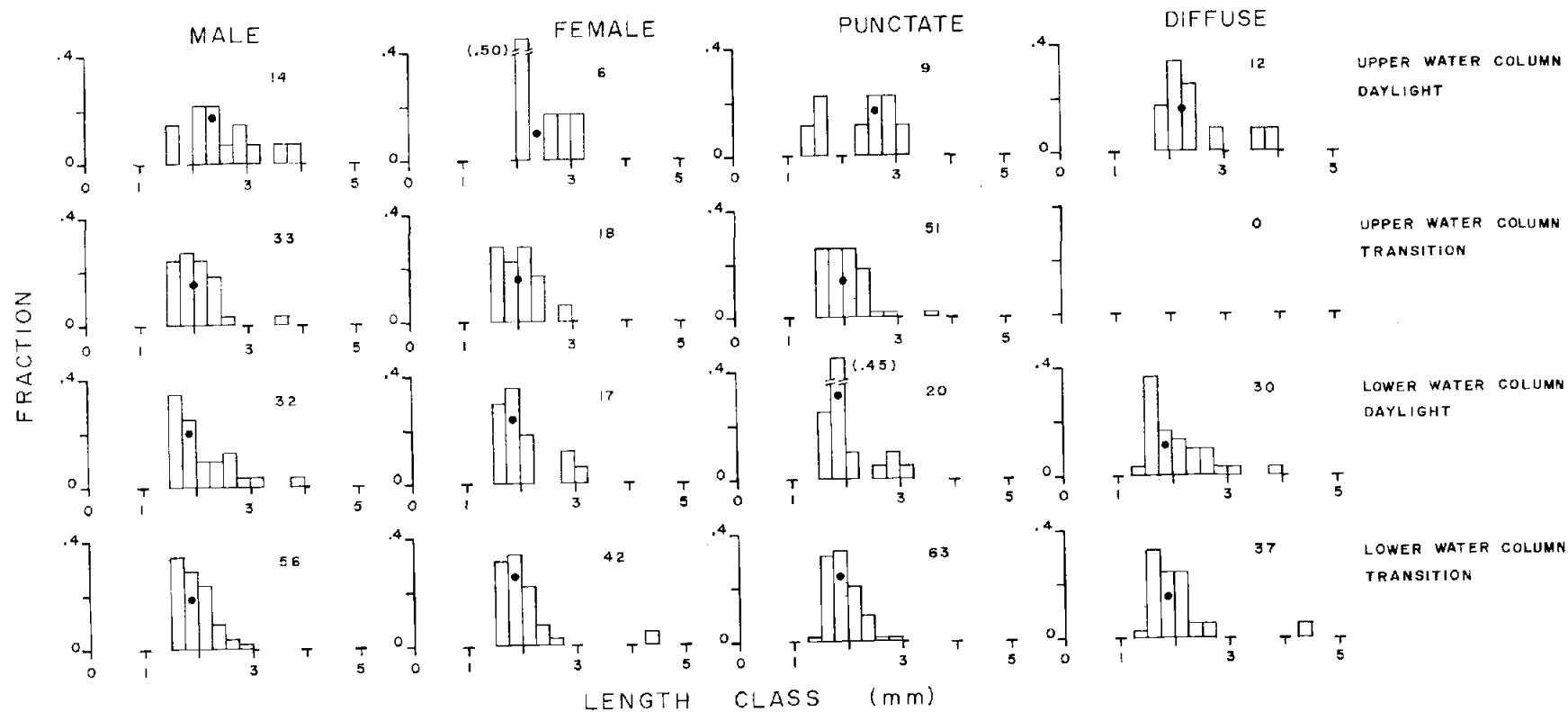
Figure 20. Length-frequency distributions of Corophium salmonis from daylight and transition light samples. Data are combined first by sex, then by melanophore state. Surface and midwater data have been combined as upper water column, and epibenthic data are presented as lower water column. Sample size is shown at the upper right of each histogram. Medium length class is indicated by ● .

In the lower water column during both daylight and transition light, the length distributions of males and females and of punctate and diffuse individuals were remarkably similar. As pointed out in Figure 17, the individuals longer than 3.50 mm, characteristic of the epibenthic-darkness distribution, were generally absent. Likewise, in the upper water column-transition light condition, male and female length distributions were very similar. Upper water column-daylight comparisons were hampered by small sample sizes.

Reproductive and gravid female C. salmonis were essentially only captured in the epibenthic and benthic strata (Table 5). Reproductive females have marginal setae on their oostigites, indicating breeding condition. Only a single reproductive female was captured in the upper water column, while 5% of the females in the epibenthic stratum and 15% in the benthic stratum were reproductive; most were also gravid. The mean length of these gravid females was near 4.50 mm, and most of the females longer than 3.50 mm, seen almost exclusively in the epibenthic and benthic strata (Figure 18), were gravid.

Corophium spinicorne

Some characteristics of active Corophium spinicorne were intriguingly different from active C. salmonis. Most C. spinicorne captured by net during each of the light conditions had expanded

Table 5. Body length and relative frequency of reproductive and gravid female Corophium salmonis and C. spinicorne. Water column data have been combined into three light categories: (1) daylight, (2) transition (dusk and dawn), and (3) darkness. Benthic data are from daylight and darkness samples. Data from water column samples have been combined as a separate category (water column). Reproductive females have marginal setae on oostigites, and gravid females have one or more eggs or juveniles in a brood pouch. All counts of clutch size were used, although some females appeared to have lost eggs.

Corophium salmonis	Surface			Midwater			Epibenthic			Water Column			Benthic
	Day	Trans	Dark	Day	Trans	Dark	Day	Trans	Dark	Day	Trans	Dark	
Total No. female	1	0	113	5	18	101	17	42	130	23	60	344	286
No. reproductive	0		0	0	0	1	0	2	8	0	2	9	44
No. gravid						0		1	6		1	6	38
Fraction reproductive	0		0	0	0	.01	0	.05	.06		.03	.03	.15
Fraction gravid								.02	.05		.02	.02	.13
Mean clutch size								7.0	5.0		7.0	5.0	10.0
Mean length reproductive females						4.375		4.375	4.531		4.375	4.514	4.494
Standard error of the mean								0	.241		0	.213	.081

Corophium spinicorne	Surface			Midwater			Epibenthic			Water Column			Benthic
	Day	Trans	Dark	Day	Trans	Dark	Day	Trans	Dark	Day	Trans	Dark	
Total no. female	18	16	12	3	1	2	0	1	8	21	18	22	
No. reproductive	7	12	4	2	1	0		0	1	9	13	5	
No. gravid	1	1	3	0	1				1	1	2	4	
Fraction reproductive	.39	.75	.33	.67	1.00	0		0	.13	.42	.72	.23	
Fraction gravid	.06	.06	.25		1.00				.13	.05	.11	.18	
Mean clutch size	5.0	5.0	2.3		22.0				15.0	5.0	13.5	5.5	
Mean length reproductive females	3.911	4.063	3.375	5.000	4.625				4.125	4.153	4.106	3.525	
Standard error of the mean	.240	.188	.323	.125						.245	.178	.292	

melanophores while C. salmonis, particularly at night, had contracted

melanophores (Table 2). In no case did the sex ratios of C. spini-

corne deviate significantly from 1:1, and no consistent trend in the

direction of deviation was evident. However, sample sizes are

rather small, and more observations are needed before reliable

conclusions can be drawn.

The range of lengths of C. spinicorne in the water column

(Figure 21) was quite large when compared to C. salmonis (Figure 17).

At the surface, lengths of individuals ranged from near 1.00 mm to

over 5.00 mm. Most, however, were between 1.50 mm and 3.00 mm.

Although very few from the lower two strata were measured, the data

suggested that the length ranges also tended to be quite broad. All

individuals over 3.75 mm in length were female, and the length dis-

tribution of males, in comparison, seemed quite narrow. Punctate

animals appeared shorter than diffuse animals; however, the small

sample sizes preclude a reliable comparison.

Most of the large females seen in the water column (Figure 22)

were reproductive, and many were gravid (Table 5). Of all females,

however, 40% were reproductive and 10% were gravid. Most of these

reproductive C. spinicorne were observed from surface stratum

samples, while reproductive C. salmonis were from the epibenthic

and benthic strata.
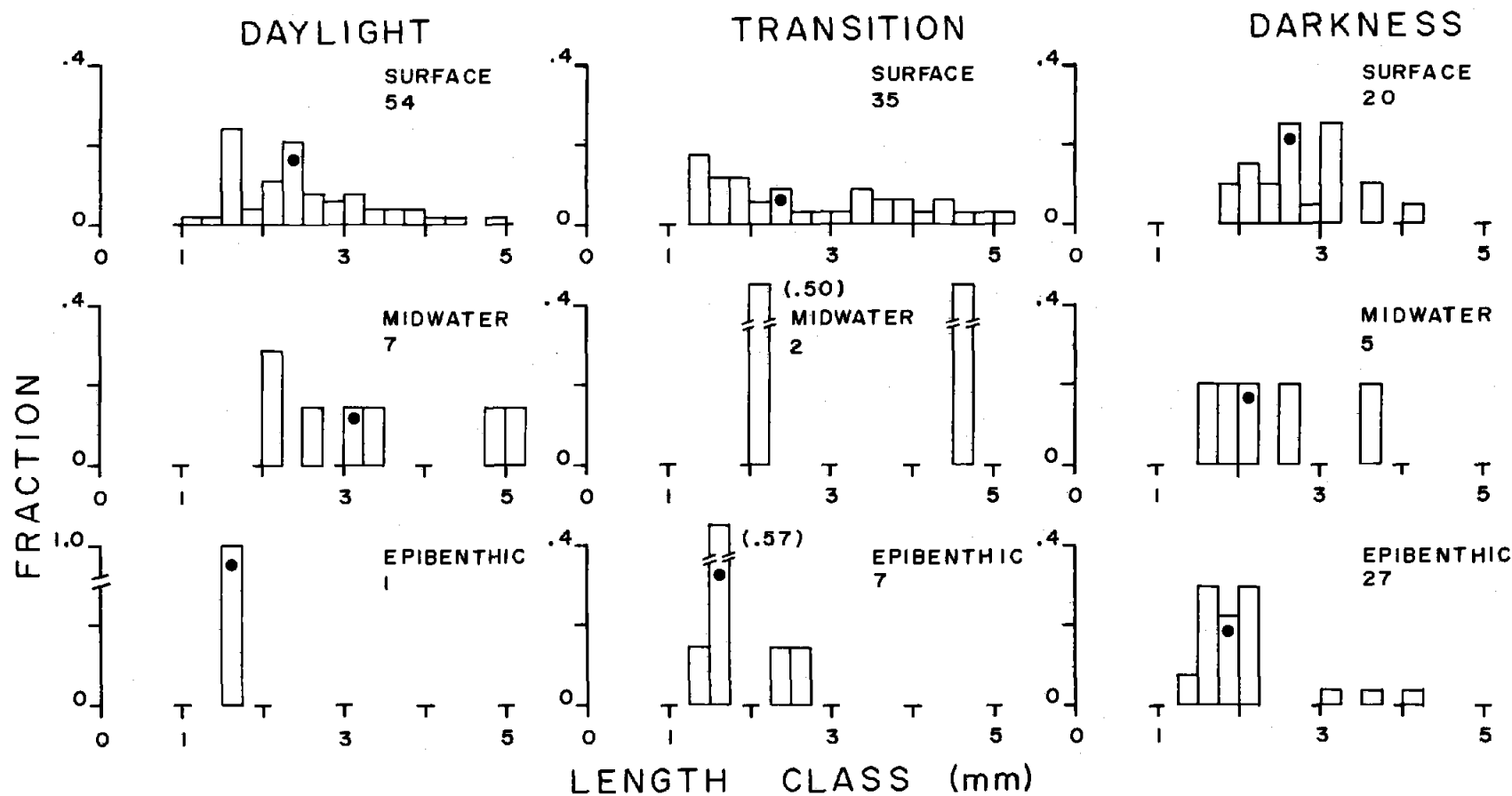
Figure 21. Length-frequency distributions of <u>Corophium</u> <u>spinicorne</u> from water column samples. Data have been combined into three light categories: (1) daylight, (2) transition (dusk and dawn), and (3) darkness. Sample size is shown at the upper right of each histogram. Median length class is indicated by ● .
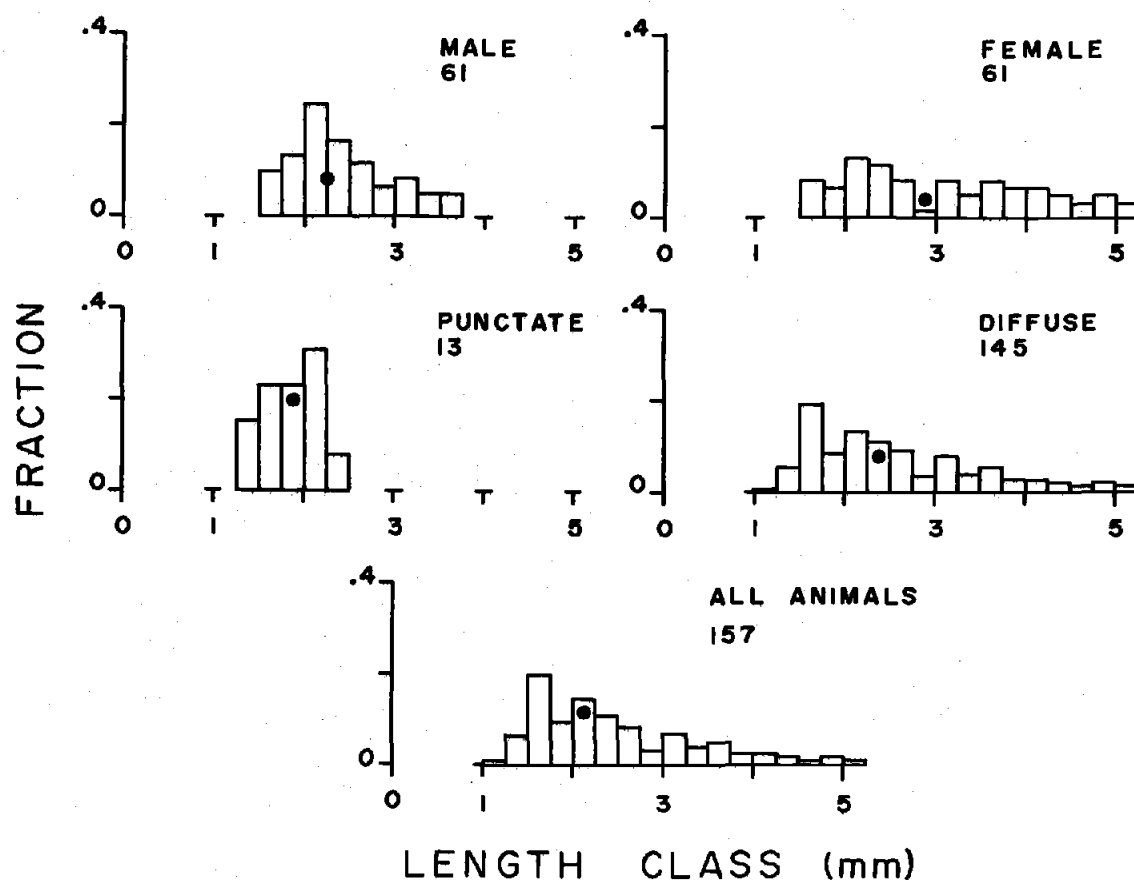
Figure 22. Length-frequency distributions of <u>Corophium</u> <u>spinicorne</u> from water column samples, according to sex and melanophore state. Data from all strata and light conditions have been combined. Sample size is shown in the upper right of each histogram. Median length class is indicated by ● .

Length, Sex, and Reproductive Condition
of Eohaustorius estuarius

Body length, sex, and reproductive condition of 281 Eohausto-rius estuarius from water column and benthic samples were determined. Water column data was collected during transition light and darkness and will be considered to represent nocturnally-active animals. Benthic data was collected during daylight and darkness, and will be considered to represent the benthic population structure.

Females consistently outnumbered males by a slight margin in each stratum (Table 6). However, these deviations were not significant when tested in the same manner as used in Table 2. Reproductive females were captured in the epibenthic and benthic strata but were absent from the upper water column samples. None of the females were gravid. Restriction of reproductive females to the lower two strata was also noted in C. salmonis, but the lack of gravid females may represent a difference in the reproductive seasons between the two amphipod species.

Most E. estuarius taken in the water column and substrate were between 1.00 mm and 2.00 mm in length, while the benthic stratum contained a small, but distinct, proportion of individuals longer than 3.00 mm (Figure 23). The epibenthic stratum may also have contained a greater proportion of these individuals longer than 3.00 mm, but more observations are needed before this contrast can reliably

Table 6. Sex ratio and female body length of Eohaustorius estuarius. Water column data are from darkness and transition samples, while benthic data are from daylight and darkness samples. Reproductive females have marginal setae on oostigites.

	Surface	Midwater	Epibenthic	Benthic
Eohaustorius estuarius				
Total number	96	25	52	108
No. male	28	5	12	33
No. female	33	8	19	45
Fraction male	.46	.38	.39	.42
Fraction females reproductive	0	0	.16	.22
Mean length			3.708	4.225
Std. err. mean			.363	.145
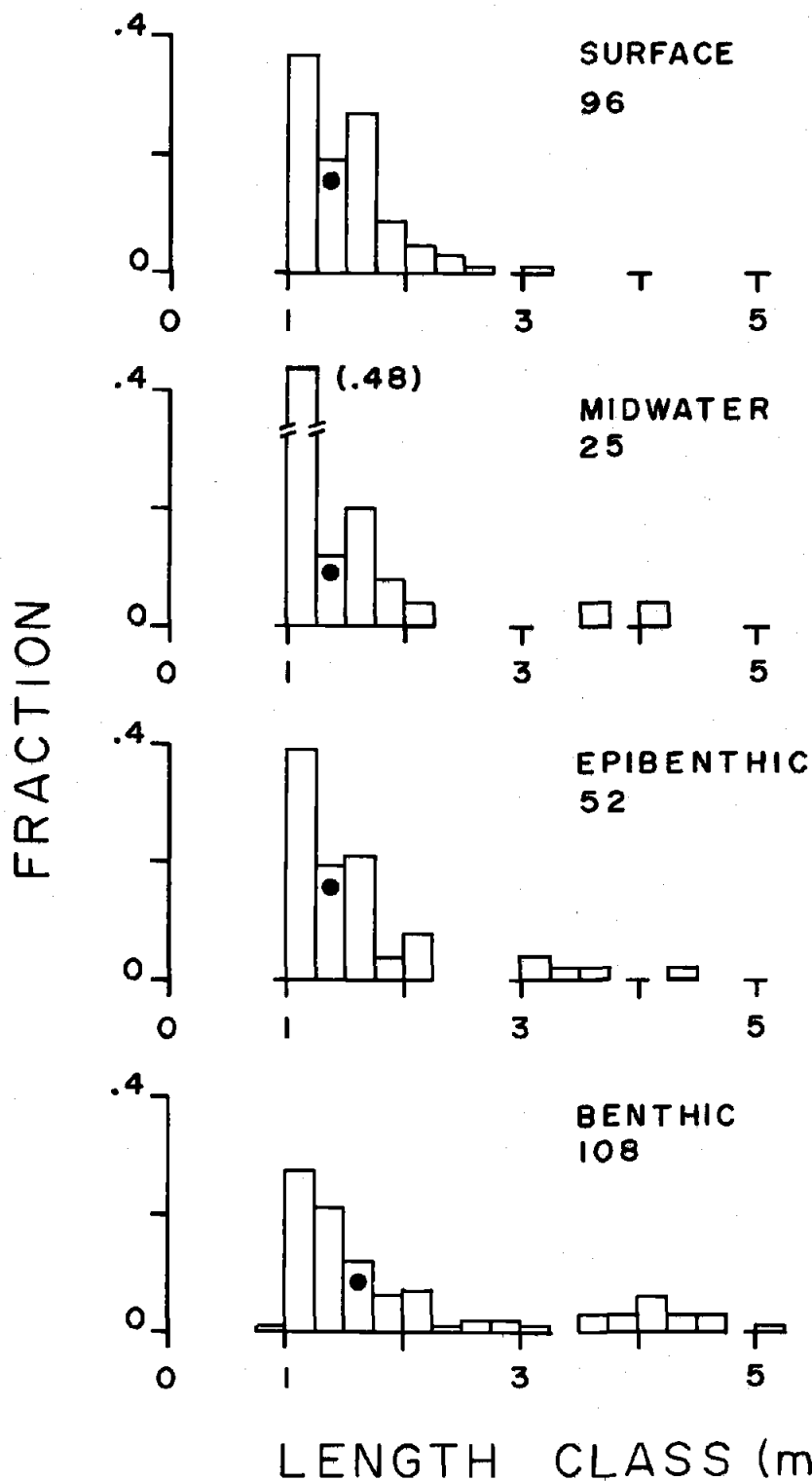
Figure 23. Length-frequency distributions of _Eohaustorius_ _estuarius_
from water column and benthic samples. Water column
data are from darkness and transition samples, and
benthic data from daylight and darkness samples. Sample
size is shown at the upper right of each histogram. Median
length class is indicated by ● .

be made. The surface and benthic data had similar sample sizes,
lending support to the conclusion that fewer large individuals were
in the surface stratum. This length distribution trend was seen for
C. salmonis (Figure 17), but the slight tendency for more females
than males in the water column at night may represent a slight differ-
ence in the behavior of these species. More female C. spinicorne
were observed in the water column, but many of them were large and
gravid (Figure 22 and Table 5).

Length of Neomysis mercedis and
Anisogammarus confervicolus

Body length of 361 Neomysis mercedis and 341 Anisogammarus
confervicolus from nighttime water column samples was determined.
Subsamples of approximately 100 individuals of each species were
examined from each stratum. These sample sizes were adequate to
determine gross differences in length distributions among strata.

Most N. mercedis in the surface stratum were between 1.25 mm
and 2.25 mm in length, with some reaching 7.00 mm, while in the
epibenthic stratum, there was a broad length range of individuals from
1.25 mm to 10.50 mm (Figure 24). It appears, therefore, that like
C. salmonis and E. estuarius, predominantly small N. mercedis
swam up to the surface stratum at night. In contrast, length distri-
butions of A. confervicolus were quite similar among the three
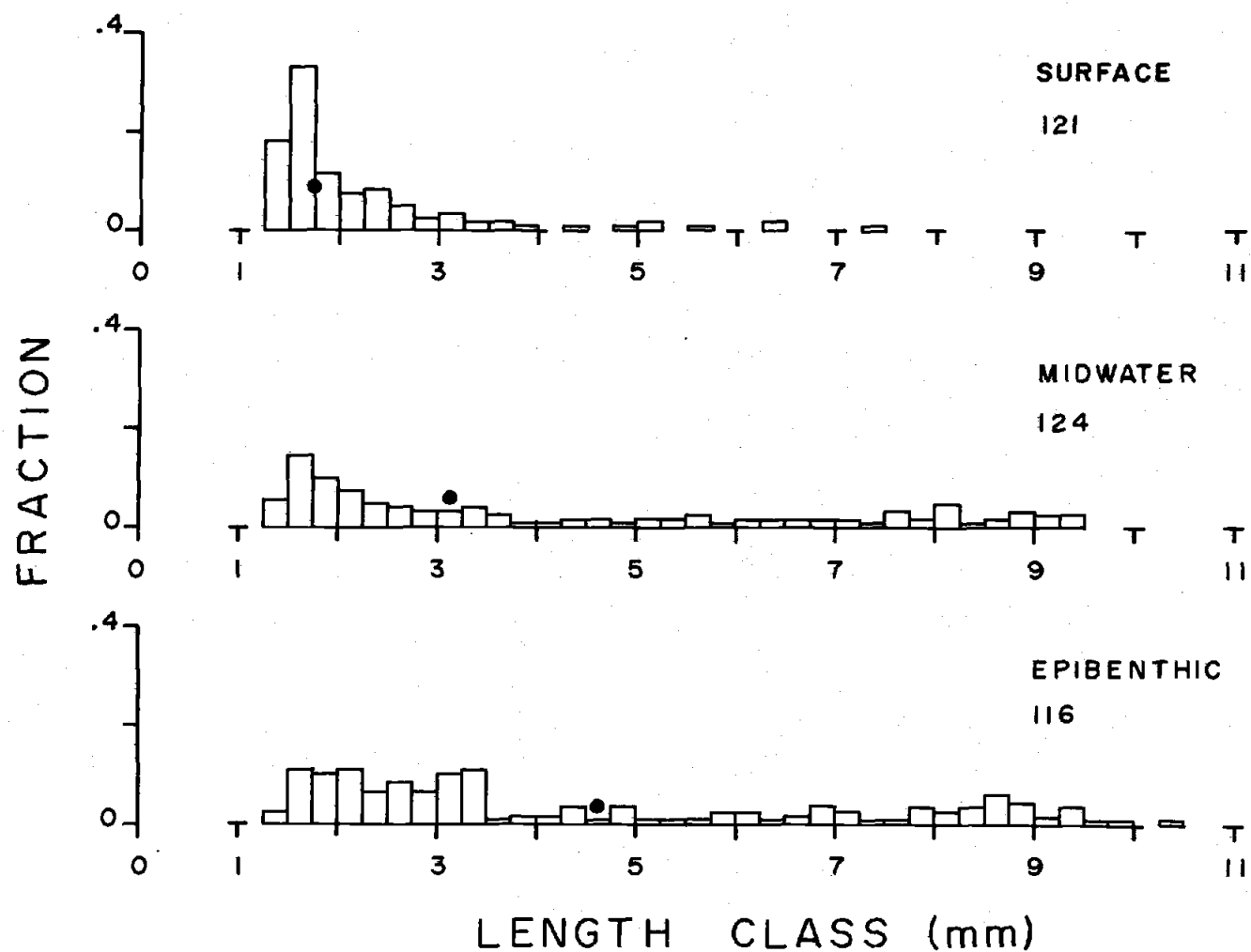
Figure 24. Length-frequency distributions of <u>Neomysis</u> <u>mercedis</u> taken in darkness samples. Sample size is shown in the upper right of each histogram. Median length class is indicated by ● .

strata (Figure 25).

Life-History of Corophium salmonis

The densities of benthic fauna in 12 grab samples taken over 17 months in 1974 and 1975 in Youngs Bay are presented in Table 7. Data for the 1974 samples, except the August 6 sample, were taken from Higley and Holton (1975). Other samples had not been previously analyzed, and only C. salmonis were counted. Data from the sample taken on September 2, 1975 is presented in monthly sequence between the August 6 and October 12, 1974, data. It is assumed that the September 1975 population structure satisfactorily represented the September 1974 population. C. salmonis density in the September 2, 1975 sample was similar to the 1974 late fall densities. Unfortunately, density could not be estimated from the August 6, 1974 sample. In addition, as will be shown, the population structure in the September 1975 sample is consistent with trends in structure seen in the summer and fall 1974 samples.

Females slightly exceeded males in number in 10 out of the 12 benthic samples (Table 8). However, in only two samples (August 6 and January 2) did the sex ratios deviate significantly from 1:1. For sexable animals from all samples combined, 46% were female, a significant departure from a 1:1 ratio.

Young juvenile C. salmonis less than 1.50 mm dominated the
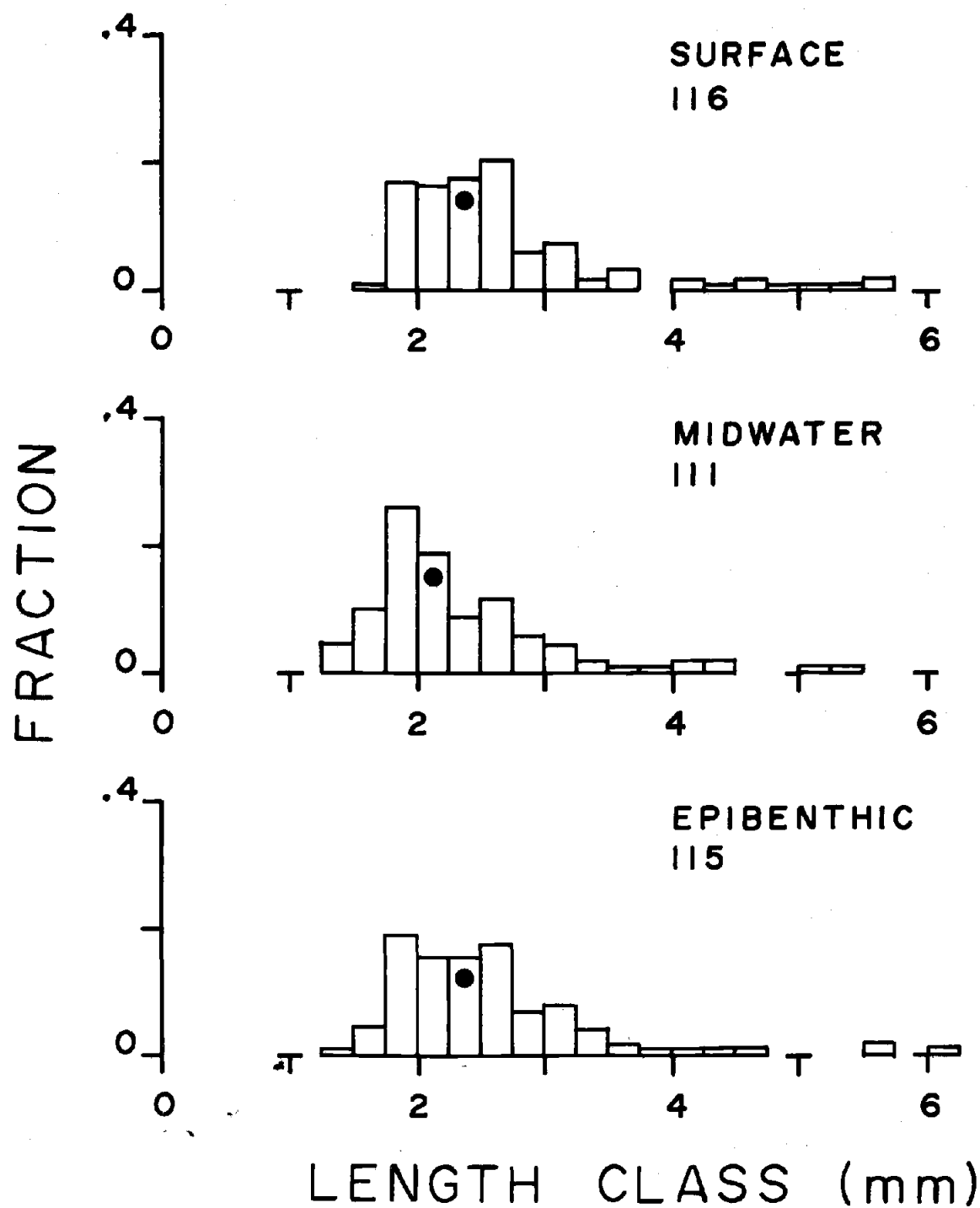
Figure 25. Length-frequency distributions of <u>Anisogammarus</u> <u>confervicolus</u> taken in darkness samples. Sample size is shown in the upper right of each histogram. Median length class is indicated by ● .

Table 7. Densities (no./m^2) of benthic fauna and substrate texture for grab samples used in life-history study of _Corophium salmonis_ from Youngs Bay, Oregon. Data for samples of April 17, May 7, May 30, June 18, July 9, October 12, and December 3, 1974, are taken from Higley and Holton (1975). Only _C. salmonis_ was counted in samples of January 2, January 29, February 24, and September 2, 1975. Densities for the August 6, 1974 sample could not be calculated. Substrate textures are based on volumetric determination of sediment size fractions. Location of stations is shown in Figure 4.

Station	PW5	PW5	PW5	PW5	PW2	PWT3	PWT3	PW5	PW5	PW5	PW5	PW5
Date	17 Apr	7 May	30 May	18 Jun	9 July	6 Aug	2 Sep	12 Oct	3 Dec	2 Jan	29 Jan	24 Feb
Year	1974	1974	1974	1974	1974	1974	1975	1974	1974	1975	1975	1975
Fraction of sample counted	.51	.52	.25	.25	1.00		.0313	1.00	.38	.0313	.0313	.0313
Substrate particle size fractions												
>0.991 mm	.7	.4		.4	1.4			.2	.8			
0.246 mm-0.991 mm	14.3	15.5		93.0	91.0			19.2	10.6			
0.063 mm-0.246 mm	71.7	65.9						76.0	72.6			
<0.063 mm	13.3	18.2		6.6	7.6			4.6	15.9			
Sample depth in grab sampler (cm)	6	3		10	6	11		11	12	11.5	11	8.5
Taxon												
Nemertinea									73			
Nematoda	3661	1722	1080	686	174			252	678			
Annelida												
Polychaeta				1290								
Ampharetidae	20											
Nereidae		906	348	840		51			449	1114		
Oligochaeta	2480	1702	2080	3226	194			112	775			
Mollusca												
Bivalva												
Macoma baltica					10							
Arthropoda												
Crustacea												
Amphipoda												
Corophium salmonis	36043	23017	45920	13790	17725		37091	30523	57845	31250	53154	63960
Eohaustorius estuarius	20				61			280	24			
Anisogammarus confervicolus	39	135		40	31				48			
Mysidacea												
Neomysis mercedis				40					24			

Table 8. Length, sex, maturity and clutch size of _Corophium salmonis_ from life-history study. Mean clutch size is based only on complete clutches. Location of stations is shown in Figure 4.

Date	Apr 17	May 7	May 30	Jun 18	Jul 9	Aug 6	Sep 2	Oct 12	Dec 3	Jan 2	Jan 29	Feb 24	All
Year	←		1974			//	1975	//		→	← 1975	→	
Station	PWS	PWS	PWS	PWS	PW2	PWT3	PWS	PWS	PWS	PWS	PWS	PWS	
No. animals examined	134	123	134	122	289	155	127	215	129	107	182	219	2011
No. smaller than 1.50 mm		12	25	21	127	71	58	16	3	2		2	
Fraction smaller than 1.50 mm		.10	.19	.17	.44	.46	.46	.07	.02	.02		.01	
No. male	63	51	46	42	84	30	30	98	66	37	90	106	743
Fraction male	.47	.46	.42	.42	.52	.36*	.43	.49	.52	.35**	.49	.49	.46**
No. female	71	60	63	59	78	54	39	101	60	68	92	111	856

Females

	Apr 17	May 7	May 30	Jun 18	Jul 9	Aug 6	Sep 2	Oct 12	Dec 3	Jan 2	Jan 29	Feb 24	All
Fraction without enlarging oostigites	.54	.28	.54	.44	.73	.32	.44	.59	.87	.93	.75	.85	
Mean length	2.309	2.449	1.971	2.115	1.901	2.096	1.860	2.317	2.226	2.093	2.216	2.181	
Std. err. mean	.057	.098	.078	.095	.044	.085	.055	.051	.069	.043	.043	.039	
Fraction with enlarging oostigites	.25	.33	.06	.39	.17	.07	.10	.18	.08	.06	.21	.11	
Mean length	3.097	2.975	3.500	3.201	2.913	3.188	3.250	3.042	3.525	3.438	3.546	3.354	
Std. err. mean	.083	.058	.072	.074	.062	.213	.161	.064	.170	.157	.119	.109	
Fraction with full-sized oostigites	.07	.18	.06	.09	.05	.04	.10	.03	.03	.02	.02	.02	
Mean length	3.975	3.661	3.500	4.225	3.563	4.000	3.375	3.792	4.500	4.125	4.625	4.875	
Std. err. mean	.285	.393	.323	.379	.239	.177	.102	.144	.177		.500		
Fraction with marginal setae	.14	.27	.33	.09	.05	.57	.36	.20	.02		.02	.03	
Mean length	4.400	4.281	4.589	4.525	4.750	4.706	4.214	4.213	5.125		4.750	4.708	
Std. err. mean	.126	.139	.100	.150	.161	.057	.122	.112			.625	.220	
Number females gravid	7	9	14	3	3	22	10	9			2	2	
Fraction	.10	.15	.22	.05	.04	.41	.26	.09			.02	.02	
Mean length	4.411	4.264	4.589	4.458	4.625	4.693	4.175	4.097			4.750	4.500	
Std. err. mean	.176	.139	.098	.220	.144	.066	.138	.147			.625	.125	
Number with intact clutches	2	1	3	1		15	4	4			1		31
Mean length	4.750	4.125	4.458	4.125		4.808	3.938	4.250			5.375		
Std. err. mean	.625		.167			.057	.188	.260					
Mean clutch size	14.0	11.0	14.0	12.0		17.5	13.8	13.0			12.0		15.3
Std. err. mean	8.0		2.3			1.7	1.5	1.4					.8

*0.05 > P > 0.01.

**P < 0.01.

benthic population during the summer of 1974 (Table 8, and Figure 26).
During this time they comprised nearly half of the population, but were
nearly absent in the spring and winter. These juveniles were just
recently released from brood pouches.

Overwintering females apparently produced the year's first
offspring by the beginning of May. The population in April was com-
posed of a large proportion of males and females near 2.50 mm in
length, and a moderate proportion between 3.00 mm and 4.75 mm in
length (Figure 27). About 10% of these females were gravid, but
new juveniles less than 1.50 mm in length were not present (Table 8
and Figure 26). However, during May, new offspring appeared and
comprised 20% of the population by the end of the month. The 2.50
mm size group in April apparently grew to near 3.00 mm by May 7
and perhaps near 4.00 mm by May 30 (Figure 27). In this last sam-
ple, females were more prevalent than males in the larger length
classes. The proportion of reproductive females increased to over
30% during this time (Figure 26). It is probable, therefore, that some
females were mature yet reproductively inactive during the winter
(those 3.00 mm to 4.75 mm in April) and produced broods by the begin-
ning of May. In addition, immature females which overwintered appar-
ently grew to maturity by the end of May and began producing broods.

There was an apparent decrease in the proportion of reproduc-
tive females and an accompanying sharp rise in the proportion of new
offspring through June and July (Figure 26). The reduction in the
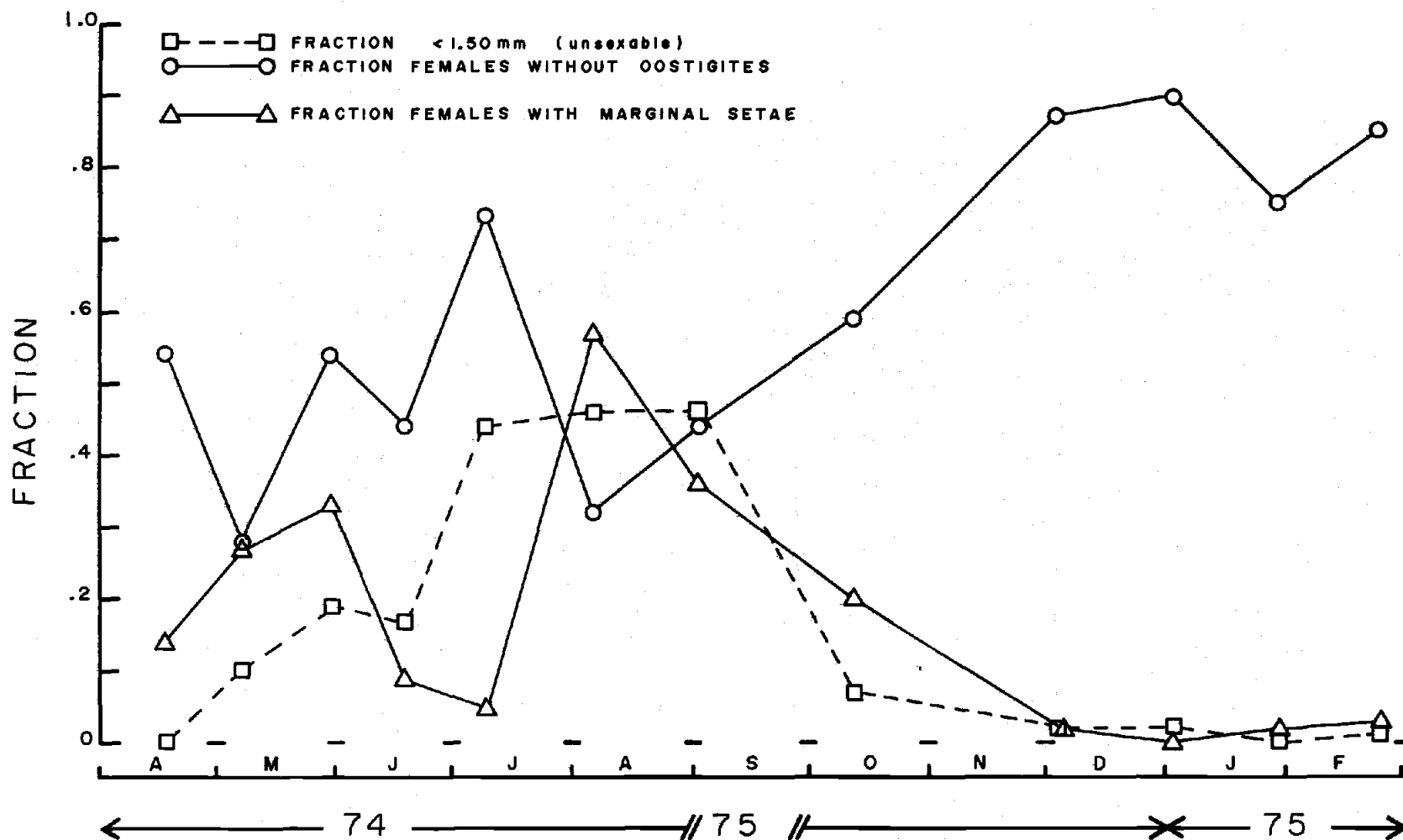
Figure 26. Seasonal changes in maturity of female Corophium salmonis and fraction of juveniles less than 1.50 mm in length. Data are based on benthic samples taken between April 1974 and September 1975 from Youngs Bay, Oregon. Sample stations are listed in Table 7 and shown in Figure 4.

Figure 27. Length-frequency distributions of infaunal <u>Corophium</u>
<u>salmonis</u> from Youngs Bay, Oregon. Data are based
on benthic samples taken between April 1974 and
September 1975. Distributions for all individuals, and
according to sex (for only those greater than 1.50 mm
in length), are shown. The size of each length class for
males and females is expressed as a fraction of all
sexable individuals, not as a fraction of the particular
sex. These histograms thus show the relative propor-
tion of each sex and the relative proportion of length
classes with each sex. Sample size is shown in the
upper right of each histogram. Median class is indi-
cated by   . Sample stations are listed in Table 7 and
shown in Figure 4.
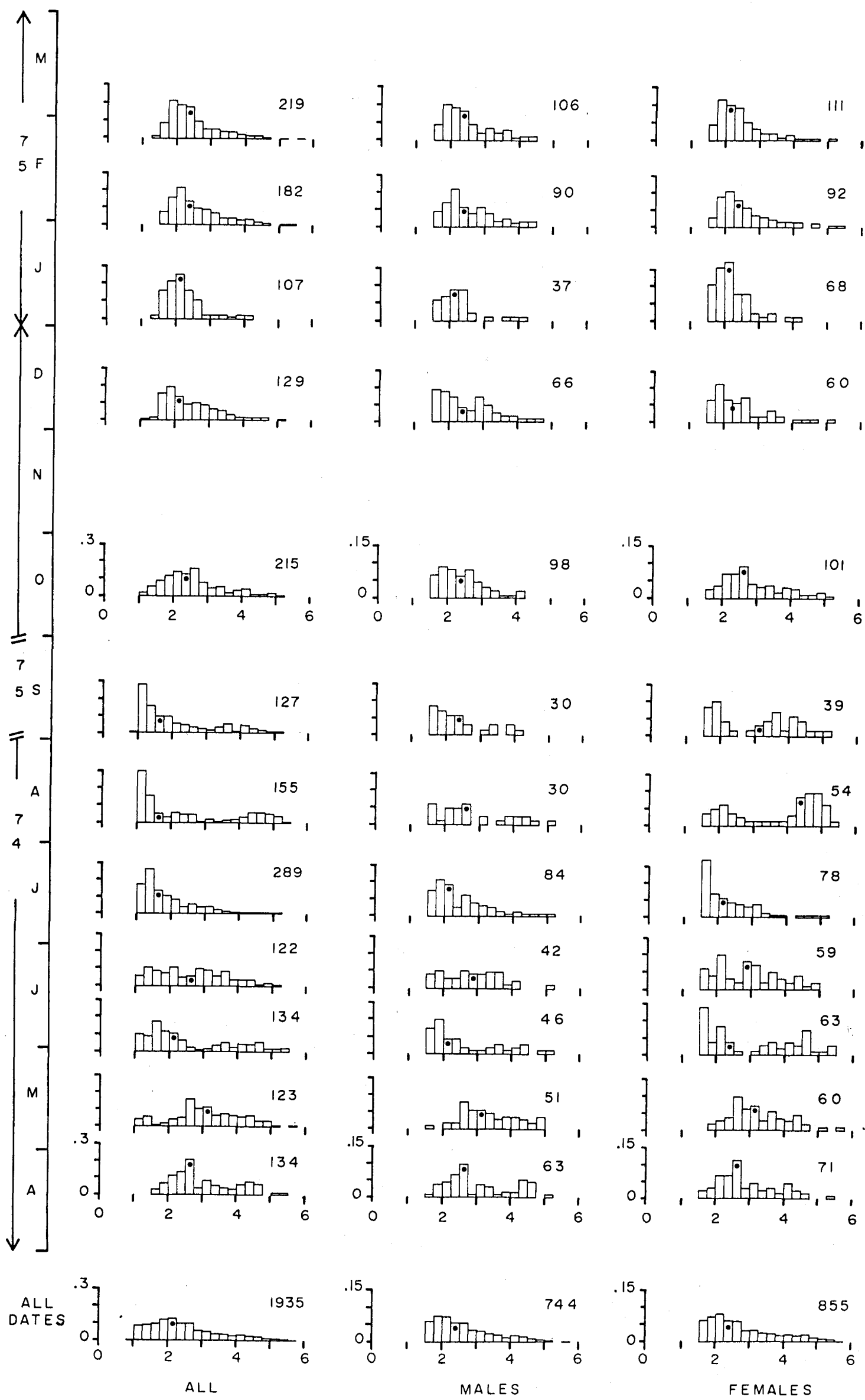
LENGTH CLASS (mm)

Figure 27

proportion of the older females was probably the result of mortality of "spent" overwintered females and dilution caused by the many new offspring. The peak of older juvenile females between 1.50 and 3.00 mm in July were probably produced in the spring.

Reproductive females represented only about 10% of the population in June and July, but increased to 60% in August, then decreased to 40% in September (Figure 26). Most of the total population was made up of new juveniles, but a distinct proportion of these large females can be seen in Figure 27. These females were probably produced in spring and matured rapidly during the warm summer months. Production of offspring declined rapidly from September to October, along with the proportion of reproductive females (Figure 26). The population from October through February was composed of immature older juveniles between 1.50 mm and 2.50 mm, probably produced in the fall broods, and a small proportion of larger adults, probably produced in summer (Figure 27).

Gravid females were captured almost throughout the year. Only the December 3 and January 2 samples contained none (Table 8). Of the 81 gravid females observed, only 31 were judged to have intact clutches. Mean clutch sizes for each sample fluctuated near 15 eggs per female, with no apparent seasonal trend for these limited data. Thus, the overall mean clutch size (n=31) of 15.3 eggs is the best estimate of average fecundity for female C. salmonis in the

mouth region of Youngs Bay.

Length distribution data of all female C. salmonis shown in Figure 27 are presented in Figure 28 broken up into the four maturity categories based on oostigite morphology. Most females in breeding condition were between 4.00 mm and 4.75 mm in length; however, some fell into the 3.25 mm to 3.50 mm length class (Figure 28a). Females with full-length oostigites (Figure 28b) may upon next molting acquire marginal setae and lay eggs, and thus are nearly mature sexually. Most of these were between 3.50 mm and 4.25 mm in length. As shown earlier, individuals between 1.50 mm and 3.00 mm were nocturnally active. These are immature older juveniles belonging to the group of females seen in Figure 28d; those without enlarging oostigites.

The life-history of C. salmonis in Youngs Bay during 1974 and 1975 was similar to the life-histories reported for C. volutator in coastal Northeast Atlantic waters. Watkin (1941b) noted that C. volutator in Dovey estuary, North Wales overwintered in two groups; one group matured the previous fall and produced some of the year's last broods, and another group hatched in the fall. Breeding commenced in February, and the year's first offspring matured by July. Muus (1967) noted that C. volutator in Niva Bay, Denmark did not commence breeding until May or June. Females breeding in late
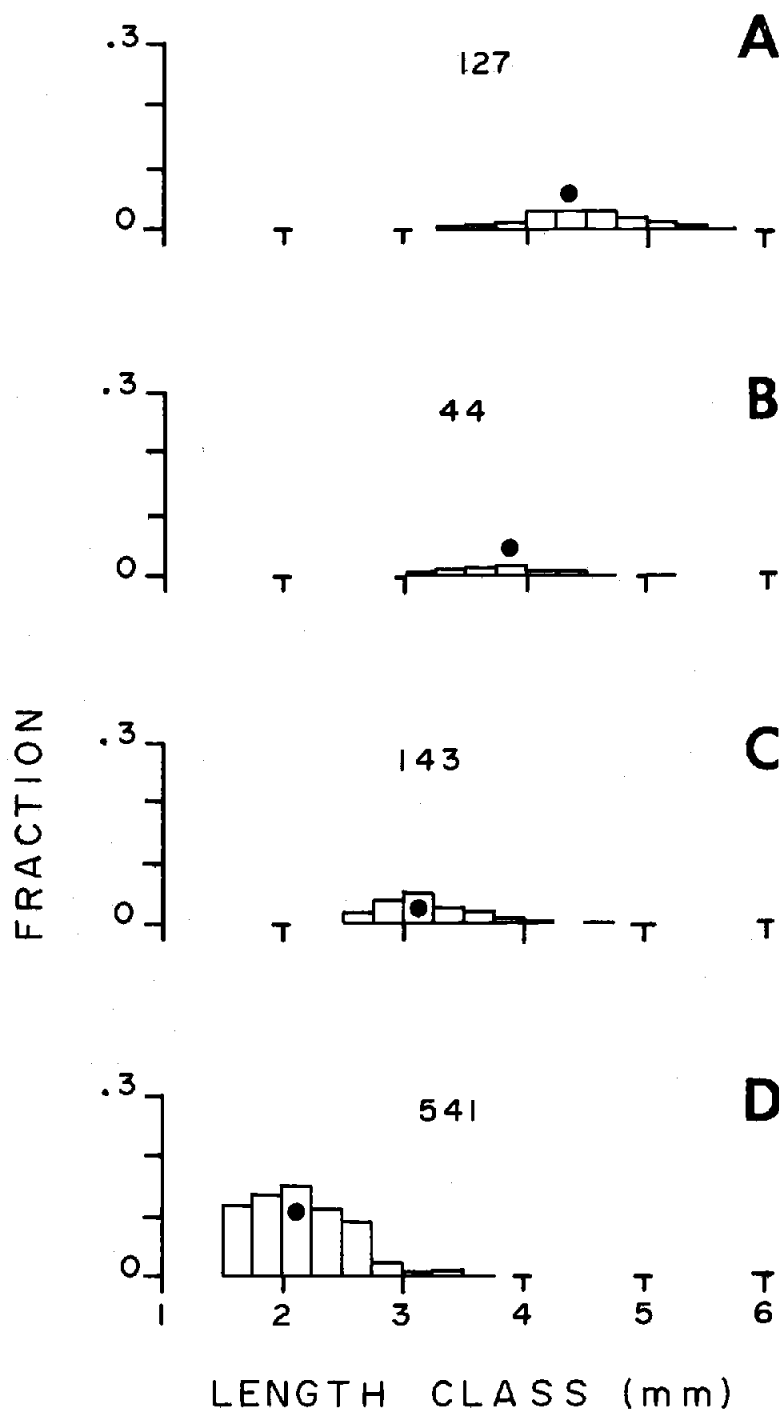
Figure 28. Length-frequency distributions according to maturity of
female Corophium salmonis from Youngs Bay, Oregon.
Based on pooled data from benthic samples taken between
April 1974 and September 1975. A. Females with
oostigites bearing marginal setae. B. Females with
full-sized oostigites. C. Females with enlarging
oostigites. D. Females without enlarging oostigites.
Sample size is shown at the top of each histogram.
Median class is indicated by ● .

spring and early summer apparently produced three broods, while

females later in the season only produced one or two broods.

DISCUSSION

Several benthic peracarids and a decapod swam in Youngs Bay during the sampling period in September, 1975. The objectives of this study included definition of the patterns of activity and an assessment of their possible functions. This section first addresses the patterns of the rhythms. Included is a discussion of the period of activity, lateral movement towards the intertidal and shoreline regions, the pattern of melanophore states in _Corophium salmonis_, and the avoidance of predation as the probable selective advantage of confining activity to darkness. Secondly, possible functions of the activity of juveniles in the upper water column, based primarily on the more extensive data on _C. salmonis_, is discussed. Conclusions here should also apply to the other species with active juveniles (particularly _Eohaustorius estuarius_ and _Neomysis mercedis_). Evidence is presented to suggest that, among the alternatives, dispersal is the most likely function. Finally, the results of some studies on crustacean neurohormonal control of several rhythmic behavioral and physiological responses are discussed, and used as the basis for a model of the regulation of these responses by swimming benthic crustaceans.

Activities, Melanophores, and Fish Predation

Swimming Activity Rhythms

Nocturnal rhythmicity of swimming activity is common in subtidal benthic communities, based on the literature reviewed. Benthic crustaceans found in the mouth region of Youngs Bay also strongly exhibited this rhythm. Water circulation in this region is dominated by large tidal oscillations, which may also influence swimming activity. However, the present data do not indicate a tidal period of activity. Extensive study would be needed to allow strong conclusions on this point.

Distinctly more C. salmonis, A. confervicolus, N. mercedis, E. estuarius, and C. franciscorum were captured during the evening ebb flow of the first epibenthic series than during the high slack of the second series. This can be explained as a physical displacement due to tidally-driven water currents (a form of "tidal influence" on activity), rather than volitional movements. It seems probable that animals were swept out of high density areas above the tow zone by tidal currents.

The relative proportion of active and non-active animals can be estimated for the two infaunal amphipod populations. For this purpose, swimming animals are assumed to come from the sediment beneath the tow zone. Average infaunal densities of C. salmonis

and $\underline{E}$. $\underline{estuarius}$ in this region were about 10,000 per m^2 and 500

per m^2, respectively, and nearly 70% of these were active types

(older juveniles). Nighttime densities of swimming $\underline{C}$. $\underline{salmonis}$

and $\underline{E}$. $\underline{estuarius}$ approached 10 per m^3 and 1 per m^3, respectively,

in a water column about 6 m deep. These represent about 1% of the

older juveniles. A similar estimate can not be made for the other

species because the densities of non-active individuals have not been

estimated.

The infaunal amphipods $\underline{C}$. $\underline{salmonis}$ and $\underline{E}$. $\underline{estuarius}$ in

Youngs Bay are distributed broadly over intertidal and subtidal de-

posits. Intertidal residents are obviously restricted to high tides

for swimming activities. Observations by Morgan (1965) and Vader

(1964) on intertidal $\underline{C}$. $\underline{volutator}$ revealed a tidal activity where

animals emerge in flooding water, migrate shoreward near the wa-

ter's edge, and re-enter burrows at late ebb tide. Likewise, several

intertidal haustoriid species studied by Watkin (1939, 1941a) and

Fincham (1970a) exhibited a nocturnal-high tide activity rhythm.

Thus, the intertidal amphipods in Youngs Bay may also express an

activity rhythm with tidal periodicity. If so, it would be interesting

to assess possible exchange of subtidal and intertidal amphipods,

and the adjustment of previously-acquired rhythmicity to new habitat

conditions.

In Youngs Bay, $\underline{C}$. $\underline{spinicorne}$ is primarily distributed along

the shoreline. Its presence in the subtidal tow zone suggests that movement from the shoreline to the subtidal, across the intertidal region, has occurred. Although this species was most abundant at night in the tow zone, it was also consistently present in the surface region during daylight. Perhaps a few individuals active at night were unable to return to the shoreline or find other suitable substrates and thus remained swimming at the surface in daylight; such animals may eventually be flushed out of the bay.

Similarly, many $\underline{A}$. $\underline{confervicolus}$ congregate along the shoreline. At high tide, individuals swim among vegetation and at low tide remain among plant rhizomes or beneath rocks to avoid desiccation. However, this species is also commonly found in the subtidal epibenthic zone, leaving the question open as to the exchange between shoreline and subtidal portions of the population.

The absence of the non-burrowing $\underline{A}$. $\underline{confervicolus}$ and $\underline{N}$. $\underline{mercedis}$ from the tow zone during daylight is harder to explain than that of infaunal species, which can leave the water column by re-entering the substrate. It is possible that these non-burrowing species moved laterally into the tow zone at night and away from it at day. Two patterns of movement may occur. First, individuals may move either up or downstream. Such a migration should, however, be influenced by tidal flow, and their presence and absence in the tow zone does not correlate with tidal cycle. Secondly, and this

seems more likely, individuals may move shoreward during the day and bayward at night.

Daytime movements to shore may, perhaps, be supported by the shoaling behavior of some mysids (Steven, 1961; Clutter, 1967, 1969; Zelickman, 1974). In daylight, some coastal mysids aggregate in dense shoals, using visual cues to assume a closely-packed parallel alignment. The use of vision for orientation is so strong that the integrity of the shoal is rapidly disrupted by the shadow of a pencil passed quickly over the shoal (Zelickman, 1974). At night, as a result, the aggregations break up, and the mysids disperse through-out the water. Similarly, Neomysis mercedis may aggregate near the periphery of Youngs Bay during daylight and disperse into the region of the tow zone at night.

Corophium salmonis Color Changes and Flatfish Predation

The distribution of pigment in the melanophores of C. salmonis was strongly correlated with nocturnal swimming activity of this species. Presumably body coloration is related in some manner to the activity. Observations on the chromatophores of other crus-taceans suggest possible mechanisms of mealnophore control and its coordination with the swimming activity.

The chromatophores of malacostracan crustaceans are clusters of cells with radiating, fixed processes extending out in the

integument (Kleinholz, 1961; Fingerman, 1963; Barnes, 1974). When pigment granules within the cytoplasm diffuse out in the processes, they color an area of the body. When they are concentrated in a dense spot, the area is mostly free of color. Chromatophores may contain one or several different colors of pigment granules, and each may be controlled independently. Various hormones control the diffusion of pigments, each one usually causing the diffusion or concentration of a single pigment type. Many species have melano-phores, which are chromatophores containing only a dark brown or black pigment.

The only studies of peracarid chromatophores have been per-formed on isopods and mysids. The isopods <u>Ligia</u> and <u>Idothea</u> have melanophores (Fingerman, 1963), while mysids generally have chro-matophores containing a dark brown pigment and a reflecting sub-stance, usually white or yellow (Tattersall and Tattersall, 1951). Chromatophore response in both groups, therefore, only causes a simple darkening or blanching of body coloration.

Two systems of chromatophore response operate concurrently in these peracarids. First, under diel light/dark illumination, animals are dark in daylight and blanched in darkness. This re-sponse is usually a circadian endogenous rhythm. Secondly, body color adjusts to match the background shade. Animals darken when placed on a black background and blanch when placed on a white

background. The background response generally dominates the diel

response, and animals on a white background remain blanched during

daylight.

Similar information on gammaridean amphipod melanophores

is not available. However, an interaction of background and diel light

intensity responses may be sufficient to explain the various states

observed in C. salmonis. The presence of only diffuse amphipods in

the sediment both day and night may be explained as a background

response. The presence of only punctate amphipods in the upper water

column at night may be explained as a light intensity response. Too

few animals were captured in the upper water column in daylight to

confirm the presence of diffuse animals predicted by the light intensity

response. The epibenthic region contained both diffuse and punctate

individuals, which is difficult to explain by either response.

The correlation of swimming activity and melanophore state

suggests that another control system may operate in C. salmonis.

Melanophore state may be hormonally coupled with movement into

the upper water column. Under this system, animals in burrows have

diffuse pigment granules, but upon their emergence into the epi-

benthic region at the start of their swimming activity, the granules

concentrate. Thus, the mixture of punctate and diffuse animals found

in the epibenthic region represents amphipods preparing to swim up

or to re-enter the substrate.

Several adaptive functions of melanophore responses have been

suggested (Fingerman, 1963). The most obvious is a camouflage

effect used to reduce predation. In clear water, translucent animals

have low visibility. The advantage that this would provide for

nocturnally-active C. salmonis may not accrue in darkness, but dur-

ing the low-light transition periods of dusk and dawn, as will be

discussed in the next section on fish predation. Thermoregulation

and protection from harmful UV radiation have been suggested for

the semi-terrestrial isopods. These animals are generally dark

during the day. Finally, mating displays have been suggested, par-

ticularly for the polychromatic decapods.

Benthic crustaceans perform a variety of biological activities

while swimming; however, most of this activity is restricted to

darkness. The most plausible explanation for this timing is the

avoidance of predation by sight-feeding fish (see, for example,

Bossanyi, 1957; Preece, 1971; Jones et al., 1973). The starry

flounder (Platichthys stellatus), a sight-feeding flatfish, is the

most abundant predator on C. salmonis in Youngs Bay (Higley and

Holton, 1975). It certainly is not able to capture as many prey in

darkness as in daylight, but large numbers of C. salmonis are still

taken. Some fish guts contain only large adult males which charac-

teristically have very long second antennae (personal observation).

Corophium forage with these antennae while in burrows, and the

flounders may move about grabbing the largest antennae. Other

types of C. salmonis are also captured, and observations discussed below on the feeding behavior of other flatfish suggest that nocturnally active prey may still be captured.

Several species of flatfish have been classified as sight feeders based on laboratory observations and on decreasing gut fullness during the night. Interestingly, these fish were more active in the water at night than during the day. These fish were the plaice Pleuronectes platessa (Jones, 1952; Hempel, 1964; Edwards and Steele, 1968), the flounder Platichthys flesus (Bregnballe, 1961; Muus, 1967), and the summer flounder Paralichthys dentatus (Olla et al., 1972). During the day, these fish either remained buried just under the substrate or moved slowly over the surface in search of prey. At night, however, they were active either over the substrate or high in the water column.

Fish may capture much of their food during the dim light conditions near dusk and dawn when nocturnally-active prey are leaving or returning to the substrate (Bregnballe, 1961; Hempel, 1964; Muus, 1967). At these times, the punctate melanophores of C. salmonis may be adaptive as protective coloration. In darkness, body coloration can not be detected by the fish except perhaps under bright moonlight.

Feeding in darkness, though less efficient, may still occur. Plaice and flounder were able to detect a jet of clam or mussel juice

pumped into an aquarium through the substrate (de Groot, 1971).

Thus, the fish may be able to detect prey by either chemical or

tactile sense. The swimming activity high in the water at night

may be a searching behavior for active prey utilizing non-visual

cues.

Possible Functions of Activities

A small, but distinct, group of adult C. salmonis longer than

3.50 mm were active in the epibenthic region at night. These were

mostly gravid females (Figure 18, and Table 5) with diffuse melano-

phores (Figure 19). This suggests an activity related to the

suite of reproductive processes associated with nocturnal activity

of peracarids. C. volutator releases offspring inside the maternal

burrow (Watkin, 1941b; Meadows and Reid, 1966). Active gravid

female C. salmonis may be dispersing to new burrows before releas-

ing offspring. If offspring are cast into the water by this species

in the epibenthic stratum at night, then molting, egg laying, and

copulation may also occur immediately after.

Many gravid female C. spinicorne with diffuse melanophores

were also captured, but in the surface stratum. Probably because

of differences in distribution and habitat preference, however,

the apparent reproductive behavior may have been performed at

a different location in the water column.

Juvenile C. salmonis in the upper water column at night was the dominant activity expressed by this species. Reproduction and feeding are not plausible explanations for this activity. First, the juveniles captured were probably not large enough to reach maturity upon their next molt and copulate. Active animals were generally between 1.50 mm and 3.00 mm in length (Figure 17; median = 2.125 mm). Based on the 1974-1975 life-history data, the smallest possible mature females ranged in size from about 3.00 mm to 5.00 mm (Figure 28B, median = 3.875 mm). Apparently the active females would have to about double in size to reach a length comparable to the smallest mature females, which is unlikely to occur in a single molt. Secondly, these juveniles were not swimming to feed because they are detritovors which deposit- and/or filter-feed while in or on sediment.

Molting may have been the sole purpose of the older juveniles' activity, but this seems unlikely. If only older juveniles were molting during the two days of sampling the upper water column, then there must have been strong synchronization of intermolt periods within developmental stages and differences between. Presumably, then, younger juveniles and adults must have molted on other nights.

Dispersal may confer a selective advantage on some individuals inhabiting heterogeneous environments. Two environmental properties leading to dispersal are habitat patchiness and local instability.

First, most species occupy recognizable patches of habitat that are dispersed in various patterns throughout their entire range, and individuals are more or less confined to local populations. Environmental conditions may differ between patches; some are usually more favorable to survival or can support higher densities than others. Local adaptations may arise. Secondly, conditions in a local habitat change over time by physical and biological processes. Some habitats may deteriorate in quality, occasionally leading to local extinctions. On the other hand, new habitat may be created which can be colonized and support population growth.

Lidicker (1962) outlined three possible selective advantages for dispersing individuals. First, an individual moving among several local populations may realize a greater chance of mating, or of leaving more offspring over a wider area, and thus increase the likelihood that some of its offspring will prosper. Secondly, mating with individuals from different demes may increase offspring fitness from heterozygosity and favorable recombinations. Finally, individuals may avoid local population crashes by dispersing from crowded or deteriorating habitats. However, all of these advantages must be measured against the probable increase in mortality.

Dispersal is often biased with respect to age and sex. Wilson (1975) noted that organisms tend to emigrate at the time of their maximum reproductive value. For a female, the maximum

reproductive value is the relative number of offspring remaining to

be born to a female of a given age. This value is typically highest

for older immature and early reproductive females. Younger ones

are less likely to survive and older ones will produce fewer offspring.

Lidicker (1962) suggested that under favorable, but crowded, condi-

tions, the young should disperse first because they are least able to

compete for food and space.

Juvenile C. salmonis may disperse at night by swimming in

the upper water column at night. In the Columbia River estuary, this

species is restricted to the muddy deposits in bays, along shores, and

in the lees of islands and shoals. These habitats are potentially un-

stable. Deposits are frequently modified by scour and burial, while

new habitats are created by sedimentation. Storm discharge can

rapidly destroy habitat. Overcrowding may cause deterioration by

reducing space for tube building, reducing available food, or causing

a buildup of harmful metabolites. Older juveniles, perhaps with the

greatest reproductive value or most responsive to environmental con-

ditions, may leave overcrowded areas and colonize new areas within

the estuary.

The behavior of two other amphipod species supports the idea

that swimming involves dispersal by older juvenile C. salmonis.

C. volutator offspring are liberated while in the maternal burrow

(Watkin, 1941b; Meadows and Reid, 1966). Thamdrup (1935; cited in

Green, 1968) described small side burrows which at first were con-
nected to the maternal burrow. But as the young grew, they became
progressively more independent and moved away. Watkin (1941b)
observed that through the early breeding season small juveniles
tended to move away from dense areas of adults to new areas of
their own. Juveniles and adults do co-occur at lower densities,
however. Mills (1967, 1969) observed that suspension feeding by
the tube-dwelling Ampelisca abdita in stable intertidal sand flats
reduces the mean particle size, making the deposit susceptible to
washout. During the breeding season, all developmental stages
swim at night during high tide. Newly released juveniles soon
appear in uncolonized stable sand deposits.

It seems plausible, therefore, to suspect that C. salmonis,
like other amphipods, may migrate away from crowded areas. If
so, swimming activity may be a response to habitat conditions, and
a model depicting a possible control mechanism is shown in Figure 29.
The amphipods receive stimuli related to crowding conditions, such
as hunger, increased intraspecific encounters, and detection of
harmful metabolic buildup. All incoming relevant stimuli are inte-
grated, perhaps with some more important factors given more
emphasis. Dispersal is initiated when the collective stimulus ex-
ceeds a critical threshold value. Once initiated, activity will be
elicited only at night. This model suggests, therefore, that during
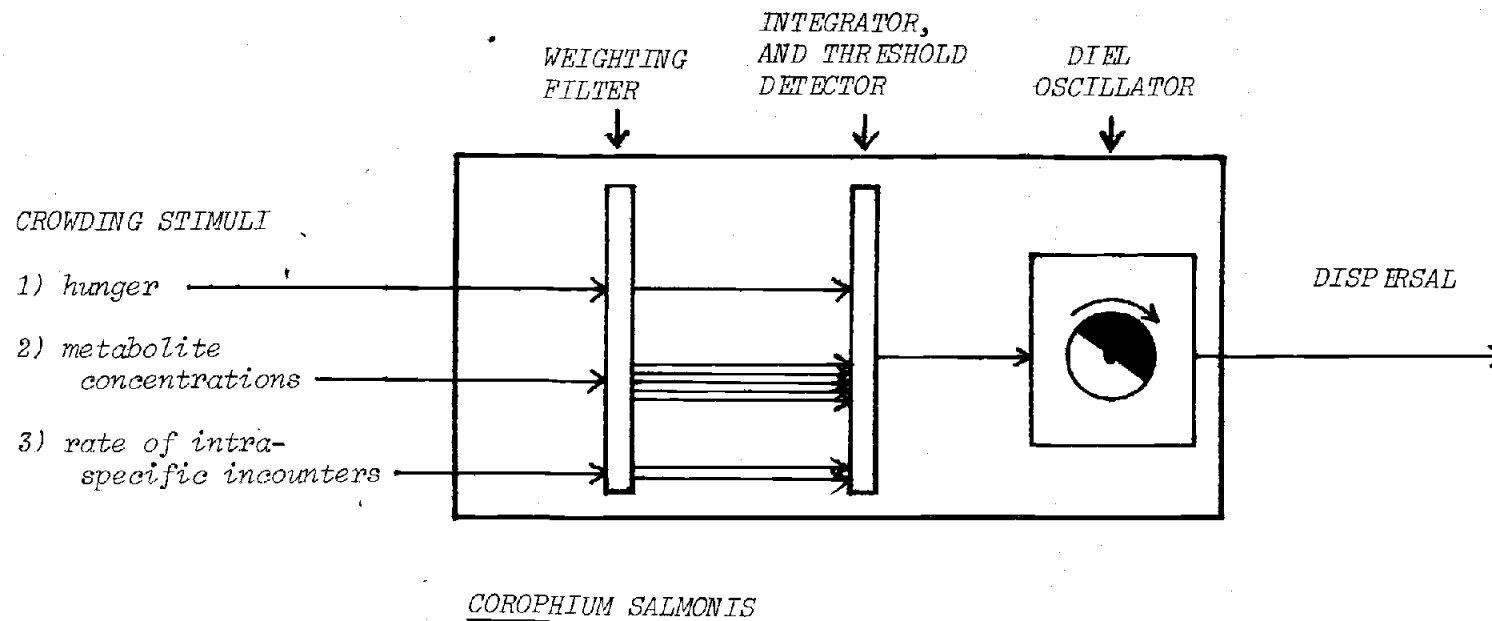
Figure 29. Threshold response model of dispersal by Corophium salmonis. Dispersal is assumed to be a response to crowding conditions in the habitat. See text for a discussion of the model.

the sampling period in September, 1975, only about 1% of the resident

infaunal juveniles were stimulated to swim by crowded conditions.

These juveniles were usually the most abundant developmental

stage present in the Youngs Bay population, and were present through-

out the entire 17 month sampling period in 1974 and 1975. Thus,

swimming activity by this stage appears possible at any time of the

year. If activity is a response to crowding, then most activity should

probably occur during summer and early fall, just after peak offspring

production.

Near-surface current speeds in the mouth region of Youngs Bay

during sampling varied between 1/2 to 1 m/s. At these speeds,

C. salmonis could be transported from 1.8 to 3.6 kilometers each

hour, and from 7.2 to 14.4 kilometers in one direction during a 4

hour tidal run. Long distances can thus be traversed throughout the

brackish water region of the estuary in a few hours. The exact dis-

tances and directions of transport can be quite variable depending on

individual activity. However, if the broad assumption of continual

activity throughout the water column at night is true, then asynchrony

with the tidal flow reversals suggests net flushing downstream in the

estuary with net river discharge.

The effectiveness of using the nocturnal activity to disperse

throughout the estuary depends on the timing and frequency of the

activity in relation to the water circulation pattern. Too many details

of the activity are unknown to assess the effectiveness of dispersal.
Activity in the channels outside Youngs Bay where net upstream flow
can occur needs to be studied. The consequence of activity is affected
by an animal's preference for tide stage and its location in the water
column.

Another important unknown concerning the activity is the
behavior of individual amphipods. The present work determined
only that the species C. salmonis occurred in the upper water column
at night. Nothing is directly known about the duration of individual
activity in the water at night, how frequent an individual is active on
different nights, and the variability in individual expression of
rhythmicity. These questions are best answered by controlled labora-
tory observations.

Neurohormonal Integration

Swimming activity by benthic peracarid and decapod crustaceans,
as has been shown by this study and in the literature, is a complex,
and sometime bewildering, behavior. Several diverse functions may
be facilitated, such as feeding, molting, various reproductive proc-
esses, and dispersal. Some species apparently swim only to perform
one function, while others, at different times or on the same night,
fulfill most of the functions. Depending primarily on habitat, activi-
ties may be diel and/or tidal in period. Interestingly, all of these

functions are, in at least some species, expressed as endogenous rhythms, and, along with other responses, are under neurohormonal control: swimming activity (Naylor and Williams, 1968; Naylor et al., 1973), molting (Passano, 1960; Charniaux-Cotton and Kleinholz, 1964), chromatophores (Fingerman, 1963), retinal eye pigment migration (Kleinholz, 1961; Tombes, 1970), metabolic level (Charniaux-Cotton and Kleinholz, 1964; Tombes, 1970), and reproductive activity (Charniaux-Cotton, 1960; Charniaux-Cotton and Kleinholz, 1964).

These responses are-either controlled by the rhythmic release of a single hormone or the rhythmic interaction of two or more antagonistic hormones. Neurosecretory cells are located throughout the central nervous system. These neurons, which possess some cytological characteristics of gland cells, receive nervous stimulation and release hormones from the terminal ends of the axons to structures of the circulatory system (Highnam and Hill, 1969; Tombes, 1970). Arechiga and Naylor (1976) reason that endogenous control of rhythmic responses operates through at least two links in a stimulus-response chain. First, there must be an as yet unknown couple between the entraining stimulus and the internal oscillator. For example, stimulation of the retinal or extraretinal photoreceptors may synchronize a circadian clock by direct nervous or indirect neurohormonal control. Secondly, there is some form of hormonal couple between the internal oscillator and the effector.

These observations on neurohormonal regulation of endogenous rhythmic responses suggest a plausible framework on which to structure the various observations on the complex behavior of benthic crustacean swimming activity. Figure 30 presents a neurohormonal model depicting the possible interaction and coordination of the factors regulating the suite of responses associated with swimming. Various stimuli carrying information about the timing of environmental cycles to which overt responses are adaptively synchronized are received by central nervous system (CNS) receptors. These stimuli may first be processed. Irrelevant information may be filtered out and relevant information weighted and combined. Entraining information is then conducted either by neurons or by hormones secreted by neurosecretory cells to the internal oscillator complex. In addition, stimuli from various other physical and biological factors in the environment are received by CNS receptors. This information may be integrated with the entraining stimuli to aid in synchronization of the oscillators, may affect the oscillators directly, or may aid in determining which appropriate responses are needed. The internal oscillator complex thus receives two types of information, entraining stimuli and the decisions to elicit various appropriate responses. The oscillator complex then effects the response at the appropriate time directly or indirectly by hormonal release.

This model, then suggests how various responses can be

Figure 30. Neurohormonal model of the coordination and regulation of several rhythmic overt responses in crustaceans. See text for a discussion of this model. a. The exact nature of the oscillator complex is not known, and may vary among species. There may be several independent oscillators set at different frequencies, or a single oscillator coupled in various ways to the effecters. b. The threshold response model described in Figure 29 may operate through this link in the model, with the integrator and threshold detector associated with the CNS integrator.

Figure 30.

CNS
RECEPTORS AND
COORDINATOR

INTERNAL   a.
OSCILLATOR

EFFECTORS

NEURONS
AND/OR
HORMONES

NEURONS
AND/OR
HORMONES

ENTRAINING STIMULI

OVERT
RESPONSE

1) diel light/dark
   cycle

chromatophores

2) daylight

swimming activity

3) hydrostatic pressure

molting

4) turbulence

egg development

5) others

others

ADDITIONAL ENVIRONMENTAL   b.
AND BIOLOGICAL FACTORS
AFFECTING OVERT RESPONSES
e.g.   temperature
       salinity
       stress
       social interactions
       food intake
       others

coordinated into a complex overt behavior. Contracted pigment granules in melanophores and nocturnal activity in the upper water column were closely associated in Youngs Bay C. salmonis juveniles. Both responses are probably hormonally mediated, and it is plausible to expect that they are coupled in a manner like that depicted in the neurohormonal model. In addition, the threshold response model (Figure 29), suggesting that environmental conditions indicative of crowding elicit an activity response, should operate in the neuro-hormonal model (Figure 30) through the pathways labelled "b." Crowding stimuli are received by CNS receptors, integrated, and passed to the threshold detector associated with the CNS coordinator.

Tattersall and Tattersall (1951) and Clutter (1969) reported that gravid female mysids release offspring, molt, lay eggs, and copulate during a brief swimming excursion into the water column at night. During the breeding season, the females of some species will repeat this suite of activities every ten days. The neurohormonal model suggests how all of the necessary processes can be synchro-nized. The intermolt period must be adjusted to the egg yolk deposi-tion cycle so that ripe eggs may be released immediately after molting. Once molting and egg release are imminent, then activity is elicited by the circadian oscillator.

Many details of the hormonal systems regulating individual overt responses and the nature of coordination between responses are

not known. Without this information, the specific links in the neuro-

hormonal model can not be described. However, the model is a

good conceptualization, based on current knowledge, of the interac-

tion of endogenous rhythmicity and neurohormonal effectors, and

should be a useful guide in the formulation of new studies of benthic

crustacean swimming activities.

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APPENDICES

APPENDIX A

Appendix A presents all samples from which individuals of various species were removed for examination of such characteristics as length, sex, melanophore state, and maturity.

Table 9 is a list of all water column samples from which some Corophium salmonis, C. spinicorne, Anisogammarus confervicolus, Neomysis mercedis, and Eohaustorius estuarius were removed for examination. The table is presented in three sections, one section for each sampling stratum. Light condition is represented by a L for daylight, T for transition (dusk and dawn), and D for darkness. The number captured in each sample and the number examined is shown. Only Corophium whose total length and sex could be determined were examined. A. confervicolus and N. mercedis were taken from only a few darkness samples. Those other samples not considered are shown by -- under the "caught" column. E. estuarius were taken from all darkness and transition samples shown by the brackets, and those other samples not considered are shown by -- under the "caught" column.

Table 10 is a list of all benthic samples from which some infaunal C. salmonis and E. estuarius were removed for examination. Replicate set #2 was taken in daylight, while sets #5 and #6 were taken in darkness.

Table 9. Water column samples selected for examination.

Surface samples	Light condition	Corophium salmonis		Corophium spinicorne		Anisogammarus confervicolus		Neomysis mercedis		Eohaustorius estuarius	
		Caught	Examined	Caught	Examined	Caught	Examined	Caught	Examined	Caught	Examined
1	L	5	5	5	5	--		--		--	
2	L	2	2	6	6	--		--		--	
3	L	2	2	7	7	--		--		--	
4	L			2	2	--		--		--	
5	T			17	17	--		--		--	
6	D	2142		40		48	40	22	11		
7	D	1088	86	32	3	54	47	--			
8	D	892		20		--		--			
9	D	982	125	20	2	19	19	222	110	127	96
10	D	593		22		--		--			
11	D	120	46	4	3	--		--			
12	D	30	29	12	12	--		--			
13	T			18	18	--		--		--	
14	L	1		15	15	--		--		--	
15	L	3		5	5	--		--		--	
16	L			3	3	--		--		--	
17	L	3	2	7	7	--		--		--	
18	L	1	1	3	3	--		--		--	
19	L			1	1	--		--		--	

Table 9. (Continued).

Midwater samples	Light condition	Corophium salmonis		Corophium spinicorne		Anisogammarus confervicolus		Neomysis mercedis		Eohaustorius estuarius	
		Caught	Examined	Caught	Examined	Caught	Examined	Caught	Examined	Caught	Examined
1	L	5	5	5	5	--		--		--	
2	L			6	6	--		--		--	
3	L			7	7	--		--		--	
4	L			2	2	--		--		--	
5	D	4	4	17	17	--		--			
6	D	306		40		62	20	11	11		
7	D	304	75	32	3	61	61	32	29		
8	D	375		20		--		79	56	25	25
9	D	652	82	20	2	58	29	60	28		
10	D	252		22		--		--			
11	D	78	47	4	3	--		--			
12	T	52	51	12	12	--		--			
13	L	2	1	18	18	--		--		--	
14	L	1	1	15	15	--		--		--	
15	L			5	5	--		--		--	
16	L			3	3	--		--		--	
17	L	1	1	7	7	--		--		--	
18	L			3	3	--		--		--	
19	L	1	1	1	1	--		--		--	

Table 9. (Continued).

Epibenthic samples	Light condition	Corophium salmonis		Corophium spinicorne		Anisogammarus confervicolus		Neomysis mercedis		Eohaustorius estuarius	
		Caught	Examined	Caught	Examined	Caught	Examined	Caught	Examined	Caught	Examined
1	L	16	13			--		--		--	
3	L					--		--		--	
4	L					--		--		--	
5	L					--		--		--	
6	L	2	2			--		--		--	
7	L	1	1			--		--		--	
8	L	6	6	1	1	--		--		--	
9	L					--		--		--	
10	L					--		--		--	
11	L	3	3			--		--		--	
12	L					--		--		--	
13	L	12	12			--		--		--	
14	T	20	19	1	1	--		--			
15	D	53	53	1	1	143	50	26	26	(summed below)	
16	D	135	58	6	1	253	65	97	29		
17	D	153	63	6	3	--		53	19		
18	D	140	69	7	3	--		--			
20	L	13	12			--		--		--	
21	T	24	24			--		--		--	
22	T	50	20	6	4	--		--		--	

Table 9. (Continued)

Epibenthic samples	Light condition	Corophium salmonis		Corophium spinicorne		Anisogammarus confervicolus		Neomysis mercedis		Eohaustorius estuarius	
		Caught	Examined	Caught	Examined	Caught	Examined	Caught	Examined	Caught	Examined
23	D	55		7		--		8	7		
24	D	87	34	7	4	--		--			
25	D	74		20		--		8	8		
26	D	40	18	22	11	--		10	8		
27	D	52				--		2	2	59	52
28	D	47	31	4	4	--		17	17		
30	D	45	22	4		--		--			
31	T	34	30	1	1	--		--			
32	T	8	7	1	1	--		--			
34	L	1	1			--		--		--	

Table 10. Benthic samples selected for examination.

Benthic samples	Corophium salmonis		Eohaustorius estuarius	
	Caught	Examined	Caught	Examined
2 (1/4 A + 1/4 B + 1/4 C)[1]	10442	355	1583	51
5 (1/2 A)[2]	2000	134	--	
6 (1/2 A + 1/2 B + 1/2 C)[3]	52	25	2410	58

[1] One-quarter from each of the three replicate samples was pooled for examination.

[2] One-half from one of the three replicate sample was examined.

[3] One-half from each of the three replicate samples was pooled for examination.

APPENDIX B

Table 11 contains salinity and temperature data by depth in Youngs Bay, Oregon from 1421 h on September 26 to 0710 h on September 30, 1975. Water depth was measured by shipboard fathometer. Station locations are shown in Figure 4.

Table 11. Salinity and temperature data.

Station	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D
Date	←				26 Sept. 75					→	←				
Time	1421	1602	1650	1735	1841	1935	2015	2147	2240	2355	0115	1450	1550	1650	1755
Water depth (m)		4.9	4.9	4.9	4.6	4.3	4.3	3.0	3.7	2.4	2.9	5.5	5.8	5.8	6.1

Salinity ($^0/oo$)

Depth (m)															
0	2.5	3.4	3.2	3.4	3.4	4.2	5.8	3.4	3.1	4.8	4.9	2.4	2.7	5.3	5.6
1	2.5	4.2	3.8	3.5	2.9	4.0	6.2	3.7	4.2	4.9	4.9	2.5	4.9	6.5	5.6
2	2.6	6.1	8.6	6.1	3.9	5.0	7.2	3.4	4.6	5.1	4.9	5.8	6.8	7.7	7.2
3		9.0	11.8	10.3	7.0	5.8	8.4						7.2	10.5	11.0	16.0
4	10.1	11.3	14.5	13.8	8.2							10.4	14.3	21.5	19.5
5														22.8	23.2
6															
7															

Temperature (^{o}C)

Depth (m)															
0	18.1	18.1	18.3	18.2	18.0	18.4	17.3	18.0	17.7	17.7	17.8	17.9	17.7	17.0	17.1
1	18.2	17.7	18.2	18.2	18.2	18.0	17.3	17.9	17.7	17.7	17.8	17.8	17.3	16.9	17.1
2	18.0	17.5	16.4	16.9	17.5	17.8	17.3	18.0	17.7	17.7	17.4	17.1	16.5	16.7	16.8
3		16.4	15.9	16.3	16.7	17.3	16.8						16.9	15.9	15.7	14.6
4	16.3	15.4	15.2	15.4	16.5							15.7	15.0	13.3	13.8
5														12.9	12.9
6															
7															

Table 11. (Continued).

Station	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D
Date		27 Sep 75 →		←	28 Sep 75										
Time (PDT)	1855	2100	2320	0116	0200	0245	0330	0415	0525	0600	0650	0807	0845	0930	1015
Water depth (m)	6.1	5.2	4.6	4.3	4.3	4.4	4.4	4.4	4.9	5.0	5.3	5.8	5.2	4.9	4.9

Salinity ($\permil$)

Depth (m)															
0	6.1	6.9	6.5	6.4	5.4	6.9	3.4	3.6	3.2	4.9	4.7	4.9	5.2	5.0	5.6
1	6.1	7.7	6.5	6.8	5.9	6.8	5.0	5.4	4.9	6.2	5.6	5.3	5.3	5.2	5.4
2	6.9	8.6	6.5	8.4	6.9	6.8	7.0	6.0	7.7	8.6	7.9	5.8	5.2	5.2	5.5
3	12.5	3.8	7.1	10.2	9.0	11.9	7.6	6.7	11.4	10.3	12.3	10.8	6.9	5.6	5.6
4	17.5	12.0	8.8	10.5	10.0	12.7	10.5	9.0	12.4	11.4	14.7	15.2	10.5	6.5	6.0
5	22.0										16.3	16.4	11.4	9.1	6.8
6															
7															

Temperature (°C)

Depth (m)															
0	16.7	16.9	16.7	16.3	16.8	16.3	16.3	16.8	17.0	16.7	16.7	16.5	16.4	16.6	16.5
1	16.6	16.8	16.4	16.3	16.5	16.0	16.8	16.3	16.7	16.4	16.6	16.9	16.4	16.5	16.6
2	16.7	16.4	16.4	16.1	16.5	16.2	16.2	16.2	16.2	15.9	16.1	16.7	16.4	16.4	16.6
3	15.5	15.9	16.5	15.7	16.0	15.0	16.3	16.0	15.4	15.4	15.3	15.6	16.4	16.4	16.5
4	14.1	15.7	16.3	15.6	16.0	14.8	15.5	15.8	14.9	15.4	14.5	14.5	15.7	16.1	16.4
5	13.2										14.2	14.4	15.4	15.9	16.3
6															
7															

Table 11. (Continued).

Station	D	D	D	B1	B1	B1	B1	B1	B2	B2	B2	D	D	D
Date				28 Sep 75 ────────────────────→					←──────29 Sep 75 ──────→					30 Sep 75
Time (PDT)	1245	1410	1510	1810	2025	2125	2244	2317	0250	0500	0700	2020	2230	0710
Water depth (m)	3.7	5.5	5.8	4.3	5.6	4.9	4 3	4.9	5.8	6.1	7.3		6.1	

Salinity (‰)

Depth (m)	D	D	D	B1	B1	B1	B1	B1	B2	B2	B2	D	D	D
0	5.6	4.7	4.2	3.6	3.4	3.5	5.0	3.9	5.5	3.6	4.0	5.7	6.6	6.4
1	6.0	4.7	4.2	3.6	3.5	3.6	5.2	3.9	6.9	4.9	4.9	5.6	6.5	6.4
2	5.5	4.7	4.3	3.6	3.5	3.5	5.5	4.6	7.6	7.4	6.5	5.9	6.9	6.5
3	6.1	4.8	6.8	10.3	9.0	3.5	6.5	5.6	7.8	8.5	9.6	9.1	7.4	6.6
4		12.3	11.8	13.4	8.9	3.6	13.5	9.4	9.0	8.1	10.4	14.2	7.8	10.0
5			12.8		11.5				11.5	8.6	12.8		8.0	14.5
6										18.7	14.6			
7											15.2			

Temperature (°C)

Depth (m)	D	D	D	B1	B1	B1	B1	B1	B2	B2	B2	D	D	D
0	16.5	17.0	16.8	17.0	16.5	16.6	16.1	16.4	15.7	16.8	16.3	16.6	16.7	16.1
1	16.5	16.7	16.9	17.1	16.6	16.6	16.0	16.3	16.1	16.2	16.3	16.2	16.7	16.0
2	16.2	16.8	16.9	16.9	16.6	16.7	16.2	16.5	15.9	16.1	16.2	16.7	16.3	16.1
3	16.3	16.7	16.4	15.5	15.7	16.4	16.3	16.4	16.2	15.5	15.3	15.8	16.1	16.1
4		15.1	15.1	15.0	15.5	16.7	14.8	15.8	16.0	15.8	15.1		16.2	15.3
5			15.0		15.2				15.4	15.7	14.8		15.9	14.5
6										13.1	14.4			
7											14.6			

APPENDIX C

Appendix C contains the densities of benthic crustaceans in the water column and the densities of infauna in the substrate during the swimming activity rhythms study in Youngs Bay, Oregon, 1975.

Table 12, 13, and 14 present the densities (no./100 m^3) of benthic crustaceans in the surface, midwater and epibenthic strata, respectively. Sample collection data are given below. Light condition is indicated by L for daylight, T for transition (dusk and dawn), and D for darkness. Salinity and temperature data were interpolated from data in Table 11.

Table 15 presents the densities (no./m^2) of infauna in the substrate. Sample collection data are given below. Substrate texture is based on dry weight analysis in six size fractions.

Table 12.   Densities (no. /100 m^3) of benthic crustaceans in the surface stratum.

Sample number	1S	2S	3S	4S	5S	6S	7S	8S	9S	10S	11S	12S	13S	14S	15S	16S	17S	18S	19S
Taxon																			
Arthropoda																			
Crustacea																			
Mysidaceae																			
Neomysis mercedis	1					13	120	122	193	218	108	40	1						
Isopoda																			
Gnorimosphaeroma oregonensis						1				1									
Amphipoda																			
Corophium salmonis	6	1	1			1289	634	527	854	577	117	23		1	3		2	1	
Corophium spinicorne	6	4	3	1	10	24	19	12	17	21	4	9	14	11	5	2	4	2	1
Corophium brevis																			
Anisogammarus confervicolus	3				1	89	63	56	35	47	14	9	1						
Eohaustorius estuarius						26	28	6	19	12	3	3							
Decapoda																			
Crangon franciscorum								1											
Environmental and Sample Data																			
Date	←			27 Sep 75			→	←						28 Sep 75					→
Time net down (PDT)	1456	1616	1720	1801	1908	2043	2340	0146	0322	0405	0517	0555	0647	0721	0842	1000	1252	1329	1433
Tow duration (min)	5.0	10.0	10.0	10.0	10.0	11.5	10.0	10.0	7.0	6.5	9.0	9.0	10.0	10.0	7.0	9.0	10.0	10.0	10.0
Speed of tow (cm/s)	128	116	110	108	139	117	139	137	133	128	92	115	106	110	113	124	130	116	106
Volume of water sampled (m^3)	79.1	134.3	135.9	133.4	171.7	156.2	171.7	169.2	115.0	102.8	102.3	127.9	130.9	135.9	97.7	137.9	160.6	143.3	130.9
Light condition	L	L	L	L	T	D	D	D	D	D	D	D	T	L	L	L	L	L	L
Surface salinity at Station D ($^0/oo$)	2.4	3.5	5.4	5.7	6.3	6.8	6.5	5.6	3.4	3.6	3.3	4.9	4.7	4.8	5.2	5.5	5.6	5.0	4.7
Surface temperature at Station D ($^\circ$C)	17.9	17.6	17.0	17.0	16.7	16.9	16.7	16.6	16.3	16.7	1619	16.7	16.7	16.6	16.4	16.5	16.5	16.7	17.0

Table 13. Densities (no. /100 m^3) of benthic crustaceans in the surface stratum.

Sample number	1M	2M	3M	4M	5M	6M	7M	8 M	9M	10M	11M	12M	13M	14M	15M	16M	17M	18M	19M
Taxon																			
Arthropoda																			
Crustacea																			
Mysidacea																			
Neomysis mercedis	2				1	13	32	104	82	80	126	55	2						
Isopoda																			
Gnorimosphaeroma oregonensis					1	1		1			4		1						
Amphipoda																			
Corophium salmonis	8				3	348	306	493	891	255	105	62	2	1			1		1
Corophium spinicorne					2	8	3	5	3	3	2	4					1	1	1
Corophium brevis												1			1				
Anisogammarus confervicolus	8					70	61	267	79	29	130	26							
Eohaustorius estuarius						15	3	1		5		1							
Decapoda																			
Crangon franciscorum								1		6	1								

Environmental and Sample Data

Date	←		27 Sep 75			→	←					28 Sep 75							→
Time net down (PDT)	1537	1635	1741	1818	1948	2109	0120	0221	0345	0450	0535	0634	0706	0814	0926	1029	1312	1349	1459
Tow duration (min)	5.0	7.0	7.0	7.0	7.0	7.5	7.0	7.0	6.2	9.0	8.0	7.0	7.0	6.0	10.0	7.0	7.0	7.0	7.0
Speed of tow (cm/s)	102	125	111	85	135	95	115	88	95	89	75	97	103	107	78	109	100	90	110
Volume of water sampled (m^3)	63.0	108.1	96.0	73.5	116.7	88.0	99.4	76.1	73.2	99.0	74.1	83.9	89.1	79.3	96.4	94.3	86.5	77.8	95.1
Light condition	L	L	L	L	D	D	D	D	D	D	D	T	L	L	L	L	L	L	L
Midwater salinity at Station D (‰)	9.0	10.5	15.0	15.0	10.0	9.6	9.4	7.9	7.5	8.0	9.0	11.0	12.0	10.0	6.0	5.6	5.0	4.7	7.0
Midwater temperature at Station D (°C)	16.9	15.8	14.6	14.7	15.5	16.2	16.1	16.3	16.2	16.2	16.0	15.5	15.0	15.3	16.4	16.5	16.5	16.8	15.0

Table 14. Densities (no. /100 m^3) of benthic crustaceans in the epibenthic stratum.

Sample number	1E	3E	4E	5E	6E	78	8E	9E	10E	11E	12E	13E	14E	15E	16E	17E	18E
Taxon																	
Arthropoda																	
Crustacea																	
Mysidacea																	
Neomysis mercedis	11									10		13	14	96	383	251	372
Isopoda																	
Gnorimosphaeroma oregonensis													2				
Amphipoda																	
Corophium salmonis	43				8	2	13			10		26	41	195	534	725	316
Corophium spinicorne							2						2	4	24	28	16
Corophium brevis													10	15	12	14	
Anisogammarus confervicolus	5						67		3	17			79	526	1134	678	571
Eohaustorius estuarius													6	4	55	43	97
Decapoda																	
Crangon franciscorum															20	24	27
Environmental and Sample Data																	
Date							← — — 26 Sep 75 — — →										
Time net opened (PDT)	1010	1116	1330	1349	1404	1440	1521	1621	1715	1741	1807	1901	1935	2013	2057	2202	2333
Tow duration (min)	5.0	5.0	5.0	2.5	5.0	5.0	5.4	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	4.0	6.0
Speed of tow (cm/s)	87	37	115	102	56	105	102	95	87	69	92	110	116	64	59.5	62	87
Volume of water sampled (m^3)	36.9	15.7	48.8	21.6	23.8	44.6	46.3	40.3	36.9	29.3	39.1	46.7	49.2	27.2	25.3	21.1	44.3
Light condition	L	L	L	L	L	L	L	L	L	L	L	L	T	D	D	D	D
Epibenthic salinity at Station D (‰)	6.1	7.5	8.4	9.3	10.1	10.5	10.7	12.0	14.5	13.0	10.0	7.0	5.8	5.0	4.0	4.0	4.6
Epibenthic temperature at Station D (°C)	15.3	15.4	16.3	16.3	16.4	16.2	16.2	15.4	15.2	15.4	16.0	16.7	17.3	17.0	17.9	18.0	17.7

Table 14. (Continued).

Sample number	20E	21E	22E	23E	24E	25E	26E	27E	28E	30E	31E	32E	34E
Taxon													
Arthropoda													
Crustacea													
Mysidacea													
Neomysis mercedis	34	34	11	21	26	24	27	6	47	72	37	13	
Isopoda													
Gnorimosphaeroma oregonensis				3									
Amphipoda													
Corophium salmonis	44	63	137	147	148	221	108	159	130	104	89	20	3
Corophium spinicorne			16	19	12	60	60	.	11	9	3	3	
Corophium brevis					2	3	3						
Anisugammarus confervicolus	13	3			2	3	5	9	39	106	10	3	
Eohaustorius estuarius			5	5	2	3	5	18	14		3		
Decapoda													
Crangon franciscorum				11	5	12	8		3				

Environmental and Sample Data

	20E	21E	22E	23E	24E	25E	26E	27E	28E	30E	31E	32E	34E
Date	←				29 Sep 75				→	←	30 Sep 75		→
Time net opened (PDT)	1900	1919	1949	2007	2036	2107	2130	2207	2238	0530	0623	0653	0804
Tow duration (min)	5.0	5.0	6.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	6.0	5.5
Speed of tow (cm/s)	70	90	73	88	138	79	87	77	85	102	90	79	87
Volume of water sampled (m^3)	29.7	38.2	37.1	37.4	58.6	33.5	36.9	32.7	36.1	43.3	38.2	40.0	38.8
Light condition	L	T	T	D	D	D	D	D	D	D	T	T	L
Epibenthic salinity at Station D (‰)	15.0	15.0	14.3	10.0	9.6	8.7	8.0	8.0	9.5	13.5	14.0	14.5	13.0
Epibenthic temperature at Station D (°C)	15.2	14.5	15.2	15.6	15.8	16.3	16.5	16.3	15.9	15.0	15.0	14.5	15.0

Table 15. Densities (no./m^2) of infauna in the substrate.

Sample number	1A	1B	1C	1D	Mean	2A	2B	2C	Mean	5A	6A	6B	6C	Mean
Taxon														
Nemertinea		28	37	19	21	150	37	75	87	87				
Annelida														
Polychaeta	401	1075	710	626	703	1627	2019	1570	1739	1196	748	1103	541	797
Mollusca														
Bivalvia	430	1897	2121	2561	1752	2748	3364	2355	2822	4860	1739	1284	1813	1645
Arthropoda														
Crustacea														
Amphipoda														
Corophium salmonis		93	224	131	112	34711	26355	36523	32530	18092	131	159	206	162
Anisogammarus confervicolus	29	19	28		19					37	19	56	55	44
Eohaustorius estuarius	383	206	290	449	332	225	636	822	551	75	1290	430	690	603
Environmental and Sample Data														
Date: 28 Sep 75														
Time (PDT)	1540	1605	1610	1617		1749	1739	1742		2215	2304	2310	2315	
Sample depth in grab (cm)	13	12	12	11		13	12	12		13	11.5	11	11	
Fraction of sample counted	1.0	1.0	1.0	1.0		.50	.25	.25		.25	.50	.50	.50	
Substrate praticle size fractions														
>1.000 mm	.2	.2	.2	0		.1	0	1.2		.5	.6	1.4	.2	
0.500 mm - 1.000 mm	.6	.9	1.0	.6		1.4	.9	.8		.7	1.7	1.5	1.4	
0.250 mm-0.500 mm	71.4	61.6	50.1	57.4		52.2	61.4	46.9		36.0	66.7	52.0	71.4	
0.125 mm-0.250 mm	23.2	29.7	35.2	35.2		40.0	31.6	41.8		49.9	23.8	19.5	22.8	
0.063 mm-0.125 mm	3.6	5.0	9.2	4.7		4.3	4.2	4.7		8.3	4.7	9.2	3.2	
<0.063 mm	.9	2.6	4.3	2.1		2.0	1.9	4.5		4.6	2.4	9.3	1.1	